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Global versus Local Changes in Upwelling Systems

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To the memory of Itaf Deme Gningue

Itaf est morte accidentellement le 26 octobre 1997 sur la route entre Rosso et Saint-Louis en revenant d'une mission de travail. Elle avait 41 ans.

Itaf avait démarré sa carrière au CRODT en tant qu'ingénieur chimiste. Elle avait su surmonter de nombreux obstacles pour réaliser une thèse, devenir chercheur, puis diriger la section Environnement du CRODT. Tous ceux qui l'ont connue et côtoyée dans son travail saluent avant tout sa volonté, son courage et sa gentillesse. Les auteurs de ce livre n'oublieront pas non plus son rire et sa bonne humeur. En 1994, lorsque Itaf étaient venue à Monterey participer au colloque CEOS, elle était enceinte de sa petite fille Khadidja. Notre pensée va à sa famille et à ses deux petites filles Ndeye Anta et Khadidja.

Ku ko guissone sope na ko, ku ko xamone gnak na ko, yala na ko Allah yeureum te xare ko adiana Amine.

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Preface and Acknowledgments

THE EDITORS

This volume is comprised of 33 contributions, most originally presented at an international conference held on 6-8 September 1994 in Monterey, California, USA under the auspices of the Climate and Eastern Ocean Systems Project (CEOS).

The CEOS was a collaborative project linking a variety of research institutions, notably ORSTOM, NMFS and ICLARM and devoted to a study of the potential effects of global change on the resources of upwelling systems through identification of global and local effects impacting on these systems.

This volume is one of the two major products of CEOS, the other being a set of CD-Roms that will empower more researchers, especially in developing countries, to study oceanographic processes (see Roy and Mendelssohn, this vol.).

We apologize for the delay in publishing this volume, due mainly to the inherent difficulty of coordinating a vast cast of authors in different parts of the world, and most with first languages other than the English we have chosen to present the result of CEOS.

We thank our respective institutions, ORSTOM, NMFS and ICLARM for their support of the effort that led to this volume. Also we take this opportunity to thank Ms Marie-Christine Pascal for the typing and layouting of this book and also Ms Nathalie Richard, Ms Barbara Chollet, Ms Sandra Gayosa, Mr Emmanuel Suisse de Sainte-Claire and Mr Francisco Torres Jr. for their assistance in the production of this volume.

Also we thank the PNDR (Programme National sur le Déterminisme du Recrutement, France) and SEAH (Systèmes Ecologiques et Actions de l'Homme, CNRS-France) for their support of our effort.

The Climate and Eastern Ocean Systems Project (CEOS)

ANDREW BAKUN
PHILIPPE CURY
MARIE-HÉLÈNE DURAND
ROY MENDELSSOHN
DANIEL PAULY
CLAUDE ROY

1. CEOS: AN INTERNATIONAL NETWORK WORKING ON CLIMATE AND FISHERIES

The injection of millions of tonnes of greenhouse gases into the earth's atmosphere may be viewed as a gigantic experiment aimed at exploring the earth's reaction to such challenge. Unfortunately, this experiment is run without proper 'controls', and hence the heated debates about the actual impact of those gases may last too long, beyond the time where the 'experiment' should be called off. The international scientific community is forced, however, to address this problem in spite of the lack of scientific controls. One way to address this is through the comparative method, a major tool in those disciplines in which experiments are hard to perform, e.g. evolutionary biology (Mayr, 1982), fisheries science (Bakun, 1985, 1996).

Given the importance of the four major upwelling systems off Peru, Chile, California, Northwest and Southwest Africa both as sources of fish and as CO_2 'pumps', scientists from the Pacific Fisheries Environmental Group (PFEG), of the National Marine Fisheries Service (NMFS), the Institut Français de Recherche Scientifique pour le Développement en Coopération (ORSTOM), and the International Center for Living Aquatic Resources Management (ICLARM) and partners from other institutions, teamed up to investigate these systems in the context of global changes, through a project called CEOS (Climate and Eastern Ocean Systems), funded by NOAA and

ORSTOM. Several national research laboratories working on similar systems were associated with this project through a cooperative agreement with ORSTOM. The African research institutes associated to the CEOS project were the Institut Scientifique des Pêches Maritimes (ISPM) in Morocco; the Centre de Recherches Océanographiques d'Abidjan (CROA) in Côte-d'Ivoire; the Fisheries Research Utilization Branch (FRUB) in Ghana; the Centre de Recherches Océanographiques de Dakar-Thiaroye (CRODT) in Senegal, and the Sea Fisheries Research Institute (SFRI) in South Africa which focus on regional case studies of climatic variability, coastal ecosystem dynamic and associated human responses. In Latin America, the Instituto del Mar del Peru (IMARPE) in Peru; the Instituto de Fomento Pesquero (IFOP) and the Universidad Catolica de Valparaiso in Chile are also involved in this project. The collaboration of scientists from these institutes with the CEOS project was also partly funded by the Scientific Committee on Dynamics and Use of Renewable Resources (DURR) of ORSTOM and PNDR (Programme National sur le Déterminisme du Recrutement).

2. BACKGROUND

The great stocks of sardines and anchovies, and other small pelagic fishes, account for about one third of the world's yield of marine fish and are of key economic importance in many nations. Production from these great stocks depends upon a delicate balance of physical ocean processes. The optimal environmental window for small pelagic fish depends upon a triad of physical factors (Bakun, 1996): *enrichment processes* that lead to the production of the zooplankton upon which the young stages depend for food; *concentration processes* that aggregate foods and thereby increase their availability to growing larvae; and *retention processes* that keep the young in their favored nursery habitats. Without a doubt, global heating will alter this 'triad' of physical processes. These processes are functions of atmospheric forcing, ocean dynamics, and fresh water inflow; all of which are expected to be altered by climate change.

The most immediate response to greenhouse warming would occur within the atmosphere rather than within the ocean, affecting the wind field over the ocean, and hence, patterns of upwelling. Bakun (1990) presents evidence that this is already occurring over the past several decades. Thus global climate change could substantially alter these factors that determine favorable reproductive habitat long before ocean temperature changes due directly to greenhouse warming may be evident. Some initial scenarios are already available. For example, Bakun (1990) has argued that one consequence of increased greenhouse effects that can be confidently expected is that temperature gradient between the ocean and the continents will increase during the Spring-Summer upwelling seasons in these systems. This would be reflected in increased alongshore wind and enhanced sea breeze circulation, which would impact recruitment (Mendelssohn and Mendo, 1987). Evidence exists for an 'optimal environmental window' (Cury and Roy, 1989; Cury *et al.*, 1995; Serra *et al.*, this vol.) with respect to wind effects such that changes in characteristic wind speed may disrupt finely tuned reproductive strategies of the small pelagic fishes.

A related project on climatic change and pelagic fish stock dynamics was recently concluded in West Africa (Mauritania, Senegal, Côte-d'Ivoire and Ghana) (Cury and Roy, 1991). One important result of this project was to establish the existence of recurrent patterns between the environment and the pelagic fish dynamics. The aim of the CEOS project was thus to build on this analysis through a comparative approach and to generalize previously obtained results. Upwelling ecosystems in the Pacific are dominated by large interyear variability whereas in the Atlantic they are characterized by a more seasonal variability. To compare the dynamics of two different functioning upwelling systems would help to understand the impact of environmental constraints on pelagic fish dynamics. Through the CEOS network it was possible to assemble and compare knowledge and data that were collected during several decades in the different upwelling areas.

Eastern ocean upwelling ecosystems present certain advantages that may make the study of effects of climate change on marine ecosystems particularly tractable; thus the study may serve an even wider purpose as an illustration of the sorts of impacts that could affect a variety of more complex marine ecosystems. As environmental changes may affect fish population dynamics in many ways and at different time and space scales, local case studies and comparative global studies are presented for the different upwelling systems. A better understanding of the links between environmental changes and fish population response is expected using various approaches. By analyzing time series data from similarly functioning regional ecosystems distributed over the globe, we hope to tease out the significant global trends from within the 'noise level' of naturally-occurring regional climatic variability.

Disentangling global versus local environmental changes appears to be a major challenge when analyzing environmental time series. New statistical techniques are developed and applied to environmental indices relevant for fish population dynamics in order to extract trends and sometime changing seasonal patterns. Another approach to separating global from local ecosystem processes is constructing trophic models of the ecosystems, then computing the values of indices expressing their emergent properties. The Ecopath software of Christensen and Pauly (1992) was used for construction of several models for each of the investigated systems and to compare their properties.

Human activities facing local and global changes are also studied. The exploitation of marine renewable resources in the different upwelling areas appears to be a real challenge due to the fact that these resources are unstable. Here, new insights are presented e.g., on how markets cope with variability of supply (Durand, this vol.).

The general theme copes with variability and instability: instability of the environment in which the resources evolve, intrinsic instability of the pelagic fish stocks and uncertainty which govern the economic exploitation of a natural resource. All these dynamics are intrinsically linked. The CEOS project was, therefore a multi-disciplinary project, where physical, biological and econometric methods could be focussed on this common theme.

3. GOALS AND OBJECTIVES OF THE CEOS PROJECT

The CEOS project was an international collaborative study of potential effects of global climate change on the living resources of the highly productive eastern ocean upwelling ecosystems and on the ecological and economic issues directly associated with such effects. A major focus of the study were the clupeoid fishes (anchovies, sardines, etc.) that are heavily exploited in the world's large marine ecosystems and which have recently been exhibiting episodes of collapse, rebound, or switches in dominance. The major objectives of the CEOS project were thus: (1) to assemble, summarize, and analyze the data record of the past four decades regarding the four eastern ocean boundary upwelling ecosystems mentioned above and other upwelling areas, (2) to apply the comparative method to identify key physical processes and ecosystems responses, (3) to resolve underlying global-scale trends that in each individual regional system may be obscured by local interyear and interdecadal variability, (4) to investigate the relationship of these global trends to accumulating greenhouse effects, (5) to construct scenarios for future consequences of global climate change on upwelling resources, and (6) to analyze and project ecological and social impacts on associated human activities and values.

More generally CEOS aimed at promoting scientific exchanges on the theme of the environment, the resource and the fisheries in upwelling areas and consequently to:

- promote relevant scientific themes on the environment, on marine resources and on fisheries;
- develop research and to promote scientific exchanges between developed and developing countries;
- promote the multidisciplinary approach in the management of the marine renewable resources;
- exchange data, methods and models in order to improve scientific knowledge;
- promote comparative ecosystem analyses in order to generalize process or to identify specificities in the environmental, the ecological or the economical dynamics;
- consider news ways for managing fisheries that take into account social and economic processes that are involved in fisheries.

4. LINKAGES OF THE CEOS PROJECT

The CEOS project addressed most of the strategic and integrating priorities listed in the U.S. 'Global Research Program Priority Framework', especially the 'Ecological Systems and Dynamics' category, and also addressed in some way most of the issues listed under that category: e.g. '(assembly and analysis of) Long-Term Measurements of Structure/Function', 'Response to Climate and Other Stresses', 'Interactions Between Physical and Biological Processes', 'Models of Interactions, Feedbacks, and Responses', 'Productivity/Resource Models', etc.

The project was designed within the general framework of the International Program of Ocean Science in Relation to Living Resources (OSLR), co-sponsored by the Intergovernmental Oceanographic Commission and the Food and Agriculture Organization of the United Nations (Bakun *et al.*, 1982). It can be considered an initial effort in the newly proposed subprogram of OSLR and Ecosystem Dynamics and Living Resources (EDLR). Elements of CEOS directly related with 'recruitment' constitute contributions to the Sardine-Anchovy Recruitment Project (SARP), a major component of the International Recruitment Program (IREP) of OSLR. It also interacted with the GLOBEC/SPACC initiative and in the Programme National pour le Déterminisme du Recrutement (PNDR GLOBEC-FRANCE, France).

5. THE MONTEREY MEETING

The present, multi-authored volume presents the results of an international conference held in Monterey (California) at PFEG (Pacific Fisheries Environmental Group) on September 6-8, 1994 where fifty CEOS participants met to exchange their results. The book is composed of thirty three papers ranging from descriptive and comparative analyses of the major upwelling ecosystems, presentation of new statistical analyses and modeling techniques, to the analysis and modeling of human activities exploiting renewable resources. We hope that the CEOS network reached, through the present book and its other products and activities, at least some of the ambitious objectives that were shared at the beginning.

REFERENCES CITED

Bakun A. 1985. Comparative studies and the recruitment problems: searching for generalizations. *CalCOFI Rep.*, 26: 30-40.

Bakun A. 1990. Global climate change and intensification of coastal ocean upwelling. *Science*, 247: 198-201.

Bakun A. 1996. *Patterns in the ocean: ocean processes and marine population dynamics.* Calif. Sea Grant College Syst. Univ. of Calif., La Jolla, 323p.

Bakun A., J. Beyer, D. Pauly, J.G. Pope and G.D. Sharp. 1982. Ocean science in relation to living resources. *Can. J. Fish. Aquat. Sci.*, 39(7): 1059-1070.

Christensen V. and D. Pauly. 1992. The Ecopath II - a software for balancing steady-state ecosystem models and calculating network characteristics. *Ecological modelling*. 61: 169-185.

Cury P. and C. Roy. 1989. Optimal environmental window and pelagic fish recruitment success in upwelling areas. *Can. J. Fish. Aquat. Sci.*, 46: 670-680.

Cury P. and C. Roy. (eds.). 1991. Pêcheries ouest-africaines : variabilité, instabilité et changement. Paris, ORSTOM, 525p.

Cury P., C. Roy, R. Mendelssohn, A. Bakun, D.M. Husby and R.H. Parrish. 1995. Moderate is better: exploring nonlinear climatic effect on Californian anchovy (*Engraulis mordax*). Climate change and fish population. R.J. Beamish (ed.). *Can. Spec. Publ. Fish. Aquat. Sci.*, 121: 417-424.

Mayr E. 1982. The growth of biological thought. Harvard Univ. Press, Cambridge, Mass., 974p.

Mendelssohn R. and J. Mendo. 1987. Exploratory analysis of anchoveta recruitment off Peru and related environmental series. *In*: D. Pauly and I. Tsukayama (eds.). The Peruvian anchoveta and its upwelling ecosystem: three decades of change. *ICLARM Studies and Reviews*, 15: 294-306.

The CEOS Comparative Analysis Framework: Motivations and Perceived Opportunities

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ABSTRACT

A number of features of the CEOS (Climate and Eastern Ocean Systems) scientific analysis framework are cited and discussed: (1) the specific focus on application of the comparative method, (2) the use of nonlinear empirical techniques, (3) inclusion of both biological-ecological and socioeconomic aspects within a common investigative design, (4) installation of integrative conceptual bases (e.g., the 'triad') for organizing multidisciplinary research activity.

Radical interdecadal variability may be intrinsic to many important fish populations and may introduce serious difficulties with respect to certain conventional tools of fisheries science. If, however, the apparent global synchrony in interdecadal-scale fluctuations reflects true mechanistic linkages, it may signify some substantial simplifications in the problem of developing scientific predictive capability.

RÉSUMÉ

Un certain nombre de caractéristiques du réseau scientifique CEOS (climat du bord est des océans) sont énumérées et discutées : (1) l'application de la méthode comparative,

(2) l'utilisation de techniques d'exploration dans le domaine non-linéaire, (3) l'intégration des aspects biologiques-écologiques et socio-économiques au sein d'une même approche, (4) mise en place de concepts de base (par exemple, la "triade") pour organiser une recherche pluridisciplinaire.

D'une décennie à l'autre des changements drastiques peuvent être observés pour de nombreuses populations de poisson et cela est difficilement explicable avec les outils classiques développés en halieutique. Si, cependant, la synchronie apparente de ces fluctuations décennales reflète l'existence d'un véritable mécanisme causal, cela peut singulièrement simplifier le problème de la capacité prédictive.

1. BACKGROUND

The oceans cover nearly four-fifths of the earth's surface and more than a billion people rely on fish as their main source of animal protein. In some countries, fish are nearly the sole source of animal protein. Demand for food fish and various other useful attributes obtainable from the sea has been accelerated by population growth and by the global trend toward population migration toward coastal areas.

Fisheries and fish products provide employment to nearly 200 million people. Globally, the bulk of the people employed in fisheries are poor and many are without acceptable alternative sources of work and sustenance. In addition, fish and fishing are enormously important to the cultural life of many coastal societies, and may often define a 'quality of life' for people having a cultural tradition of harvesting the sea. Hence, maintenance of viable fishery resources may be extremely important to preserving traditional ways of life, associated economic activities, tourism, etc. In addition, fish represent the fastest growing food commodity entering international trade. Accordingly, fish and fish products represent an extremely valuable source of foreign exchange to many countries, in some cases providing as much as half of total available foreign exchange income.

The methodologies of fisheries science are intended to ensure sustainable resource populations to support productive and profitable fisheries. Unfortunately, the conventional methodologies are not working very well. Over and over again, extremely important fish stocks around the world have been collapsing, causing economic dislocations and personal suffering to people whose livelihood depends on fishing or on related commercial activities. Some would say that it is not the methodologies that are at fault, but that the problem lies in imperfect application of the methodologies; there is always somewhat of an adversary relationship between conservation-minded fishery scientists and the fishing industry, and at any time there are always some who say less fish should be taken. But it seems fair to say that the sudden onset of most of the collapses comes as a relative surprise to the 'mainstream' of fishery scientists involved.

Figure 1 is an illustration of an aspect of the conventional conceptual basis for scientific management of an exploited fishery. The concept is one that may apply well to many terrestrial systems, such as to the management of buffalo on a prairie grassland or of wild deer in a natural forest area. The idea is that at high population sizes (to the far right of the diagram) the population may be using up its available resources of food, habitat space, etc. In such a case, if the population size is reduced by harvesting, the productivity of the stock may actually be improved (i.e., in the diagram the system moves to the left toward the 'peak' of the stock-recruitment curve where the rate of production of new members of the population is highest). This has the comforting implication that accumulation of new individuals that would tend to increase the population to stock sizes that lie to the right of the peak, represents a 'surplus production' that can be safely (and, in fact, beneficially) harvested.

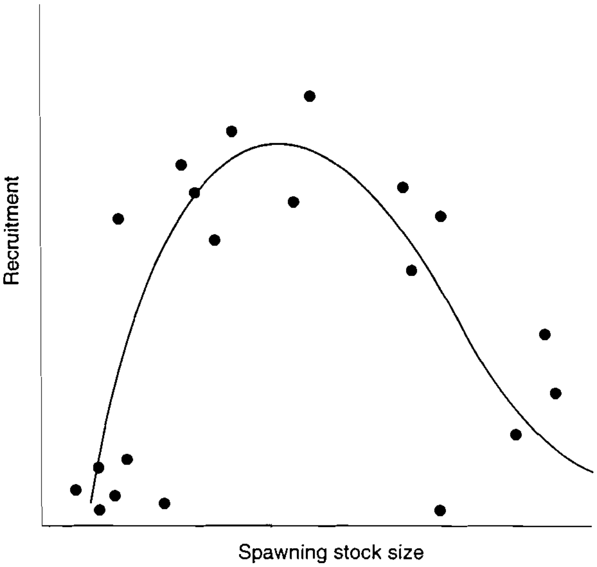


Fig. 1: A dome-shaped 'stock-recruitment curve' fitted to the same data points as used to construct Fig. 2 (modified from Bakun, 1996).

The fact that the methodologies based on a conceptual model that reflects experience with wild terrestrial populations are not generally working very well for marine fish populations has led some to the notion that marine ecosystems may represent 'chaotic systems', in which unexpected results are a feature intrinsic to the system's dynamics. Certainly, the coupled nonlinear equations that describe the dynamics of predator-prey systems represent classic examples of mathematical chaos (May, 1979). Even very simple models of biological population interactions tend to exhibit chaotic behavior. But, the idea that one is working with chaos in attempting to manage fishery resource populations seems defeating. If tiny changes in initial conditions could indeed lead to widely differing outcomes, then there would appear to be little hope of beneficially affecting the outcome by intelligent and prudent adjustments of the rate of exploitation. Happily, there are some recent developments that seem to contradict such a point of view.

2. RADICAL INTERDECADAL POPULATION VARIABILITY

It is only recently becoming widely recognized by fishery scientists that extreme variability may be an intrinsic feature of many fish populations. Contributing to the developing change in outlook has been the evidence derived from deposits of fish scales in sediments (Soutar and Isaacs, 1974; DeVries and Pearcy, 1982; Baumgartner *et al.*, 1992). These sedimentary records indicate that radical fluctuations in fish population abundance have been common occurrences long before the advent of large-scale fishing.

Moreover, in the period for which data records from fisheries have been available, abrupt population declines have been recurrent features. The decadal period from the mid-1970s to the mid-1980s was particularly remarkable in this respect. A pattern of population increases during that interval, followed by population declines after its end in the mid-1980s, seems to have been extremely widespread and consistent (Lluch-Belda *et al.*, 1989, 1992; Bakun, in press). For example, this mid-1970s to mid-1980s period was one of phenomenal productivity and growth of the major groundfish populations of the Subarctic North Pacific which sustained the massive expansions of the fisheries of that region through the period (FAO, 1993). Conversely, since the mid-1980s these populations are in decline, in spite of continuing elaborate stock assessment activities and state-of-the-art fishery management efforts. Alaskan salmon stocks also increased dramatically during the mid-1970s to mid-1980s period. Total chlorophyll in the water column appears to have increased north of Hawaii (Venrick *et al.*, 1987). Lobsters, sea birds, seals, and coral reef fishes in the northwestern Hawaiian Islands all seem to have experienced increased production (Polovina *et al.*, 1994); conversely, since the period ended in the mid-1980s, lobster landings from this area have dropped by two thirds (Anon., 1993) and other biological populations are in a downward trend.

On the other hand, North Pacific Albacore tuna appear to have suffered a steep population decline during the mid-1970s to mid-1980s period (FAO, 1993). Many salmon stocks of the California Current also declined during this period (Pearcy, 1992; Francis and Hare, 1994).

Remarkably, the very large populations of anchovies and sardines that dominate the fish biomass in the major eastern ocean upwelling regions of the world, as well as the northwestern Pacific off Japan, seem to have been rising and falling somewhat in phase (Kawasaki, 1983). Both the Californian and Japanese fisheries grew during the 1920s and early 1930s to peak in the mid to late 1930s. (There were no corresponding landings off western South America because no significant fishing occurred.) Both populations remained at extremely low numbers for some three decades. The sardine fisheries in both regions then commenced sudden rapid growth near the mid-1970s, the same period in which enormous numbers of sardines appeared off South America initiating a massive fishery in that region. Now, toward the latter part of the 1980s, the above-mentioned additional simultaneous reversals in trend have occurred (Lluch-Belda *et al.*, 1989, 1992).

Since the advent of substantial fisheries, anchovy populations have been generally out of phase with the sardine populations in the three regions. In the California Current, after a time lag of about a decade following the sardine collapse, the anchovy population increased to the point that over 340 000 tonnes were taken in 1981. Off Japan, the anchovy catches grew during the period of low sardine abundance following the initial sardine collapse, attaining maximum levels of nearly half a million tons during the late 1950s and the 1960s. The anchovy catches then gradually declined as the sardine population proceeded in its rebuilding phase. More recently, as the Japanese sardine population declined, extremely large shoals of anchovy were reported (Lluch-Belda *et al.*, 1992)

In the Peru-Humboldt Current system, the fishery for anchovy (anchoveta) peaked in 1970 at more than 13 million tonnes, constituting by far the largest single fishery that has ever existed on earth. It then collapsed to less than 1 million tonnes after the 1972 El Niño, rebounded briefly to about 2 million tonnes for several years, and then fell back following the 1976 El Niño to below 1 million tonnes and remained at this relatively low level during the period of sardine abundance up to the mid-1980s (see contributions in Pauly *et al.*, 1989). Now as the sardines are plunging, once again the anchoveta population is explosively building to the point that it promises to return Peru to its former position as the world's 'number one' fishing nation (Mendo, 1994), at least until the next El Niño event. These radical alternations between sardines and anchovies occurring on interdecadal time scales have been given the name 'regime change' by Lluch-Belda *et al.* (1989).

Thus, we have a situation in which fish populations distributed in widely distant parts of the Pacific, and in other oceans of the world as well (Bakun, 1996), appear to be fluctuating in a degree of synchrony. The populations are certainly far too widely separated to interact in any direct way. For example, the populations of sardines in the different 'corners' of the Pacific were considered until very recently (Parrish *et al.*, 1989) to be separate distinct species. But as one views the variability of more and more populations, and notes the same apparent rhythms, the idea that the variabilities are somehow interlinked becomes compelling.

3. THE BAD NEWS

This presents us with somewhat of a 'bad news' versus 'good news' situation. In large part, the parameter estimations for the various conventional models used in fisheries science depend in one way or the other on equilibrium assumptions. Without the assumption that the various data points can be regarded as reflections of an identical process, albeit with a substantial random noise component superimposed, the degrees of freedom available to produce estimates vanish. Thus one can't obtain the needed parameters even if the methodologies should be appropriate.

However, radical variability on interdecadal scales may also introduce serious problems in the methodologies themselves. For example, consider the following heuristic example, taken from Bakun (1996). Let us artificially construct a stock-recruitment 'history' (Fig. 2) for some hypothetical fish stock that followed the dome-shaped productivity pattern discussed above, using only the concept that good recruitments contribute to population growth and poor recruitments to population decline. Let us say, for example, that in the early 1970s recruitment and stock size both remained low. Then suddenly, near the mid-1970s, a series of good recruitments caused the stock to progressively build (i.e., the points move progressively to the right in the diagram). Then, suppose that near the mid-1980s the recruitment levels fell back to a lower mean state and so stock size progressively decreased (i.e., the points move back toward the origin of the diagram).

If a 'stock-recruitment curve' is fitted to these points (see Fig. 1 which was purposely constructed from these same 'data' points), the fit is really quite good compared to many examples one sees in the fisheries scientific literature (e.g., see examples in Rothschild, 1986). Following the usual logic, the fact that the fitted curve turns sharply downwards at the high biomass side of the diagram would imply strong compensatory density-dependence and therefore surplus production that could be freely exploited with no damage to stock productivity (in fact improving average reproductive success) as long as the stock biomass is not allowed to fall to the left of the peak of the curve. Under such a logic, all management would need to do would be to keep the stock size somewhere toward the middle of the curve and all should be well.

But of course, this is a delusion. The concept used to generate the data points underlying this curve was not density-dependence, but simple addition: a group of good recruitments adds up at some later time to large spawning biomass (see for example, Sharp *et al.*, 1983). It is recruitment controlling population size, not population size controlling recruitment. Any apparent density-density dependence in this particular example is illusory. There is nothing in the example to support an implication of 'surplus production', and a methodology based on such an implication may be comforting to those trying to balance exploitation and conservation, but totally wrong in this case.

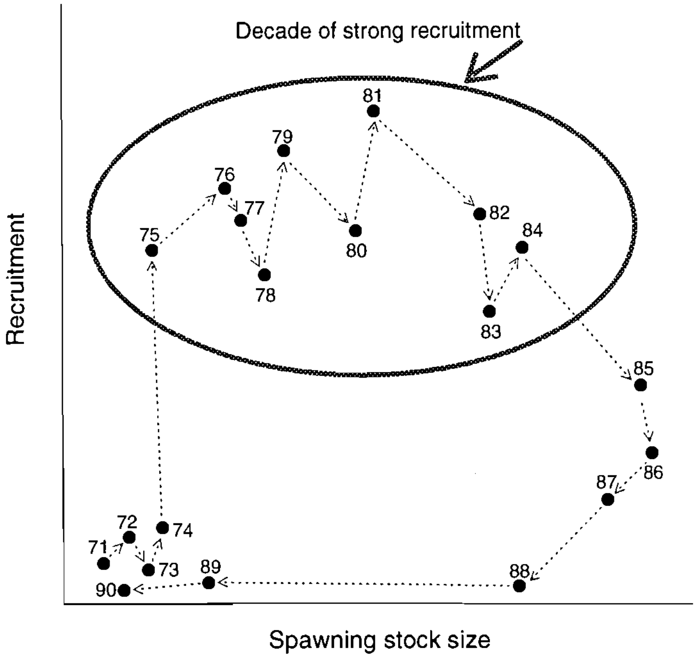


Fig. 2: Hypothetical stock recruitment diagram for a fish population that has exhibited a 'dome-shaped' productivity curve, with particularly high recruitments in the period from the mid-1970s to mid-1980s. Numbers next to each point indicate the year ('71' refers to 1971, etc.). Dotted lines connecting points indicate the temporal sequence (modified from Bakun, 1996).

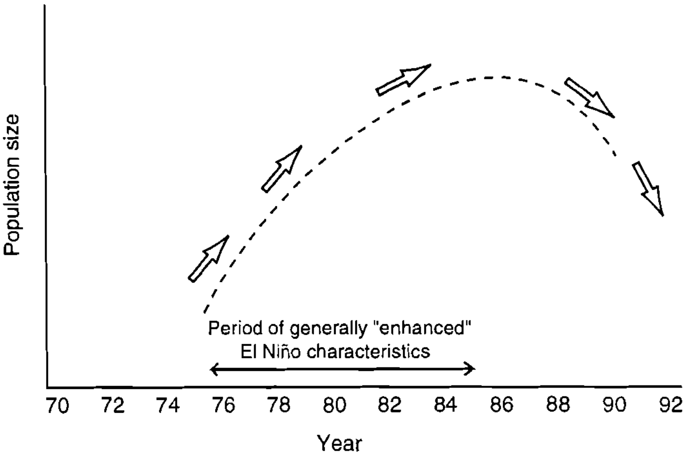
4. THE GOOD NEWS

But on the other hand, there may also be some good news in the situation. If radical interdecadal variability is indeed occurring synchronously in distantly separated fish populations distributed over the world's oceans, there would appear to be some very hopeful implications for the future of our science.

One would think that the separation between the populations must in most cases be far too great for any significant population exchanges or other purely biological interactions that might provide linkage mechanisms which could explain the synchrony. And it seems unlikely that a set of separate autonomous ecosystems, each dominated by its own internal chaotic dynamics, could somehow 'self-organize' themselves to generate mutual synchronous variability on a global scale. Thus, if these populations are indeed varying synchronously, the conclusion seems to be that they must not be functioning primarily as chaotic systems, at least on the time scales of the synchronized variability. There would, in such a case, be no implied tendency toward unstable responses to minute changes in initial conditions and therefore no reason for the earlier-mentioned pessimistic viewpoint concerning potential benefits of careful, skillful fishery management.

It would seem that such synchronous behavior would have to be generated by some type of very large-scale external forcing, most probably through climatic teleconnections acting through the atmosphere. Actually, interdecadal modulations of the El Niño—Southern Oscillation (ENSO) system appear to this writer to be the most likely type of linkage mechanism (Bakun, 1996; in press) (Fig. 3). Moreover, since biological models representing anything but the simplest of marine trophic interactions are characterized by chaotic behavior, the implication of global synchrony would seem to be

Fig. 3: Diagram characterizing the pattern of variation, observed in many marine fish populations, showing a period of increased stock productivity and rapid population growth in the decade from the mid-1970s to the mid-1980s, followed by stock declines after the mid-1980s (modified from Bakun, 1996).



that the biological dynamics involved must be very simple. The synchrony must be a rather direct effect of the external physical forcing acting either on the fish themselves, or very directly on a primary food source, at some sensitive life stage. It must not be, for example, an effect working through a complex food web.

If so, then there would appear to be a realistic hope of success in gaining a real scientific understanding of the factors determining reproductive success and population dynamics of fishery resource stocks. If the large-scale linkage is principally through the atmosphere, as seems most likely, it must probably be transferred through the local sea surface, leaving various 'signatures' in the boundary layers of the ocean and atmosphere which exist on either side of the air-sea interface. Temperature trends have not been consistent in the various regions (for example, during the mid-1970s to mid-1980s period when the eastern Pacific was in a definite warm phase, the northwestern Pacific, where sardines were expanding equally dramatically, was in, if anything, a cool phase). Thus it seems most likely that the effect must be a mechanical one. Wind stress acting on the sea surface is the predominant mechanism for transfer of momentum and mechanical energy between the atmosphere and the ocean. Accordingly, we should expect that the causal mechanism we are looking for would be a process, or more likely a sum of processes, driven by the action of the wind on the sea surface.

5. THE COMPARATIVE APPROACH

The experimental method and the comparative method have been called "the two great methods of science" (Mayr, 1982). Drawing valid scientific inference requires multiple realizations of the process of interest, preferably over a range of differing conditions, in order to separate causality from happenstance with a reasonable degree of confidence. The most direct approach to assembling the needed suite of realizations is the experimental method, wherein experimental controls are imposed that allow the scientist to systematically vary conditions of interest while holding other factors constant. But marine ecosystems are hardly amenable to experimental controls. Fortunately, the comparative method presents an alternative. And potentially it is a powerful one. For example, Mayr (1982) credits the comparative method for nearly all of the revolutionary advances in evolutionary biology. The comparative method assembles the separate realizations needed for scientific inference by a process of recognition of informative patterns of naturally-occurring temporal and spatial variations in existing conditions and phenomena. That is, different sets of seasonal and/or geographical settings, encompassing a range of natural variability in conditions and mechanisms, substitute for controlled experimental 'treatments'.

CEOS was designed to apply this approach in a collaborative, multilateral manner, using different regional fish stocks and ecosystems as sources of the multiple realizations needed to draw scientific conclusions (Bakun *et al.*, 1992). Two different general approaches have been used to apply the comparative method to addressing the fish recruitment problem (Bakun, 1985). The first is to compare the seasonality and geography of spawning to the environmental climatologies of several regions in order to try to resolve patterns of correspondence that can point out the dominant common factors appearing to determine the temporal and spatial aspects of reproductive activity. The studies of Parrish *et al.* (1983), Roy *et al.* (1989, 1992), and Bakun (1993) are examples of this type of approach.

The second type of approach involves comparative time series modeling, where empirical model formulations are compared among similar species and ecosystems. Inter-regional consistency can then enhance confidence in empirical relationships. The "optimal environmental window" (Cury and Roy, 1989) is a prime example of an empirical relationship that bears greatly enhanced credibility and influence due to its high degree of inter-regional reproducibility.

6. GOING NONLINEAR

Fish stocks would have a natural tendency to adapt their spawning habits to represent choices of seasonality and geography that would most often yield the most favorable combinations of the principle factors controlling recent reproductive success. That is how natural selection works (Weiner, 1994). Accordingly, fish populations would tend to be adapted to, and therefore fare best under, conditions which are rather typical of their habitual spawning habitats. Therefore it would seem that highest success should be associated more with typical conditions than with atypical conditions on the spawning grounds (unless, for example, the atypical conditions represented favorable circumstances which were not normally available elsewhere within the range of the population). Consequently, one would generally expect 'dome-shaped' relationships, with highest success at intermediate values of a crucial factor and lower success at more extreme values on either the high or low sides. For example, temperature can either be too high or too low, with the optimum for a given species at some intermediate value.

Over the recent period of development of fishery-environmental science, reliance on linear statistics and empirical methods has been very much the fashion. This is in spite of the fact that one would intuitively expect 'dome-shaped' relationships rather than linear ones. Thus it may not be surprising that empirical studies of environment—recruitment linkages have often yielded inconsistent, and therefore intellectually non-satisfactory, results. For example, if an empirical study addressed a situation where in most instances conditions were on one flank of such a 'dome-shaped' relationship (e.g., near an extreme end of species range, etc.), then linear analysis might pick up a significant relationship. Likewise, in another situation where most of the data were on the other flank, an equally significant result, but having opposite 'sign', could be found. In such a case, comparison of the two situations would yield directly opposing results, even though the underlying dome-shaped relationship held consistently in all cases. And of course, if data were distributed on both flanks of such a 'dome-shaped' relationship, linear methods would probably fail completely to pick up any significant empirical relationship at all.

Recently, effective nonlinear methods of empirical analysis have been introduced to marine ecology and fisheries science (Mendelssohn and Cury, 1987; Mendelssohn and Mendo, 1987; Cury *et al.*, 1995). A problem with introducing the possibility of nonlinear relationships is that it is much easier to fit data when one has an indefinite choice of functional forms. Without the discipline of a single a priori choice, such as linearity, the problem of spurious fits becomes even worse than usual. In such circumstances, the discipline of comparative interregional consistency in functional form offers a very useful alternative.

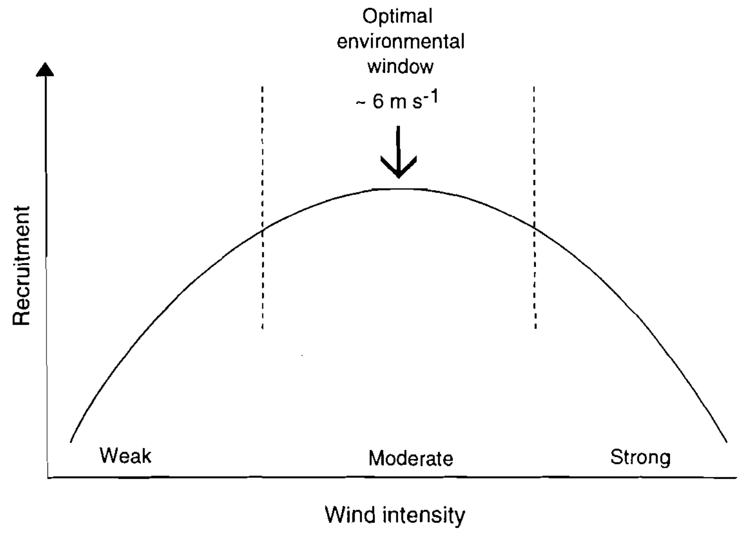


Fig. 4: 'Optimal environmental window' relationship between wind intensity and reproductive success in upwelling regions (Cury and Roy, 1989).

In the preeminent example that we have available up to this time, nonlinear methods were applied in a comparative context to an empirical investigation of effects of interyear variations in mean wind intensity on the population dynamics of various stocks of small pelagic fish in several coastal upwelling regions. The result (Fig. 4) was the famous, domed-shaped, 'optimal environmental window' relationship (Cury and Roy, 1989). This finding, and its follow-on extensions (many of which appear in this volume), finally provides some tangible empirical support for certain concepts (e.g., the 'triad' framework which is presented in the next section) that have been emerging 'inferentially' over the past decade within the context of the international SARP Project (IOC-FAO Sardine-Anchovy Recruitment Project), and more recently, within the CEOS context. It also provides empirical support to arguments such as presented above in Section 4, i.e., that the driving mechanism for synchronized 'regime'-scale population variability must most probably be simply and directly linked to inter-decadal-scale global climatic variability, probably transmitted locally through the sea surface by action of the wind.

7. THE 'TRIAD' FRAMEWORK

Comparative studies of geographical climatology of fish reproductive habitats (i.e., the first type of approach introduced in Section 5) have tended to identify a 'fundamental triad' (Bakun, 1993, 1996, in press) of three major classes of processes that combine to yield favorable reproductive habitat for coastal pelagic fishes and also many other types of fishes:

(1) enrichment processes (upwelling, mixing, etc.);
(2) concentration processes (convergence, frontal formation, water column stability); and
(3) processes favoring retention within (or drift toward) appropriate habitat.

The importance of enrichment processes is quite intuitive and, moreover, tends to be clearly evident in geographical patterns of fish abundance. Most of the ocean surface area is quite unproductive because of scarcity of certain essential plant nutrients, which are trapped below the photosynthetic layers by ocean stratification. And clearly, areas where nutrients are supplied to the illuminated ocean surface layers by upwelling or mixing tend to be highly productive and to contain large, prolific fish populations.

Perhaps less widely appreciated is the importance of concentration processes. For very small organisms, such as fish larvae and other important components of the planktonic food web, sea water represents quite a viscous fluid; major energy expenditures may be necessary just to move from food particle to food particle. Thus large amounts of energy, needed for the rapid growth that is required for quick passage through the various size-related levels of intense predation that pervade the ocean environment, may be expended in feeding activity. Consequently, availability of processes whereby food particles are concentrated tends to be vital.

This is probably a major reason why various types of interfaces, or ergoclines (Legendre and Demers, 1985), tend to be sites of enhanced biological activity in the ocean. These interfaces tend either to maintain, or to be maintained by, mechanisms of concentration (Bakun, 1996). Ocean fronts (Fig. 5) are obvious examples. The importance of processes occurring in or near ocean fronts is suggested by the widespread attraction of fish and other marine animals to drifting objects. The actual convergent water motions associated with a front are probably too subtle to be directly sensed by pelagic organisms functioning in an environment devoid of fixed reference points. However, drifting objects tend to be carried into and to accumulate within frontal structures An innate attraction to drifting objects serves to position the fish within the zones of enhanced biological activity and correspondingly improved feeding conditions (Bakun, 1993, 1996).

Conversely, turbulence is a dispersive process and so acts counter to concentration processes. Thus intense turbulent mixing events have appeared to be detrimental to larval survival (Lasker, 1978, 1981a, 1981b). On the other hand, extremely small-scale turbulence may actually act like a concentration mechanism by increasing the encounter rate of small organisms with food particles (Rothschild and Osborn, 1988).

The third factor in the 'triad' is retention. Life cycles of marine organisms tend to include at least one stage of passive larval drift. Thus, in a dispersive fluid medium, loss of early life stages from the population habitat may represent serious wastage of reproductive resources. Consequently, fish populations tend to spawn in locations and seasons that minimize such losses (Parrish *et al.*, 1981; Sinclair, 1988). The triad concept thus incorporates many of the most promising current hypotheses about environmental regulation of fish reproductive success.

Certainly, the optimal environmental window result (Fig. 4) confirms well to an interpretation based on this fundamental triad. An obvious explanation for lowered reproductive success on the 'left flank', or 'low wind' side, is a lack of nutrient-enrichment by wind-induced upwelling or mixing, leading to inadequate production of appropriate larval food (Cushing, 1969). In addition, it is possible that under conditions where the interaction of feeding behavior with stable fine-scale food particle structure may be less important than the energy savings produced by turbulent diffusion of food particles toward feeding larvae, the mechanism of Rothschild and Osborn (1988) may exert some control on the 'left flank' by increasing larval survival toward the slightly higher wind speeds within the 'window'.

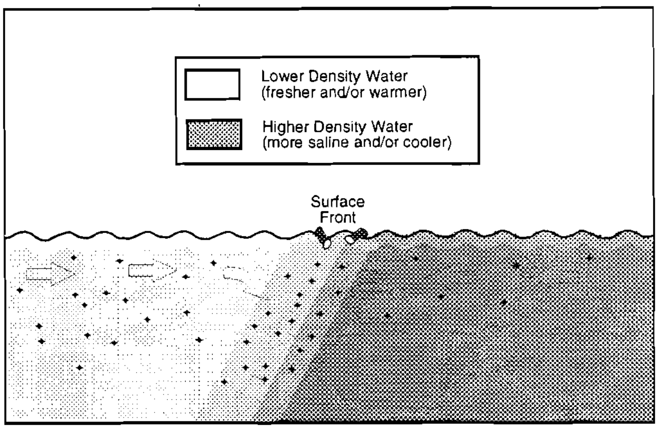


Fig. 5: Schematic diagram of a front between waters of differing density. Arrows indicate density-driven flows associated with the front. 'Particle' symbols indicate planktonic organisms capable of resisting vertical displacement. (Scales are distorted: vertical scale greatly expanded relative to horizontal; particles greatly magnified; surface waves not to scale, etc.) Redrawn from Bakun (1993).

The control on the 'right flank', i.e., the 'high wind' side, could come about either through (1) increased offshore transport leading to excessive offshore loss of pelagic larvae from the favorable coastal habitat (Parrish *et al.*, 1981; Sinclair, 1988) or through (2) overly intense turbulent mixing which could disperse fine-scale concentrations of appropriately sized food particles needed for successful first feeding (Lasker, 1978, 1981a, 1981b) as well as inhibit basic photosynthetic production by mixing phytoplankton cells beyond their 'critical depth' (Sverdrup, 1953; Steele, 1974). Strong turbulence might also impair a larva's ability to physically capture prey (MacKenzie *et al.*, in press).

As a framework for research activity, the triad concept has the advantage that it may appeal to both physical and biological scientists, and so provide a common basis for interdisciplinary studies. Moreover it avoids the defeating complexities of small-scale trophic processes that are impossible to observe directly on population scales and thus to formulate as indicator time series for empirical analysis and verification. (These of course must be extremely important processes in the overall trophic economy upon which fish populations depend. But in terms of influence on radical interdecadal population variability, if the 'good news' arguments presented in Section 4 are valid, one can reason that these trophic complexities must be operating somewhat in the background and not directly controlling the fluctuations. Thus, in this respect they would seem to be less important than the direct linkage of the physical climatic system, through the triad processes, immediately to the fish themselves).

8. INCORPORATING SOCIOECONOMICS

Fisheries scientists would like to think that if the industry would only do what the scientists advise, everything would be all right: populations would remain prolific and productive and fisheries would remain profitable and sustainable. This might not be true, and the notion may lead to a false sense of security that contributes to the disastrous level of overcapitalization of world fisheries (FAO estimates that world fisheries operate at an annual loss of US$53 billion, which must be offset by government subsidies). It seems rather likely that, for many highly variable populations, there may be no management system that would succeed in maintaining them continuously at population sizes approaching a large fraction of historical peak levels.

Even so we should be able to learn from experience to avoid some of the economic losses and social dislocations. In the cases of inherently variable classes of fishery resource populations, rather than clinging to the hope of managing the populations so as to provide secure bases for stable fisheries, it may be necessary to shift the focus toward directly managing the fisheries and to developing 'robust' strategies for economic viability under conditions of radically varying resources. For one thing, a holistic view of risk and uncertainty might help avoid the disastrous overcapacity that has made fisheries a net burden on other economic sectors. This in turn would tend to ameliorate the overfishing problems, and would certainly promote better economic return to those earning their livelihoods by fishing and associated activities.

In order to 'learn from experience' in dealing with such issues, CEOS incorporates both environmental biology and socioeconomics as major components of its comparative research framework. In fact, CEOS is the only international scientific program addressing small pelagic fisheries that includes both biology and socioeconomics as substantial components.

Of course development of robust strategies is one thing and specific scientific prediction is quite another. Taking an analogy (and jargon) from the American stock market, 'dollar cost averaging' is a robust strategy, i.e., one that may serve to maximize earnings by maximizing the likelihood that, on average, more shares are bought when the markets are in a lower price phases than when they are in higher price phases. This may a good type of strategy when no specific prediction is possible and when the markets are reasonably well-behaved. But every stock market player knows that 'dollar cost averaging' is no match for 'insider information' (i.e., specific foreknowledge of market events). In the sense of this analogy, one might say that the goal of CEOS is to generate some real, tangible 'insider information' on fishery resource variability and attendant socioeconomic consequences.

So, one might ask what level of prediction one might hope for. Well, maybe the least we might expect on the near term would be to be able to reasonably identify when we may be in a period of transition or 'regime change'. At such a time, for example, a particular level of precaution might be appropriate. One might be warned that the experience accumulated during a recent period of relative stability may not hold in the new conditions, or that equilibrium models that may have been valid to some level of approximation over the previous period may no longer be so, or that a recent high catch per unit effort may not indicate that the population is doing particularly well, but only that conditions have changed (recall the Peruvian experience of very high catch/effort occurring just before the disastrous collapse of the anchoveta fishery in the early 1970s). These may represent very valuable pieces of foresight. And that level of prediction indeed seems a realistic hope, particularly in view of the relative simplification (see Section 4) of the system response that may be implied by the apparent interregional synchronies.

9. PATHWAYS AHEAD

The retrospective analytical approach, making use of the new analysis techniques applied in a comparative context, has predominated in the first years of CEOS. The most extensive application has been on the biological-ecological side of the spectrum of issues. Here, the 'triad' idea has been implicit in the choice of independent variables (i.e., in the extensive use of wind-related indices of transport, turbulence generation, upwelling, etc.).

There would seem to be room for expanded use of a similar approach on the socioeconomic side. Of course, advances on an underlying conceptual framework (in analogy to the ecological side where we have the 'triad', for example) on which to structure empirical analysis activities will be extremely useful. To this end, some additional very basic interregional comparative 'pattern recognition' among the available histories, anecdotes, and informational fragments might be warranted. The conventional management approach of trying to keep the size of a resource population continually at a relatively high level by managing the level of fishery removals, and thus to provide a basis for a relatively static fisheries industry, is simply not working in a substantial number of cases. Fisheries science badly needs an alternative, but it must be one which can stand up to rigorous evaluation (Sissenwine, 1993). Although in many situations it may not be possible to maintain a desired population level by adjusting fishing pressure, it most clearly will always be possible to destroy a population by too much fishing. In a situation in which it is obviously in no one's interest (except perhaps in the very short-term interest of very selfish entities) to utterly destroy a resource, the conventional methodologies at least provide a formal basis for saying 'stop fishing now'. So, until there is available a specific well-founded alternative, it is clearly unwise to dismantle or discredit what is in place.

On the ecological side there seem to be some promising opportunities to become more process-oriented. The train of logic developed earlier suggested the probability that the interregional linkages are transferred from the atmospheric teleconnections to the ocean ecosystem through the sea surface. Many of the triad processes involve transfers through, or changes in properties of, the sea surface skin. Consequently they may leave 'signatures' that might be identified from satellites. This is a timely consideration because there will be shortly up to five separate ocean-specialized satellites in orbit and active; previously there has been no more than one at any one time (Kieffer, pers. comm.). This new generation of ocean-oriented satellites will also provide new tools. For example, useful direct estimates of ocean primary productivity from satellites are a strong possibility.

Satellite images represent a wealth of spatial detail that may be linked to triad processes. A key problem will be in converting this information to the longer time scales for which recruitment information, or other net population-scale outputs, may be obtainable. The standard method for transferring satellite information to longer time periods has been by making longer-term averages of the data. However, such an averaging process degrades the spatial detail which is the strongest feature of satellite-derived information. The trick will be to find a more intelligent way to deal with the short time-scale data flow.

The triad framework may be of use in identifying features or qualities that may in some way be quantifiable to the extent that index time series could be developed. Advanced statistical techniques such as spectral EOFs (Mendelssohn and Roy, 1986) may be useful in this regard. Perhaps the techniques of 'artificial intelligence', using neural network computer software, etc., might be enlisted to make use of ever more available and less expensive computer power to deal with finding and resolving the pertinent features from within the enormous data flows produced by satellite-mounted sensors (i.e., to allow the computer itself, through shear computing power, to 'learn' to recognize the relevant attributes). Another technique to rationally carry the spatial detail provided by satellite observation systems to the longer time scales associated with population-scale recruitment success is to use the satellite information to drive coupled dynamic coastal ocean models that may correctly incorporate pertinent triad mechanisms. Testing of this approach is currently being implemented in a CEOS-associated study off Senegal (C. Roy, pers. comm.).

There appear to be some key biological—ecological questions involved in the development of greater understanding of the nature interdecadal regime changes and how best to cope with them. These are often questions that are particularly difficult to address. I have often felt (Bakun, 1996) that there are two types of questions in our business. One type are questions for which we can get answers but don't need them and the other type are questions for which we need answers but can't get them.

One major one of the second type is: 'What is the nature of the interaction between anchovies and sardines?'. The classic example of regime change involves a shift of dominance between anchovies and sardines within the extremely important small pelagic fish component of the trophic structure of an ocean boundary current ecosystem. But it is unclear by what mechanism these two groups might interact to effect displacement of one by the other. Some level of 'competition' seems to be implied if indeed there is a tendency for mutual exclusion. But if the dominant mechanism were some kind of predatory exclusion such as a very major effect of predation of adults of one group on the eggs of the other, etc., it would seem to be counter to the earlier arguments about global synchrony in populations (i.e., lack of major predatory interactions, corresponding absence of chaotic dynamics, etc.).

One evident difference between the two is that sardines are larger, correspondingly stronger swimmers, and more adapted to migration, while anchovies appear to be more adaptable, being able to utilize a variety of habitat configurations yielding appropriate 'triad' tradeoffs (Bakun, 1993). Since sardines have done well in several systems which evidently experienced intensification of dynamic aspects during the mid-1970s to mid-1980s period, Bakun (1996; in press) speculated that sardines could perhaps deal best with an intensified system (stronger flows, more intense ocean turbulence, etc.). But there is no information presently available as to exactly how such an effect might act. Moreover, this particular argument seems to imply a mechanism acting at the adult stage.

On the other hand, one might think it more likely that the linkage mechanism might be acting at the early life stages through differential effects of climate-mediated alterations in characteristic configurations of triad processes. In such a case, if one could define variability in characteristic triad structures through analysis of satellite imagery, it should be possible to design quite simple and feasible programs to sample spatial distributions of larvae in relation to such structures, and to find out where and if anchovy or sardine larvae were abundant and also where they were growing well; for example, larval growth could be gauged by measuring RNA/DNA ratios (Nakata *et al.*, 1995; Buckley, 1984). Similarly, temporal patterns in survival and growth of the respective species, in relation to temporal variability in the triad physical structures, might be investigated by analyzing daily marks on larval or juvenile otoliths (Campana and Neilson, 1985; Guitierrez and Morales-Nin, 1986) collected at some later time.

Clearly, it will be well to continue to try to find innovative investigative approaches to key issues. One might expect that much of the type of results that can issue from standard conventional sampling programs, 'shotgun' approaches to data gathering, etc., might already be largely in hand and that innovation and ingenuity should be the key to getting the answers we need. CEOS has a number of relative innovations incorporated in its analytical framework: (a) use of nonlinear empirical techniques, (b) a specific focus on application of the comparative method, (c) promising conceptual bases for organizing collaborative interdisciplinary activity (e.g., the 'triad', which integrates both physical and biological aspects in a simple, relatively comprehensive framework), (d) incorporation of socioeconomic aspects together with ecological aspects. This framework has already led to certain salient results, such as the demonstration of the remarkable robustness of the estimated optimal environmental windows.

According to the arguments presented earlier in this paper, the apparent tendency for a degree of global synchrony in interdecadal population variability and 'regime changes' may allow certain conclusions to be drawn, pointing the way to narrowing the range of possible processes and degrees of complexity in the problem. If indeed the biological complexity may be minimal, as appears to follow from the argument, substantial progress on issues that have been resistant for many decades, seems a distinct possibility.

Thus, if the apparent global synchrony is real, it is indeed a 'gift'. There is no reason that such synchrony would have had to occur. But if indeed it does occur, it is surely rife with significance. We should carefully decipher the full range of implications in order to make good use of the information in directing our research activities along particularly cogent pathways. In particular, it could be very meaningful as regards fisheries science itself. For example, it would appear to imply that the key problems in our science are problems we can address, without being lost in endless complexities. Ultimately, it could mean that fisheries management need not forever be a sort of operational craft, based on 'rules of thumb' and aphorisms, but rather have at its disposal real prognostic power based on understandable mechanisms and sound scientific laws. More immediately, it could mean that, after decades of frustration, real, tangible progress on the fisheries-environment problem may be within our reach. That would be very good news indeed.

REFERENCES CITED

Anon. 1993. Why lobster boom is over? *Fishing News International*, March, 4.

Bakun A. 1985. Comparative studies and the recruitment problem: searching for generalizations. *CalCOFI Rep.*, 26: 30-40.

Bakun A. 1993. The California Current, Benguela Current, and southwestern Atlantic shelf ecosystems: A comparative approach to identifying factors regulating biomass yields. *In:* K. Sherman, L. M. Alexander, and B. Gold (eds.). *Large marine ecosystems: stress, mitigation, and sustainability*. Am. Assoc. for the Advancement of Science: 199-224.

Bakun A. 1996. *Patterns in the ocean: ocean processes and marine population dynamics*. Centro de Investigaciones biológicas del Nordeste, La Paz, Mexico and University of California Sea Grant, San Diego, USA, 323p.

Bakun A. In press. A dynamical scenario for simultaneous "regime-scale" marine population shifts in widely separated LMEs of the Pacific. *In:* The large marine ecosystems of the Pacific Ocean. Blackwells, London.

Bakun A., V. Christensen, C. Curtis, P. Cury, M.H. Durand, D. Husby, R. Mendelssohn, J. Mendo, R. Parrish, D. Pauly and C. Roy. 1992. The climate and Eastern Ocean Systems project (CEOS), *Naga*, the ICLARM Quarterly 15(4): 26-30.

Baumgartner T.R., A. Soutar and V. Ferreira-Bartrina. 1992. Reconstruction of the past history of Pacific sardine and northern anchovy populations over the past two millenia from sediments of the Santa Barbara Basin, California. *CalCOFI Rep.*, 33: 24-40.

Buckley L.J. 1984. RNA/DNA ratio: an index of larval fish growth in the sea. *Mar. Biol.*, 80: 291-298.

Campana S.E. and J.D. Neilson. 1985. Microstructure of fish otoliths. *Can. J. Fish. Aquat. Sci.*, 42: 1014-1032.

Cury P. and C. Roy. 1989. Optimal environmental window and pelagic fish recruitment success in upwelling areas. *Can. J. Fish. Aquat. Sci.*, 46: 670-680.

Cury P., C. Roy, R. Mendelssohn, A. Bakun, D.M. Husby and R.H. Parrish. 1995. Moderate is better: exploring nonlinear climatic effects on the Californian northern anchovy (*Engraulis mordax*). *In:* R.J. Beamish (ed.). Proceedings of the International Symposium on Climate Change and Northern Fish Populations. *Can Spec.Publ. Fish. Aquatic Sci.*, 121: 417-424.

Cushing D.H. 1969. Upwelling and fish production. *FAO Fish. Tech. Pap.*, 84, 40p.

DeVries T.J. and W. G. Pearcy. 1982. Fish debris in sediments of the upwelling zone off central Peru: a late Quarternary record. *Deep-Sea Res.*, 28:87-109.

FAO. 1993. Review of the state of world marine fishery resources. *FAO Tech. Pap.*, 335, 136p.

Francis R.C. and S.R. Hare. 1994. Decadal-scale regime shifts in the large marine ecosystems of the north-east Pacific: a case for historical science. *Fish. Oceanogr.*, 3: 279-291.

Gutierrez E. and B. Morales-Nin. 1986. Time series of daily growth in *Dicentrarchus labrax L* otoliths. *J. Exp. Mar. Biol. Ecol.* 103: 163-179.

Kawasaki T. 1983. Why do some pelagic fishes have wide fluctuations in their numbers? Biological basis of fluctuation from the viewpoint of evolutionary ecology. *In:* G.D. Sharp and J. Csirke (eds.) Reports of the Expert Consultation to Examine Changes in Abundance and Species Composition of Neritic Fish Resources. *FAO Fish. Rep.*, 291, 1: 1065-1080.

Lasker R. 1978. The relation between oceanographic conditions and larval anchovy food in the California Current: Identification of the factors leading to recruitment failure. *Rapp. P.-v. Réun.Cons. int. Explor. Mer*, 173: 212-230.

Lasker R. 1981a. Factors contributing to variable recruitment of the northern anchovy (*Engraulis mordax*) in the California Current: contrasting years 1975 through 1978. *Rapp. P.-v. Réun. Cons. int. Explor. Mer*, 178: 375-388.

Lasker R. 1981b. The role of a stable ocean in larval fish survival and subsequent recruitment. *In:* R. Lasker (ed.) Marine fish larvae: morphology, ecology and relation to fisheries. Univ. Washington Press, Seattle: 80-87.

Legendre L. and S. Demers. 1985. Auxiliary energy, ergoclines and aquatic biological production. *Naturaliste can.* (Rev. Écol. Syst.), 112: 5-14.

Lluch-Belda D., R.J.M. Crawford, T. Kawasaki, A.D. MacCall, R.H. Parrish, R.A. Schwartzlose and P.E. Smith. 1989. World-wide fluctuations of sardine and anchovy stocks: the regime problem. *S. Afr. J. Mar. Sci.*, 8: 195-205.

Lluch-Belda D., R.A. Schwartzlose, R. Serra, R.H. Parrish, T. Kawasaki, D. Hedgecock and R.J.M. Crawford. 1992. Sardine and anchovy regime fluctuations of abundance in four regions of the world oceans: a workshop report. *Fish. Oceanogr.*, 1: 339-347.

MacKenzie B.R., T.J. Miller, S. Cyr and W.C. Leggett. In press. Evidence for a dome-shaped relationship between turbulence and larval fish ingestion rates. *Limnol. Oceanogr.*

May R. M. 1979. Bifurcations and dynamic complexity in ecological systems. *Ann. New York Acad. Sci.*, 316: 517-529.

Mayr E. 1982. *The growth of biological thought.* Harvard Univ. Press, Cambridge, Mass., 974p.

Mendelssohn R. and C. Roy. 1986. Environmental influences on the French, Ivory Coast, Senegalese and Moroccan tuna catches in the Gulf of Guinea. *In: Special Publication of the International Skipjack Year Program*, ICCAT, Madrid: 170-188.

Mendelssohn R. and P. Cury. 1987. Forecasting a fortnightly abundance index of the Ivoirian coastal pelagic species and associated environmental conditions. *Can. J. Fish. Aquat. Sci.*, 44: 408-421.

Mendelssohn R. and J. Mendo. 1987. Exploratory analysis of anchoveta recruitment off Peru and related environmental series: 294-306. *In:* D.Pauly and I. Tsukayama (eds.) The Peruvian anchoveta and its upwelling ecosystem: three decades of change. *ICLARM Studies and Reviews* ,15: 294-306.

Mendo J. 1994. *The Peruvian anchoveta fishery and environmental changes*. Presented at the first international CEOS Meeting, Monterey, California, 6-8 September, 1994.

Nakata K., H. Zenitani and D. Inagake. 1995. Differences in food availability for Japanese sardine larvae between the frontal region and the waters on the offshore side of Kuroshio. *Fish. Oceanogr.*, 4: 68-79.

Parrish R.H., C. S. Nelson and A. Bakun. 1981. Transport mechanisms and reproductive success of fishes in the California Current. *Biol. Oceanogr.*, 1: 175-203.

Parrish R.H., A. Bakun, D.M. Husby and C.S. Nelson. 1983.Comparative climatology of selected environmental processes in relation to eastern boundary current pelagic fish reproduction. *In*: G.D. Sharp and J. Csirke (eds.). Proceedings of the Expert Consultation to Examine Changes in Abundance and Species Composition of Neritic Fish Resources. *FAO Fish. Rep.*, 291: 731-778.

Parrish R.H., R. Serra and W.S. Grant. 1989. The monotypic sardines, sardina and sardinops: their taxonomy, distribution, stock structure, and zoogeography. *Can. J. Fish. Aquat. Sci.*, 46: 2019-2036.

Pauly D., P. Muck, J. Mendo and I. Tsukayama (eds.). 1989. *The Peruvian upwelling ecosystem: dynamics and interactions.* ICLARM Conf. Proceedings 18, 468p.

Pearcy W.G. 1992. *Ocean ecology of North Pacific salmonids.* Washington Sea Grant Program. Univ. Washington Press, Seattle and London, 179 p.

Polovina J.J., G.T. Mitchum, N.E. Graham, M.P. Craig, E.E. De Martini and E.N. Flint. 1994. Physical and biological consequences of a climate event in the central North Pacific. *Fish. Oceanogr.*, 3: 15-21.

Rothschild B.J. 1986. *Dynamics of marine fish populations.* Harvard University Press. Cambrige, Mass., 277p.

Rothschild, B.J. and T.R. Osborn. 1988. The effects of turbulence on planktonic contact rates. *J. Plankton Res.*, 10: 465-474.

Roy C., P. Cury, P. Fontana and H. Belvèze. 1989. Stratégies spatio-temporelles de la reproduction des clupéidés des zones d'upwelling d'Afrique de l'ouest. *Aquat. Living Resour.*, 2: 21-29.

Roy C., P. Cury and S. Kifani,1992. Pelagic fish reproductive success and reproductive strategy in upwelling areas: environmental compromises. *In:* A.I.L. Payne, K.H. Brink, K.H. Mann and R. Hilborn (eds.). Benguela trophic functioning. *S. Afr. J. Mar. Sci.*, 12: 135-146.

Sharp G. D., J. Csirke and S. Garcia. 1983. Modelling fisheries: What was the question? *In:* G. D. Sharp and J. Csirke (eds.) Proceedings of the Expert Consultation to Examine Changes in Abundance and Species Composition of Neritic Fish Resources. *FAO Fish. Rep.*, 291: 1177-1224.

Sinclair M. 1988. *Marine populations. An essay on population regulation and speciation.* Washington Sea Grant Program. Univ. Washington Press, Seattle and London, 252 p.

Sissenwine, M.P. 1993. Comment. *In*: D.D. Platt (ed.) *The system in the sea, applying ecosystem principles to marine fisheries*, 2: Conference proceedings. The Island Institute, Rockland, Maine: 142.

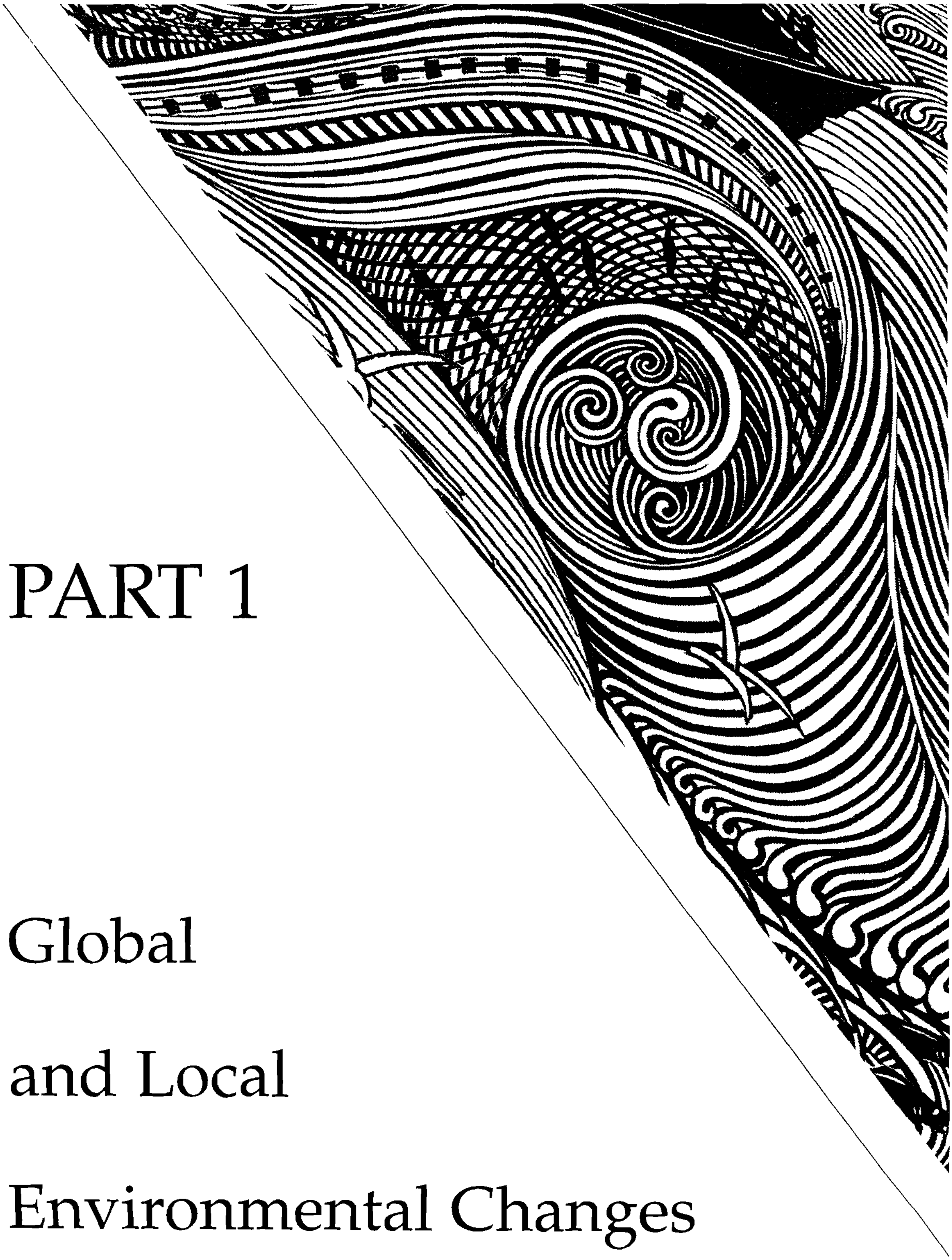
Soutar A. and J.D. Isaacs. 1974. Abundance of pelagic fish during the 19th and 20th centuries as recorded in anaerobic sediment off the Californias. *Fish. Bull.*, U.S., 72: 257-273.

Steele J.H. 1974. *The structure of marine ecosystems.* Harvard Univ. Press, Cambridge, Mass., 128 p.

Sverdrup H.U. 1953. On conditions for vernal blooming of phytoplankton. *J. Cons.*, Cons. int. Explor. Mer, 18: 287-295.

Venrick E.L., J.A. McGowan, D.R. Cayan and T.L. Hayward. 1987. Climate and chlorophyll a: long-term trends in the central North Pacific Ocean. *Science*, 238: 70-72.

Weiner J. 1994. *The beak of the finch.* Alfred A. Knopf, New York, 332 p.



PART 1

Global and Local Environmental Changes

The Development and the Use of a Climatic Database for CEOS using the COADS Dataset

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ABSTRACT

The Comprehensive Ocean-Atmosphere Dataset (COADS) was selected by CEOS for use in analyzing the climatic variability of the world upwelling ecosystems during the past four decades. The COADS database summarizes over 100 million surface meteorological observations collected by ships of opportunity and other platforms over the world. This dataset has world-wide coverage and the earliest data dates back to 1854.

A preliminary investigation of the climate variability of the world coastal upwelling regions was performed using a reduced version of the COADS dataset (the 2° by 2° monthly summary files). It appeared that these files are subject to numerous biases and are not suitable for performing the retrospective analysis of the climatic variability planned by CEOS. It was necessary to set up a database using the individual observations instead of the summary files. A version (CMR-5) of the 100 million individual records available in the COADS was provided by NCAR (National Centre for Atmospheric Research - USA). The CMR-5 version of the COADS dataset was reorganized in a fashion that allowed for rapid access to the dataset using a micro-computer, and software for processing and summarizing the data was developed. The reorganized dataset was then put onto CD-Roms for distribution. The software and the five CD-Roms represent the core of the climatic information used by the CEOS program for the retrospective and comparative analyses.

Some important biases encountered when using the COADS data are reviewed. Changes through time in the measurement procedures are the most common source of systematic errors in COADS; these biases occur in particular in sea surface temperature and wind. The sudden change that occurs after the Second World War due to the use of insulated buckets and of engine-intake measurements is thought to be responsible for the abrupt change in the SST time series that occurs at the same time. Wind data reported by ships are either measured with an anemometer or are estimated from sea-state. Estimated wind data predominate before the Second World War. Today, wind data collected using measurement devices are predominant. Several examples are given in order to illustrate the potential biases that can affect the seasonal cycle and the long term trend of the wind intensity due to the gradual shift through time from estimated wind data to measured wind data. The potential biases introduced by merging buoys data with ship data are illustrated by looking at the wind data off California during the last twenty years. Finally, a discussion on the reality of the positive trend existing in the wind data off West Africa is presented.

RÉSUMÉ

La base de données COADS (Comprehensive Ocean-Atmosphere Dataset) a été sélectionnée par CEOS pour analyser la variabilité climatique des zones d'upwelling mondiales au cours des quarante dernières années. Cette base de données rassemble 100 millions d'observations météorologiques de surface collectées par les navires marchands et d'autres plates-formes sur les océans du monde entier. La couverture est mondiale et les premières données remontent à 1854.

Un premier travail sur la variabilité climatique fut réalisé en utilisant une version réduite de COADS (moyennes mensuelles par carrés de 2°par 2°). Il est apparu que les données contenues dans ces fichiers sont affectées par de nombreux biais qui rendent hasardeuse leur utilisation pour l'étude de la variabilité climatique sur le long terme. Pour pallier ces difficultés, il fut nécessaire de bâtir une base de données rassemblant les données originales au lieu de données déjà pré-traitées. Une version de la base de données COADS (CMR-5) contenant les 100 millions d'enregistrements originaux fut acquise auprès du NCAR (National Centre for Atmospheric Research - USA). Cette base de données fut restructurée afin de permettre un accès rapide à partir d'un micro-ordinateur, et un logiciel d'extraction et de traitement fut développé. L'ensemble de la base de données fut ensuite transféré sur un jeu de 5 CD-Roms.

Les principaux biais rencontrés lors de l'utilisation de COADS sont passés en revue. Les changements au cours du temps des méthodes de mesure sont à l'origine des erreurs les plus courantes, les variables concernées sont plus particulièrement la température de surface de la mer et le vent. Des modifications des modes de prélèvement et l'introduction de nouveaux instruments de mesure à la fin de la Seconde Guerre Mondiale sont à l'origine d'un changement abrupt dans les séries de température de surface de la mer à la fin des années quarante. Les données concernant le vent, récoltées par les navires marchands, sont de deux types : "estimées" visuellement à partir de l'état de la mer ou "mesurées" à l'aide d'un anémomètre. Jusqu'aux années cinquante, l'essentiel des données de vent était du type "estimées", aujourd'hui les données "mesurées" à l'aide d'un anémomètre sont prédominantes. Plusieurs exemples sont donnés afin d'illustrer les biais introduits dans les séries temporelles de vent, construites à l'aide de COADS, par l'augmentation régulière du nombre de données "mesurées" au cours des quarante dernières années. Les biais introduits par la prise en compte de données provenant de bouées météorologiques sont illustrés à partir de séries extraites devant les côtes de Californie. Les séries temporelles de vent obtenues à partir de COADS devant les côtes ouest-africaines sont comparées à d'autres séries, et une discussion concernant la réalité de la tendance observée dans les données COADS dans cette région est réalisée.

INTRODUCTION

One of the major objectives of the CEOS program is to assemble, summarize and analyze the climatic data record of the four eastern ocean boundary upwelling ecosystems during the past four decades, as well as the record for the other upwelling areas (Bakun *et al.*, 1993). For this purpose, a climatic data base covering the last fifty years with a worldwide coverage is needed. This also should be homogeneous among areas and over time and thus allow the comparative analyses planned by the CEOS program.

The Comprehensive Ocean-Atmosphere Dataset (COADS) is one of the few datasets that meet these criteria (see Slutz *et al.* (1985) and Woodruff *et al.* (1987) for an extensive description of the source data and of the procedures used to create the COADS dataset). The COADS database summarizes over 100 million surface meteorological observations collected by ships of opportunity and other platforms over the world oceans which have been quality controlled and put into a consistent format. This dataset is the most complete record of surface marine climate to date. It has a world-wide coverage and the earliest records date back to 1854. The early studies of the CEOS program have used Release 1 of the COADS for the period 1854 to 1979; and for the period from 1980 to 1990, an interim release has been used, which is compatible in format and organization to Release 1, but is constructed using simplified procedures and preliminary input data.

Besides the individual observations, which are available in several formats containing different amounts of the data, reduced or summarized versions of the COADS dataset are available in several forms, including monthly or decadal summaries average over a spatial grid of 2° by 2° for the entire ocean. Due to the massive number of individual reports (100 million), the majority of researchers have used the monthly summaries. A preliminary investigation of the climate variability of the world coastal upwellings was performed using the 2° by 2° monthly summary files. Except for a trimming procedure which removes extreme outliers, the summary files are computed using all the available data. Biases in the long term behaviour of the time series derived from these pre-processed files rapidly arose: data from meteorological buoys are merged with ship data (see Section 3); wind data are aggregated without distinction between the measurement procedure used (estimated using the Beaufort scale or measured using an anemometer, see Section 3). The fixed 2° by 2° spatial grid is also a strong limitation for coastal studies where the spatial grid has to be flexible in order to be adapted to the shape of the coastline. After this first attempt, it appeared that the 2° by 2° degree summaries files were not suitable for performing the retrospective analysis of the climatic variability planned by CEOS. To avoid some of the bias existing in the summaries files, it was necessary that the retrospective analysis be performed using the individual observations instead of the 2° by 2° summary files.

Producing useful time series from the 100 million individual records available in COADS is a much more complicated task than working with the 2° by 2° monthly summaries files; this is even more so as the CEOS program needs to run on micro-computers rather than mainframes or workstations in order to allow dissemination of the database throughout the CEOS network. At the time the project started, large capacity optical storage devices became available which allowed for the storage and processing of large amounts of data with a micro-computer. A version of the 100 million individual records available in the COADS database which uses a compressed binary format (CMR-5) was provided by NCAR (National Centre for Atmospheric Research - USA) and transferred to a set of optical disks connected to a micro-computer. The CMR-5 version of the dataset was reorganized in a fashion that allowed for rapid access to the dataset by area, and software for processing and summarizing of the data was developed. The reorganized dataset was then put onto CD-Roms for distribution. The software and the five CD-Roms represent the core of the climatic information used by the CEOS program for the retrospective and comparative analyses.

1. DATA SOURCE USED FOR THE DEVELOPMENT OF THE CEOS CLIMATIC DATABASE

The primary data source for the CEOS climatic database is the Release 1 of COADS which covers the period 1854-1979. An interim data product is used to cover the period from 1980 to 1990 (Woodruff and Lubker, 1986). During the design and development phases of the database, our main goal was, despite the massive volume of information, to preserve access to the raw individual observations and to allow access with a microcomputer. The CMR-5 format provides a good compromise between keeping access to the raw data and a significant reduction of the total volume. It consists of approximately 100 million individual observations from 1854 to 1990. It is a packed binary format containing the most frequently used information, designed as a compact alternative to the original reports. The variables included in each report under the CMR-5 format are given in Table 1. The following observed quantities are available:

- air temperature;
- sea surface temperature;
- dew point depression;
- zonal and meridional wind components;
- sea level pressure;
- cloudiness;
- present weather.

Each record in the CMR-5 format contains data on the measurement procedure (fields BI, WI and HI in Table 1), on the precision and units (fields TI and DI in Table 1), on the type of observing vessel (field ST in Table 1) and on the origin of the record (field CD in Table 1). Quality control indicators (noted as 'flags' in Table 1) for each observed quantity area also available. The COADS documentation (Slutz *et al.*, 1985) gives a detailed description of the quality control procedures. A brief summary of these procedures is given below.

A multiple step statistical method was set up during the development of COADS in order to identify outliers for six variables: sea surface temperature, air temperature, sea level pressure, zonal wind, meridional wind and humidity. The result of this process is the definition of the smoothed lower and upper median deviation (s_1, s_2) around the smoothed mean (X) for each of the six variables; these calculations are performed with a monthly time step and a 2° spatial step. These means and limits are used to create trimming bounds for the variables. The value assigned to the quality control flags for a given observation is set according to Table 2.

The entire CMR-5 format version of the COADS dataset was reorganised and sorted in order to have an homogeneous structure over the whole time period (1854-1990). 648 folders (or subdirectories) were created, each one corresponding to a 10° by 10° geographical square. A folder (or subdirectory) contains 25 data files, one for each 2° geographical square within the 10° square. This structure allows quick access and retrieval of data for a specific ocean location.

A computer program, the Comprehensive Ocean Data Extraction or CODE was developed in order to quickly access, process and summarize using a microcomputer, the COADS dataset in the CMR-5 format. The advantage of CODE over the use of the 2° by 2° monthly pre-processed COADS files is that all calculations are performed by going back to the individual observations. This is particularly important for the calculation of derived parameters such as wind stress or wind speed cubed which are provided by CODE. It also allows a flexible spatial grid (0.1° of latitude or longitude step in the data, 0.5° in the CODE program), and makes it possible to select between several types of platform (buoys, merchant or research ship, ocean station , etc.) or between the methods used to collect the data (estimated wind using the Beaufort scale or measured wind using an anemometer).

2. BIAS IN THE COADS DATA

Some important biases encountered when using the COADS data are reviewed. Changes through time in the measurement procedures are the most common source of systematic errors in COADS; these biases occur in particular in Sea Surface Temperature (SST) and wind. Air temperature and dew point temperature are also affected by systematic

Field	Description	Value	Units
	Location		
BOX10 *	10° box number	1≤ 648	1
MONTH		1≤ 12	1
BOX2 *	2° box number	1≤ 16202	1
YEAR		1800 ≤ 2054	1
DAY		1≤ 31	1
HOUR		1≤ 23	1
LAT	(from BOX2 SW corner)	0 ≤ 2.0	0.1°
LONG	*(idem)*	0 ≤ 2.0	0.1°
	Temperature		
SST	Sea Surface Temperature	-5.0 ≤ 40.0	0.1°C
BI	Bucket Indicator	0 ≤ 2	1
AT	Air Temperature	-88.0 ≤ 58.0	0.1°C
DP	Dew Point Depression	0 ≤ 70.0	0.1°C
TI	Temperature Indicator	0 ≤ 5	1
	Wind		
U	Eastward component	-102.2 ≤ 102.2	0.1 m/s
V	Northward component	-102.2 ≤ 102.2	0.1 m/s
DI	Direction indicator	0 ≤ 5	1
WI	Wind speed indicator	0 ≤ 1	1
	Pressure and clouds		
SLP	Sea Level Pressure	870.0 ≤ 1074.6	0.1 mb
C	Total cloud amount (**)	0 ≤ 9	1
NH	Lower cloud amount (**)	0 ≤ 9	1
CL	Low cloud type (**)	0 ≤ 10	1
H	Cloud height (**)	0 ≤ 10	1
HI	Cloud height indicator (**)	0 ≤ 1	1
CM	Middle cloud type (**)	0 ≤ 10	1
CH	High cloud type (**)	0 ≤ 10	1
	Miscel.		
ST	Ship type	0 ≤ 7	1
PW (**)	Present weather (**)	0 ≤ 99	1
CD (**)	card deck (**)	0 ≤ 999	1
	Flags		
LF	Landlocked flag	0 ≤ 0	1
SF	SST flag	0 ≤ 2	1
AF	Air temperature flag	0 ≤ 2	1
RF	Relative humidity flag	0 ≤ 2	1
WF	Wind flag	0 ≤ 2	1
PF	Pressure flag	0 ≤ 2	1

Table 1: List of all variables available under the CMR-5 format.
(*) : this refers to the NCAR 10° and 2° box coordinate systems (see Slutz *et al.*, 1985) for detail.
(**) : parameters cannot be extracted using the CODE program.

Flag value	Trimming limits
0	$X - 2.8s_1 \leq x \geq X + 2.8s_2$
1	$X - 3.5s_1 \leq x \geq X + 3.5s_2$
2	$x < X - 3.5 s_1$ or $x > X + 3.5s_2$
missing	missing

Table 2: Quality control flags values in the CMR-5 format; x is the value of an individual observation, X is the smoothed median and s_1 and s_2 are the smoothed lower and upper median deviation.

errors but they are not documented here (see Isemer and Hasse, 1987; Folland *et al.*, 1984; Kent *et al.*, 1983a and 1983b for details). Along the US coastline, data coming from moored meteorological buoys have been incorporated into the COADS database during the 1980s; the effect of such changes is documented in an area where buoy data have become predominant after 1980. Comparisons between atmospheric pressure data from COADS and several other independent atmospheric pressure data have been made; the results are generally good and yield some confidence in the usefulness of the COADS pressure data (Jones *et al.*, 1986; Ward and Hoskins, 1996).

2.1. Biases in SST

The method of collecting SST samples has changed through time. Before the Second World War, SST was measured on a sea water sample collected using a bucket; engine intake measurements became predominant for the later period (Jones *et al.*, 1986). Due to evaporative cooling, measurements performed using an uninsulated bucket is thought to be about 0.5°C lower than a measurement from an engine intake (Ramage, 1984). The sudden change that occurs after the Second World War due to the use of insulated buckets and of engine-intake measurements is thought to be responsible for the abrupt change in the SST time series that occurs at the same time (Folland and Parker, 1990). This sudden shift of the mean value of SST is illustrated in Figure 1.

Several models has been developed to correct bias in bucket observations prior to the Second World War (Folland *et al.*, 1984; Folland and Hsiung, 1987; Folland and Parker, 1990; Jones and Wigley, 1992), however these corrections cannot be applied to individual observation because of the unreliability of the bucket/intake indicator and of the lack of information on the kind of bucket used in COADS.

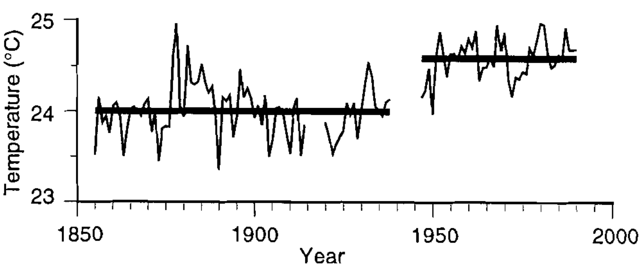

Fig. 1: Time series of Sea Surface Temperature in the tropical Atlantic (10°N-30°N, 30°W-50°W). A shift in the mean value of SST occurred in the late 1940s.

Since the beginning of the 1950s, insulated bucket or engine intake measurements are thought to be the predominant method used for measuring SST. Thus, even if some bucket measurements have been used after 1945, the biases are probably considerably less than those occurring before.

2.2. Biases in the wind data

Wind data reported by ships are either measured with an anemometer or are estimated from sea-state. Estimated wind data predominate before the Second World War. The percentage of measured wind data started to increase in the late 1940s (Fig. 2). Today, wind data collected using measurement devices is the predominant way of collecting wind data (Fig. 2). The CMR-5 format contains a flag for each wind record which indicates whether the data were estimated or measured. Several extractions were made in order to compare the characteristics of the wind signals calculated using either estimated, measured or the combination of estimated and measured wind data in several areas. These comparisons illustrate the potential biases that can affect the long term trend of the wind intensity due to the gradual shift through time from estimated wind data to measured wind data.

Measured wind data are measured in meters per second. Estimated wind data are reported using the Beaufort scale and have to be converted to an equivalent wind speed. Conversion from the Beaufort scale to wind speed expressed in m/s is done using a Beaufort equivalent scale. The scale used in COADS is the CODE 1100 (or old WMO scale). This scale is known to underestimate wind speed for Beaufort number less than 6 and to overestimate wind speed for Beaufort number greater than about 6 (WMO, 1970; Cardone, 1969; Kaufeld, 1981; Isemer and Hasse, 1991). The calculation of wind speed using measured wind data will therefore give different results than the same calculation performed using estimated wind data. Examples of the differences obtained in the determination of the mean monthly seasonal cycle of the wind speed for several areas located in different upwelling ecosystems are given in Figure 3. From those examples, it appears that the mean monthly values of wind speed calculated using measured wind data are from 0 to 0.8 m/s higher than wind speed calculated using estimated wind; the phase of the seasonal cycle does not appear to be strongly affected.

When both estimated and measured wind data are merged to calculate wind speed, the variation through time of the ratio between the numbers of estimated and measured wind observations introduces an artificial variability in the time series of wind intensity. Because estimated wind data tend to be underestimated for Beaufort scale lower than 6, wind speed will tend to be

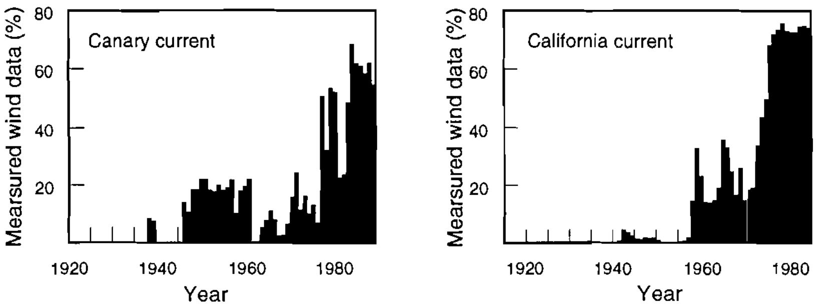

Fig. 2: Percentage of measured wind data in COADS from 1920 to 1990 in two eastern boundary current ecosystems.

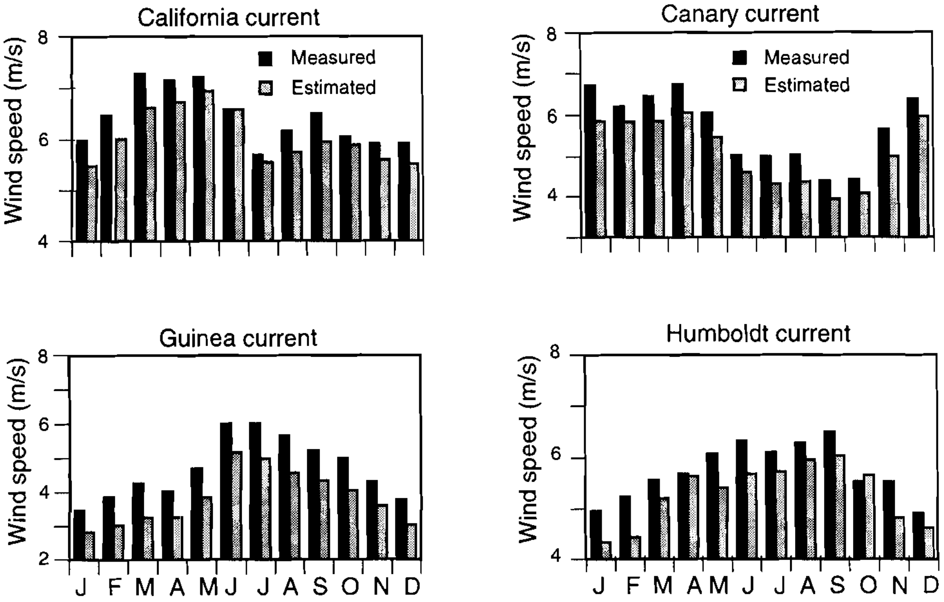

Fig. 3: Mean monthly seasonal cycle of the wind speed calculated in four areas located in the major eastern boundary current ecosystems using estimated and measured wind data (calculated for the period 1950-1990).

lower during time periods characterized by a high number of estimated wind data than during time periods when measured wind data are predominant (all other things remaining constant). The time series presented in Figure 4 illustrate the effect of the increasing percentage of measured data wind during the last 40 years on the long term variability of the wind speed. The percentage of measured wind data starts to increase significantly around the late 1960s. As a consequence, the mean annual wind speed calculated using all the available wind data (both estimated and measured, E&M time series) becomes significantly higher than the mean annual wind speed calculated using only estimated wind data (E time series).

Figure 5 shows that the difference between the annual mean of the E&M and the E wind time series is mostly explained by the interannual variability of the percentage of measured wind data. The difference reaches 0.5 m/s in the California Current and in the Guinea Current when the measured wind comprises 70% of the E&M time series.

The consequence of the increasing percentage of measured wind data in the E&M time series is the introduction of an artificial positive trend superimposed over the long term tendency given by the E wind time-series (Fig. 4). This artificial increase of the wind intensity is particularly noticeable in the California Current and the Guinea Current regions. When a linear trend is fitted from 1970 to 1990 to the time series of the California and Guinea Current wind speed, the slope of the trend of the E&M wind speed time series is 60%, respectively 80% higher than the slope of the trend given by the E wind speed time series.

A way to avoid such biases would be to use measured wind data only, but for many areas, the data density of the measured wind data in COADS is not high enough to allow the calculation of a reliable monthly time series of measured wind data before the early 1970s. Time series of wind speed based on estimated wind data can go back in some areas as far as the late nineteenth century, but the mean value of the wind speed will be affected by the bias introduce with the use of the CODE 1100 conversion table. Changes in the observation practices that were used to estimated the wind from sea-state,

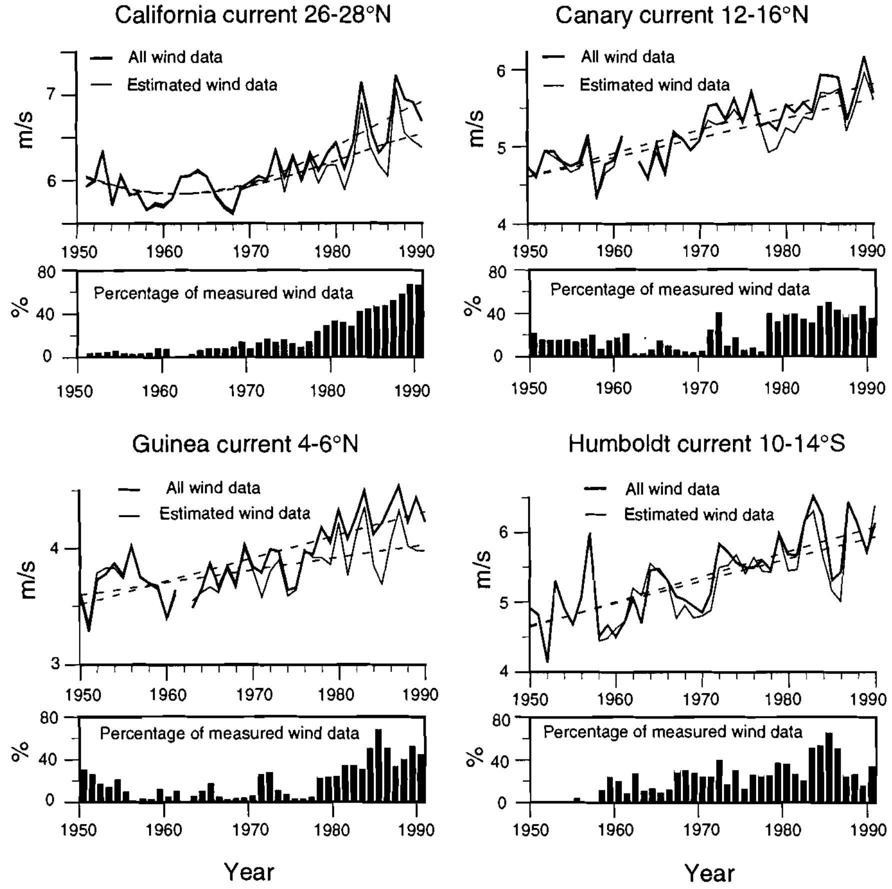

Fig. 4: Time series of wind speed calculated using all the available wind data (E&M time series) and using only estimated wind data (E time series) in four upwelling areas. For each region, the annual percentage of measured wind data is given. The long-term trend of the wind speed for each time series is also presented.

the increase of the mean size of the ships over the century and many other factors may also have introduced biases in the long term behaviour of estimated wind time series.

2.3. Meteorological buoys off the US coast

The operation of a network of moored buoys by the US National Data Buoy Centre (NDBC) started in the early 1970s. Hourly buoys data have been incorporated into the COADS interim release for the period 1980-1990 (Woodruff and Lubker, 1986). Some of the biases introduced by merging buoy and ship data are documented here using data extracted off the California coast.

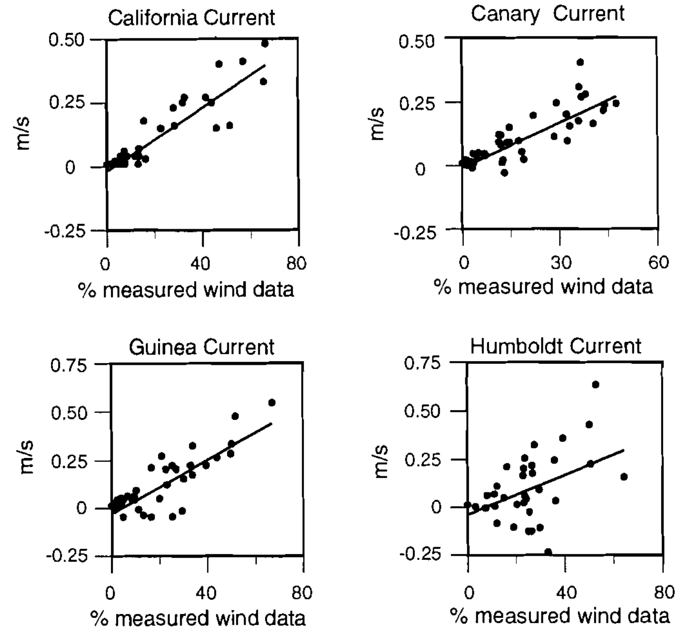

Fig. 5: Plots of the difference between the E&M and M wind speed time series against the percentage of measured wind data in four different upwelling areas.

Several buoys were installed off the California coast during the 1980s. Hourly SST, wind and atmospheric pressure data from these buoys have been incorporated into COADS. The example given in Figure 6 shows that between 36°N and 40°N the number of wind observations stays relatively constant during the 1970s (between 3000 and 4000 observations per year) and that it suddenly increases by a factor of 5 in 1981 to reach 22 920 observations. This sudden increase of the number of observations in 1981 is the consequence of the introduction of the buoy data into COADS. The reason for the decrease of the number of observations after 1984 is unknown to us.

The buoys are located in the nearshore area and the ship traffic lines are located several miles offshore. Therefore, we can suspect that the dominance of data coming from the buoys during the 1980s introduces important changes in the value of the surface atmospheric parameters in the time series. Unfortunately, the ship type indicator is missing for the interim release and therefore it is impossible to discriminate between buoy and ship observations from 1980 to 1990. The buoys are equipped with an anemometer and the buoy wind data were recorded in COADS as 'measured' data. In the COADS interim release, this is the only way to investigate the change introduced by the buoys data into COADS. The time series of the scalar wind speed calculated using 'measured' wind data in an area located off the California coast shows that a sharp decrease of the scalar wind speed occurred in 1981 when the data from the buoys are incorporated (Fig. 7). This apparent relaxation of the wind speed is likely the result of the coastal location of the buoys where the wind field presents a local minima (when compared to the offshore domain).

The time series of the scalar wind speed calculated using both measured and estimated wind is also affected by the implementation of the buoys (Fig. 7). In this series, the dominance of data coming from the buoys after 1980 results in a spurious relaxation of the wind. When wind variables are calculated using 'estimated' wind data, the buoy data are not taken into account. The time series of scalar wind speed calculated using 'estimated' wind data shows that the 1981 wind speed relaxation is an artifact resulting from the dominance of buoy data after 1980 (Fig. 7).

The COADS monthly 2°x2° summary files do not discriminate between either ship or buoy data and it is likely that wind time series off California extracted from these files will be affected by the spurious relaxation of the wind after 1980.

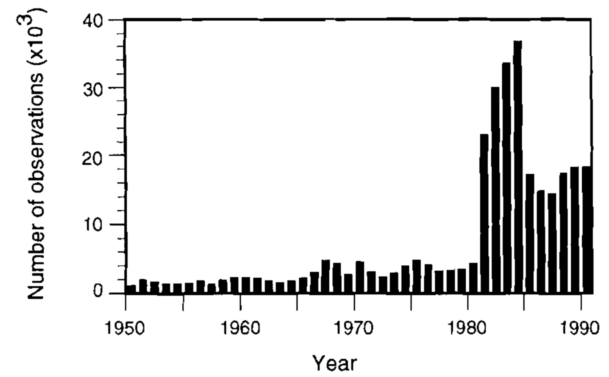

Fig. 6: Annual number of wind data available in the COADS database along the California coast between 36°N and 40°N.

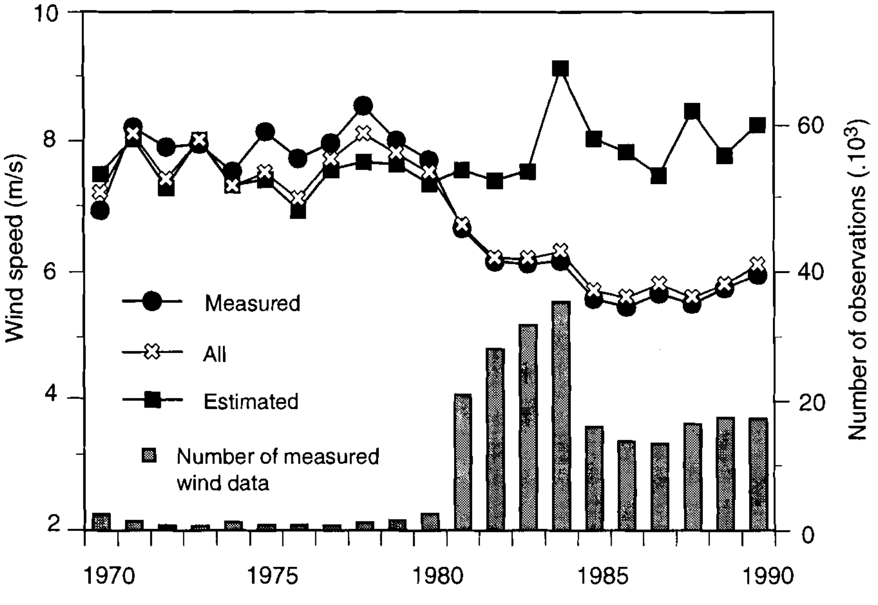

Fig. 7: Scalar wind speed along the California coast between 36°N and 40°N calculated using 1) measured wind data, 2) all wind data (estimated and measured) and 3) estimated wind data. The annual number of measured wind data in the area is also presented.

3. TREND IN THE WIND OFF WEST AFRICA: REALITY OR ARTIFACT?

A dominant feature of the time series of the COADS wind data off West Africa since the late 1940s is a continuous positive trend. Between 12°N and 22°N, wind stress (proportional to the square of the wind) increased by almost 50% from 1946 to 1990. During the upwelling season, it is expected that such an important increase of the wind stress would intensify the upwelling process and the upward flux of cold subsurface water to the surface, resulting in colder SST. Off West Africa, the magnitude of the wind stress increase from 1950 to 1990 is significant enough that drastic changes would have been introduced in the physical and biological properties of the region. However, the validity of the trend in the COADS wind data has been the subject of intense debates (Ramage, 1987; Cardone *et al.*, 1990; Isemer, 1995). In the following paragraphs, an attempt is made to examine the validity of the trend in the COADS wind off West Africa, between 12°N and 24°N.

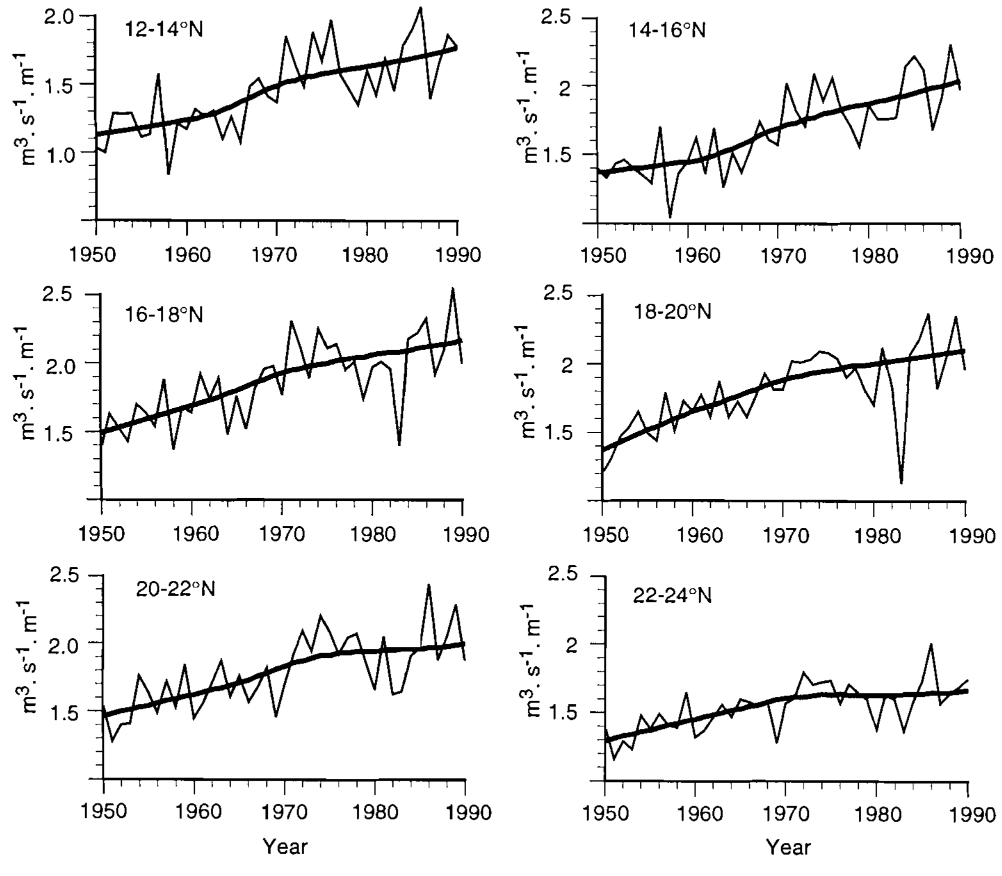

Fig. 8a: Time series of the Coastal Upwelling Index (CUI) averaged over the upwelling season (January through June) from 1950 to 1990 along the coast of West Africa between 12°N and 24°N.

Monthly time series of wind stress using the estimated wind data and of SST are extracted from the COADS database along the coast of West Africa, from 12°N to 24°N with a 2° latitudinal step. A Coastal Upwelling Indices (CUI) is calculated using the wind stress data following Bakun (1973). CUI is the offshore component of the total wind induced Ekman transport. With an upwelling favourable wind, the Ekman transport is directed toward the offshore direction and CUI is positive.

From 12°N up to 24°N, monthly CUI and SST are averaged over the upwelling season (Fig. 8a and 8b). In each area, the long term behaviour of the CUI time series is characterized by a continuous positive trend (Fig. 8a). The long term trends of the SST time series are rather stable over the whole time period with a slight cooling in the 1970s following by a warming in the 1980s (Fig. 8b). This suggests that there is no apparent relationship between the long term variability of the upwelling process and SST.

A comparison of the COADS data with other information would be extremely valuable but very few wind data exist with such a long term coverage. The wind data routinely collected every 3 hours at the Dakar-Yoff airport (14°40' N) is one of the few time series available in the region to perform such a comparison. The airport is located on the tip of the Cap-Vert peninsula

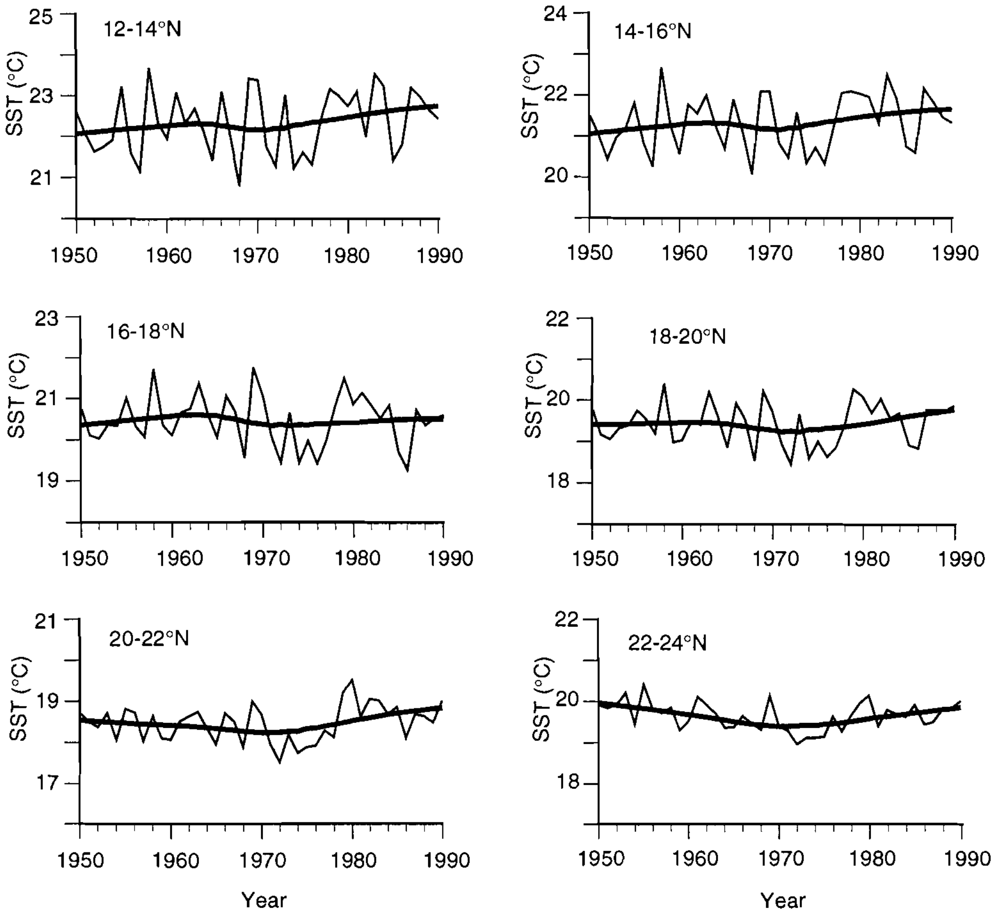

Fig. 8b: Time series of the Sea Surface Temperature (SST) averaged over the upwelling season (January through June) from 1950 to 1990 along the coast of West Africa between 12°N and 24°N.

and the wind data are thought to be representative of the wind over the offshore domain (Roy, 1989). The annual values during the upwelling seasons and the trend of the CUI derived from the Dakar-Yoff airport wind data from 1964 to 1990 are compared with the CUI time series derived from the COADS estimated wind data in the same region (14°N-16°N) (Fig. 9). The interannual variability of both time series are quite similar but there is no apparent positive trend in the CUI derived from the Dakar-Yoff wind data (Fig. 9); during the same time period, the trend in the CUI derived from the COADS wind data shows an increase of about 50% (from 1.5 to 2 $m^3.s^{-1}.m^{-1}$) of the upwelling intensity (Fig. 9). This comparison between the COADS data and the airport data gives two different pictures of the long term variability of the wind in the region.

Previous studies of the interannual variability of wind and SST in the region had shown that variability of the upwelling favourable wind accounted for a significant part of the variability of SST (Arfi, 1985; Portolano, 1986; Roy, 1989; Nikjaer and Van Camp, 1994). As an intensification of the upwelling favourable wind results in an increase of the CUI and in an intensification of the upward flux of cold subsurface water, a negative correlation is expected between CUI and SST. With the COADS data, the correlation coefficients between the mean values of CUI and SST during the upwelling seasons from 1950 to 1990 are low (between -0.22 and -0.4 except for the northern most area where it reaches 0.58) (Fig. 10). This

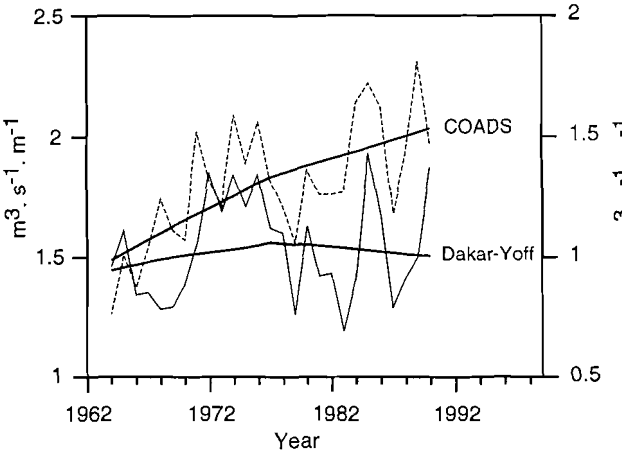

Fig. 9: Coastal Upwelling Index (CUI) averaged over the upwelling season (January through June) from 1964 to 1990 calculated using a) the wind data at the Dakar Yoff airport and b) the COADS wind data in the corresponding square (14°N-16°N, 19°W-16°W).

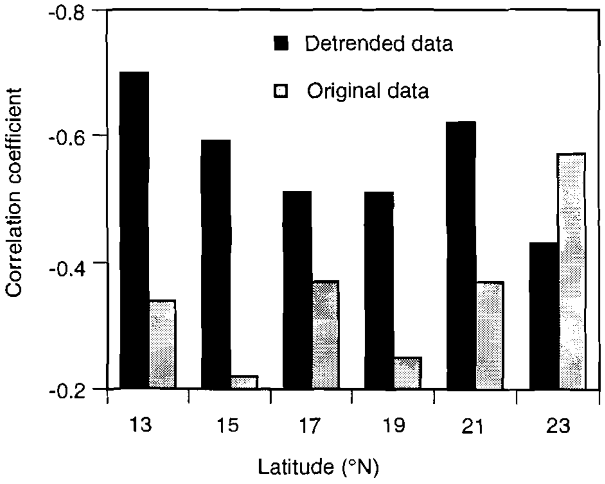

Fig. 10: Correlation coefficient between CUI and SST during the upwelling season (January through June) along the coast of West Africa between 12°N and 14°N using a) the original CUI data and b) the detrended CUI data.

suggests that the increase of the upwelling favourable wind in the COADS data over the whole time period has had little effect on the interannual variability off SST. Given the magnitude of the wind intensification (50% over 40 years) and previous studies, this is a surprising result that raises some doubt about the reality of the trend in the COADS wind data off West Africa. The use of a detrended CUI time series gives a totally different picture. The correlation coefficients between the detrended CUI and SST time series varies between -0.48 and -0.70 (Fig. 10). Except for the northern-most area, using the detrended CUI time series results in a significant increase of the correlation between the strength of the upwelling and SST.

To obtain a significant correlation between the fluctuations of upwelling and SST is in accordance with our knowledge of the dynamics of the region and with previous studies, which have shown similar results. This questions the validity of the trend in the COADS wind data off West Africa. The comparison between the wind data from the Dakar-Yoff airport and the COADS wind data also raises some doubt about the validity of this trend. If this trend is not a real phenomenon, its origin remains unknown to us. The wind data used to calculate the CUI are restricted to the estimated wind data and the origin of the trend cannot be explained by an increasing fraction of anemometer type data in the wind time series used to calculate the CUI.

CONCLUSION

The COADS database represents a very important source of information for studying the long term variability of the climate over the oceans. In many areas like in the tropics, the COADS data are the only information available regarding the variability of the environment. For fishery oceanography, it represents a very valuable tool. However this dataset is not exempt of important limitations. Time series of surface meteorological parameters constructed using the COADS data can be strongly affected by several biases and lead to erroneous interpretation.

For the wind variables, the main difficulty results from the difference between estimated wind data using the Beaufort scale and measured wind data using an anemometer. It is shown that the calculation of wind speed using the COADS dataset can be strongly biased depending on the kind of data used. Wind speeds calculated using estimated wind data will tend to be underestimated. The calculation of the mean monthly cycle of the wind speed in several areas shows that difference between estimated and measured values can be as high as 0.8 m/s but the phase of the signal does not seem to be strongly affected.

The consequence of the difference between estimated and measured wind data is that time series of wind speed can be severely biased by the progressive shift from estimated wind data to measured wind data. When both measured and estimated wind data are merged, the resulting time series is affected by an artificial positive trend. In some areas, the slope of the trend in the wind speed time series calculated using both measured and estimated wind data can be 60% to 80% higher than the slope of the trend calculated on a wind speed time series using estimated data only. Recently, Ward and Hoskins (1996) made a comparison between the reported winds in COADS (from the COADS 2°x2° monthly summaries files) and a wind derived from seasonal mean sea level pressure gradients over the world oceans. Their results show a considerable disagreement between the long term trend in the reported wind and the trend in the pressure derived wind. Globally averaged over the world oceans, there is no trend of any substance in the pressure derived wind, whereas there is an upward trend in the reported wind data of about 14% from 1949 to 1988. They conclude that the difference between the reported wind and the pressure derived wind was mainly due to the growing percentage, over time, of measured wind data in the COADS records.

For the calculation of a reliable wind time series over a long time period, it is strongly recommend to use either estimated or measured wind data and to avoid the use of time series where both wind data type are merged. This represents a strong limitation for the use of the COADS 2°x2° monthly summaries files to study long term climatic variability. In those summary files, both estimated and measured wind data are used to calculated a mean monthly wind speed.

The introduction of the buoy data along the California coast during the 1980s is another example of the bias introduced by merging data from different origins in COADS. Along the US California coast, the wind time series given by the COADS 2°x2° monthly summaries files are strongly affected by the dominance of the buoys data in the data records after 1980, resulting in an artificial relaxation of the wind. Obviously, the use of these summary files can lead to a completely erroneous interpretation of the long term variability of the wind in the region.

The positive trend in the COADS wind time series off West Africa between 12°N and 22°N is a striking feature. Using estimated wind data, the magnitude of the trend results in an increase of about 50% of the wind stress over the last 40 years. This positive trend cannot be explained by an increasing fraction of anemometer type data in the wind time series as the anemometer wind data were not included in the calculation. The comparison with an independent wind time series and the dramatic increase of the correlation between CUI and SST when the trend is removed raises some doubt as to the validity of this trend. However, one should notice that a positive trend exists in the pressure derived wind in the region (see Fig. 6 in Ward and Hoskins, 1996). The trend of the North Atlantic Oscillation (NAO), which is an indicator of the strength of the atmospheric circulation in the Atlantic Ocean related to the Acores high (Hurrell 1995, 1996), is also in accordance with the long term trend that exists in the COADS wind data in the 14°N-16°N area (Fig. 11), but with a less pronounced upward trend during the last 30 years. Given these contradictory results, the validity of the trend in the COADS wind over West Africa remains an open question.

From our experience with the use of the COADS database to study long term climatic variability over the oceans, we conclude that extreme care should be taken in the interpretation of the results. It is strongly recommended to get access to the individual records rather than using the COADS 2°x2° monthly summaries files. The five CD-Roms produced by CEOS provide an easy to use alternative to these summary files.

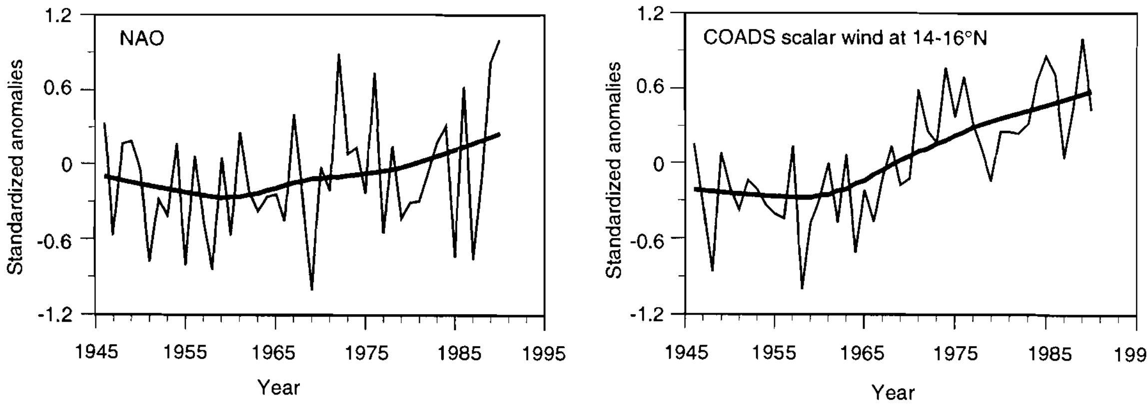

Fig. 11: Time series of the standardized anomalies of the North Atlantic Oscillation (NAO) and of the scalar wind speed during the upwelling season in an area off West Africa (14°N-16°N) from 1946 to 1990.

REFERENCES CITED

Arfi R. 1985. Variabilité interannuelle d'un indice d'intensité des remontées d'eau dans le secteur du cap Blanc (Mauritanie). *Can. J. Fish. Aquat. Sci.*, 42 (12): 1969-1978.

Bakun A. 1973. Daily and weekly upwelling indices, west coast of North America 1946-71. *U.S. Dep. Comm., NOAA Tech. Rep. NMFS SSRF*-671, 103p.

Bakun A., V. Christensen, C. Curtis, P. Cury, M.H. Durand, D. Husby, R. Mendelssohn, J. Mendo, R. Parrish, D. Pauly and C. Roy. 1993. *The Climate and Eastern Ocean Systems Project.* Naga, The ICLARM Querterly 15(4): 26-30.

Cardone V.J. 1969. *Specification of the wind distribution in the marine boundary layer for wave forecasting.* Report TR69-1, New York University, New York, NY, 131p.

Cardone V. J., J.G. Greenwood and M. A. Cane. 1990. On trends in historical marine wind data. *J. Climate*, 3: 113-117.

Folland C.K., D.E. Parker and F.E. Kates. 1984. Worldwide marine temperature fluctuations, 1856-1981. *Nature*, 310: 670-673.

Folland C.K. and J. Hsiung. 1987. Correction of seasonally varying biases in uninsulated bucket sea surface temperature data using a physical model. *Met. Office Synoptic Climatology Branch Memo.*, 154.

Folland C.K. and D.E. Parker. 1990. Observed variations of sea surface temperature. *In*: M.E. Schlesinger (ed.). Climate-ocean interaction, NATO workshop, Oxford, Kluwer Academic Publishers: 21-52.

Hurrell J. W. 1995. Decadal trends in the North Atlantic oscillation: regional temperatures and precipitation. *Science*, 269: 676-679.

Hurrell J. W. 1996. Influence of variations in extratropical wintertime teleconnections on northern hemisphere temperatures. *Geophys. Res. Lett.*, 23: 665-668.

Isemer H.J. 1995. Trends in the marine surface wind speed: ocean weather stations versus volontary observing ships. *In*: H.F. Diaz and H.J. Isemer (eds.). *Proceedings of the International COADS Winds Workshop*, Kiel Germany, 31 May-2 June 1994. US dept. of Commerce-Institut fur Meereskunde, Kiel: 68-84.

Isemer H.J. and L. Hasse. 1987. *The bunker atlas of the North Atlantic Ocean.* 2: Air-sea interactions. Springer-Verlag, 252p.

Isemer H. J. and L. Hasse. 1991. The scientific Beaufort equivalent scale: effect on wind statistics and climatological air-sea flux estimates in the North Atlantic Ocean. *J. Climate*, 4: 819-836.

Jones P.D., T.M.L. Wigley and P.B. Wright. 1986. Global temperature variations, 1861-1984. *Nature*, 322: 430-434.

Jones P.D. and T.M.L. Wigley. 1992. Corrections to pre-1941 SST measurements for studies of long-term changes in SSTs. *In* : H.F. Diaz, K. Wolter and S.D. Woodruff (eds.). *Proceedings of the International COADS Workshop*, Boulder, Colorado, 13-15 January 1992. US Department of Commerce, NOAA. 227-237.

Kaufeld L. 1981. The development of a new Beaufort equivalent scale. *Meteor. Rundsch.*, 34: 17-23.

Kent E.C., P.K. Taylor, B.S. Truscott and J.S. Hopkins. 1983a. The accuracy of voluntary observing ship's meteorological observations - Results of the VSOP-NA. *J. Atmos. & Oceanic Tech.*, 10: 591-608.

Kent E.C., R.J. Tiddy and P.K. Taylor. 1983b. Correction of marine daytime air temperature observations for radiation effects. *J. Atmos. & Oceanic Tech.*, 10: 900-906.

Nykjaer L. and L.V. Van Camp. 1994. Seasonal and interannual variability of coastal upwelling along northwest Africa and Portugal from 1981 to 1991. *J. Geophys. Res.*, 99 (C7): 14197-14207.

Portolano P. 1986. Analyse des séries vent-températures de la mer en surface le long des côtes sénégalaises. *Océanogr. trop.*, 21 (2): 205-227.

Ramage C. S. 1984. Can shipboard measurements reveal secular changes in tropical air-sea heat flux ? *J. Climate Appl. Meteor.*, 23: 187-193.

Ramage C.S. 1987. Secular change in reported wind speeds over the ocean. *J. Clim. Appl. Met.*, 26: 525-528.

Roy C. 1989. Fluctuations des vents et variabilité de l'upwelling devant les côtes du Sénégal. *Oceanologica Acta*, 12 (4): 361-369.

Slutz R.J., S.J. Lubker, J. D. Hiscox, S.D. Woodruff, R. L. Jenne, D.H. Joseph, P.M. Steurer and J.D. Elms. 1985. *Comprehensive Ocean-atmosphere Data Set*; Release 1. NOAA Environmental Research Laboratories, Climate Research Prograam, Boulder, CO, 268p.

Ward M.N. and B.J. Hoskins. 1996. Near surface wind over the global ocean 1949-1988. *J. of Climate*, 9: 1877-1895.

Woodruff S.D. and S.J. Lubker. 1986. COADS 1980-85 update. *In*: S.D. Woodruff (ed.). *Proceedings of a COADS Workshop*, Boulder, Colorado, January 22-24, 1986. US Department of Commerce, NOAA. Technical Memorandum, ERL ESG-223: 36-48.

Woodruff S.D., R.J. Slutz, R.L. Jenne and P.M. Steurer. 1987. A Comprehensive Ocean-atmosphere Data Set. *Bull. Amer. Meteor. Soc.*, 68: 1239-1250.

World Meteorological Organization (WMO). 1970. *Reports on marine science affairs.* 3: The Beaufort scale of wind force. WMO Geneva, Switzerland, 22p.

How to Detect a Change both on Global and Local Scale in Oceanographic Time Series

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ABSTRACT

Analyzing change in climatic time series requires a more complete understanding of the different way that time series can vary over time, and the different kinds of 'trends' and 'pseudo-trends' that can occur. Time series can vary in the mean in either a deterministic or stochastic manner, they can vary in the seasonal component in either a deterministic or stochastic manner, and the underlying 'innovations variance' can also vary with time. Each of these types of changes in a series can produce similar kinds of behavior over a short period of observation, but are driven by very differing processes. Multiple time series, particularly those that are spatially distributed, may exhibit these types of behavior in a seemingly unrelated manner, yet can be shown to be driven by common underlying components. These types of dynamics will be very different from those that would be estimated by EOF's or other techniques based on principal component analysis. We discuss recent advances in time series analysis and econometrics that allow us to more fully explore how time series may vary and to test for and to estimate the underlying components of change.

RÉSUMÉ

Pour analyser les changements dans une série climatique, il ne suffit pas de « repérer » les différentes sortes de « tendances » ou « pseudo-tendances » qui peuvent apparaître. Sous peine de profondes erreurs de compréhension, il est nécessaire de pouvoir caractériser correctement les différents processus d'évolution dans le temps. Une série temporelle peut évoluer de façon déterministe ou stochastique dans sa composante moyenne et/ou dans sa composante saisonnière. Les processus résiduels peuvent également avoir une variance qui évolue dans le temps. Ces différents processus d'évolution ont des propriétés très différentes et la caractérisation que l'on peut faire des changements temporels en dépend grandement. Malheureusement, sur de courtes périodes de temps, ces différents processus apparaissent très semblables. Il est donc primordial de pouvoir distinguer correctement les différentes composantes d'une série temporelle pour en caractériser les propriétés. Lorsqu'on examine conjointement un groupe de séries temporelles, par exemple des séries de température distribuées sur différentes latitudes adjacentes, il est possible de mettre en évidence des processus d'évolution sous-jacents qui leur sont communs. Ce type de dynamique est très différent de celui qui pourrait être estimé par des modèles EOF ou autres méthodes basées sur l'analyse en composante principale. Des avancées récentes en analyse des séries temporelles et en économétrie permettant d'explorer le type d'évolution d'une série temporelle, de tester et d'estimer les composantes sous-jacentes de ces changements temporels sont présentées.

INTRODUCTION

The earth's climate has been changing over the centuries, and coupled with these changes have been change in the ocean environment and in marine resources. Over the last several decades, concern has risen that anthropogenic effects, particularly in the atmosphere, may be altering or accelerating the natural pattern of climate change. However, the observed anthropogenic changes in the atmosphere are not necessarily producing concomitant changes in the ocean, or may be producing changes that are more complex than those observed in the atmosphere. Even without human influence, this natural progression of climate could have profound effects on the ocean and its resources. Understanding how the ocean has been changing, how the resources in the ocean have been changing, and detecting anthropogenic effects in either, are difficult problems that require careful thinking about what we mean by change, about the ways change can occur in the data we analyze, and whether even a global process of change could produce varying effects in different regions of the world. The types of dynamics we are presently witnessing in the ocean and the atmosphere raise questions that typically can not be answered by the usual methods of analysis. The term 'climate change' has been used loosely in the oceanographic literature, referring to almost any variation in the ocean environment. What is meant by 'climate change' must be more precisely defined if we want to characterize it properly.

Changes in the ocean environment can be transitory or relatively permanent. Even such large shocks as major El Niños can be transitory in nature when analyzed properly over a longer time-scale. Roy and Mendelssohn (this vol.) have shown that the major El Niños of 1972 and 1982 in the Humbolt Current, though large, were short-lived in their effects while the 1956-57 El Niño had long-lasting effects on the California Current system. ENSO events may be part and parcel of the long-term trend in the ocean, or they may be relatively frequent shocks to the ocean that in fact obscure the long-term signal. The upwelling regions of the world are of particular interest because of their high productivity. The upwelling process, which is local in scale, may be influenced by changes more global in scope. Bakun (1990), for example, has hypothesized that global warming would increase upwelling, making the upwelling regions cooler during the upwelling months, and perhaps affecting the oxygen content and other properties of the local ocean waters important to fish stocks. These changes, however, would not be reflected in the ocean as a whole. A change observed in the ocean environment at a particular area can be unique to that area, or part of a process observed over an entire region, or part of a process occurring over the entire globe. Moreover, there could be regional or global processes that are causing the observed change in the local environment, but with a different manifestation depending on the site it is occurring. It is then necessary to analyze variability at different spatial scales. Separating out common trends or common seasonal components from local trends and season is important to handle this type of question. Changes in the upwelling process can occur not only in the intensity of the upwelling, but also in the timing of crucial events such as the seasonal cycle, the onset of the spring transition in the California Current system for example. Identifying the proper source of these changes needs to be able to separate what pertains to a trend and what pertains to some cycle around this trend.

To properly deal with these types of problems requires precise definitions of the types of changes that might be observed and careful thinking about how change can be manifested in the data we analyze. Similar problems arose in economics where highlighting common features among variables, isolating source and timing of changes among any of numerous and always moving explicative factors, separating out a proper trend from some cycle and distinguishing a shifting trend from other cyclical fluctuations are crucial questions. Great advances have been made in econometrics and time series analysis to handle such a challenge. These new statistical techniques, which at least begin to deal with some of these issues, must be used also to analyze changes in oceanographic data, or else the results could be misleading. The aim of this paper is to describe some of these concepts and techniques; examples of their use are also presented.

1. WHAT IS CHANGE?

From the previous section, it is clear that change, particularly in the context of climate change, can be very complex in nature. Yet, when the term 'change' is mentioned, it is firstly as opposed to some sort of relatively stable state and change is therefore associated with some sort of non-stationary state. Climate change is often used in contexts such as 'global warming', meaning that the weather worldwide is progressively becoming warmer. In other words, the worldwide mean temperature has a positive time trend in the long-term. In this sense, 'change' and 'trend' in a series are almost synonymous. This is a limited view of what constitutes a 'change', particularly in regards to the climatic changes in the ocean. Only some of the examples presented in the Introduction correspond to this notion of change. Models that focus on the long-term change in the mean will not lend insight to the other problems discussed.

Even restricting ourselves to 'trends' in the data, the problem of defining the trend is more complex than finding the change in the overall mean. If a large region is being examined, this assumes that the entire region is changing in a homogeneous, uniform manner. In the ocean, due to the complex interactions between circulation processes and atmospheric forcing, the observed changes in different areas could be in different directions even if the underlying process is global in scope. Aggregate methods, or even disaggregate methods that assume a uniform trend will be misleading in identifying the change. Shifting trends are also changes that are very difficult to put to the fore if the trends are not correctly measured. 'Trend' can occur in the mean, the usual way people think of trend, but 'trend' can also occur in the seasonal component, and in the variance of the series. Properly identifying a trend will help to better characterize a change. More formally, a time series random variable is said to be stationary if its distribution does not depend on time. A time series is said to be weakly stationary if the mean and variance of the series do not depend on time. A time series is non-stationary, or has a 'trend', if either the mean or the variance of the time series (or both) are functions of time. Changes in the mean and the variance of a series can come about in several ways, for example, changes can be either deterministic or stochastic. Changes at intermediate frequencies can occur due to changes in the seasonal component. For non-stationary series, a series that has a trend in the mean has different properties than a series that has a trend in the variance. While over the short run the dynamics can appear similar, this difference has important consequences both for model building and for our understanding of the behavior of the process.

1.1. Deterministic and stochastic trends

The common understanding of trend is a changing mean level that varies deterministically. Let y_t be an observed time series, then a deterministic trend in the series y_t would be given for example by:

$$y_t = \mu + \alpha t + \varepsilon_t \qquad \text{where } \varepsilon_t \rightarrow \mathrm{N}(0, \sigma^2) \tag{1}$$

The mean or expected value of this series is $E(y_t) = \mu + \alpha t$. This mean evolves with time while the variance is constant, $Var(y_t) = \sigma^2$. Such a series is said to have a deterministic trend or to be "trend stationary" since a simple regression on time will detrend or stationarize the series, the resulting detrended series will have a constant mean μ. The mean level of a deterministic trended series increases by some fixed amount every period (Fig.1c).

However, a time series can behave in the short-run as if it has a deterministic trend in the mean, yet be generated by a different mechanism. The simplest case of such a series is the so-called "random walk" which is of the form:

$$y_t = y_{t-1} + \varepsilon_t \tag{2}$$

where the ε_t are independent, identically distributed random variables with mean of zero and variance σ^2 (Fig.1b). The series y_t can be rewritten as:

$$y_t = y_0 + \sum_{t=0}^{\infty} \varepsilon_t \tag{3}$$

Such a series has a constant mean, $E(y_t) = y_0$, and a variance which increases towards infinity over time: $Var(y_t) = \sigma^2 t$

If the ε_t are zero mean stationary but autocorrelated, the series y_t is no longer a pure random walk but the trend of the y_t series will still behave as a random walk. These types of trends are called stochastic trends. In the econometric literature, they are also referred to as 'unit root', since the random walk model is equivalent to an autoregressive model with a root of modulus one in the autoregressive polynomial (i.e. roots of $\varphi(B) = 0$ in a series such as: $\varphi(B)y_t = \phi(B)\varepsilon_t$), see Hatanaka (1996) for details. In the above example (Eq. 2), it can be noticed that the coefficient in lag term is equal to 1. Differencing the series will remove the stochastic trend, leaving the series stationary. Processes that become stationary when differenced are called 'integrated' or 'difference stationary'. Let the backshift operator B be defined as:

$$By_t = y_{t-1} \tag{4}$$

Then differencing a series can be expressed as $\Delta y_t = (1 - B)y_t$. Sometimes a series needs to be differenced d times to become stationary. It will be then necessary to calculate $\Delta^d y_t = (1 - B)^d y_t$. These series are said to be 'integrated of order d', denoted by I(d). A random walk process is a very simple case. Generally, observed series exhibit more complex behavior than that of a pure random walk. A random walk with drift process can be given by:

$$y_t = \mu + y_{t-1} + \varepsilon_t \tag{5}$$

where ε_t is given as in Equation 2. Rewriting y_t as:

$$y_t = y_0 + \mu t + \sum_{t=0}^{\infty} \varepsilon_t \tag{6}$$

we see that this series has both a deterministic trend (i.e. a trend in mean given by $E(y_t) = y_0 + \mu t$) and a stochastic trend (i.e. a trend in variance given by $Var(y_t) = \sigma^2 t$). Since differencing will cancel out both trends, $E(y_t - y_{t-1}) = \mu$ and $Var(y_t - y_{t-1}) = \sigma^2$, such a series with both a deterministic and a stochastic trend is also an integrated series (Fig.1d). A random walk with drift will change in each period by some fixed amount *on average*. The change in each period will be by a predictable amount μ, which is called the drift, plus an unpredictable random amount. For this reason it is referred to as a 'stochastic trend'.

The different behaviors produced by these types of time series can be understood by examining artificial time series generated from closely related equations (Fig. 1a,b,c,d). The SST series at 36-38°N was whitened and the resulting residuals were used as the innovations (errors) in each of the simulations. The first series (Fig.1a) is a stationary autoregressive series with one lag and an autoregressive parameter equal to 0.5. The series has a constant mean and a constant variance. When the autoregressive parameter is set to 1, a unit root is introduced in the series. The random walk nature of the series is evident (Fig.1b). Adding a deterministic trend to the stationary series (Fig.1c) and adding an intercept to the random walk series, which becomes a random walk with drift (Fig.1d), highlights the problem of differentiating between deterministic and stochastic trend. The behavior of the two last series is very similar yet generated by two very different processes. Most people would say that the random walk with drift has a deterministic trend and would wrongly detrend this series by a regression on time.

In the case of a Trend Stationary series, it is only the mean of the series which will bring information on the long-term evolution of the process. The variance of forecast errors is finite, the uncertainty attached to these forecast is then bounded. It is indeed not the case for a Difference Stationary series since the variance of a series with a unit root is infinite. The best forecast of the future value of an integrated series we can make is its present value since the prediction error is going to infinity with time. The important difference between these two classes of non-stationarity lies on the fact that a 'shock' at any given period on a trend stationary process will only have a transitory effect while it will have a lasting effect on a difference stationary process. Integrated series are 'long memory' processes since any short-lived event will influence definitively the future level of such series.

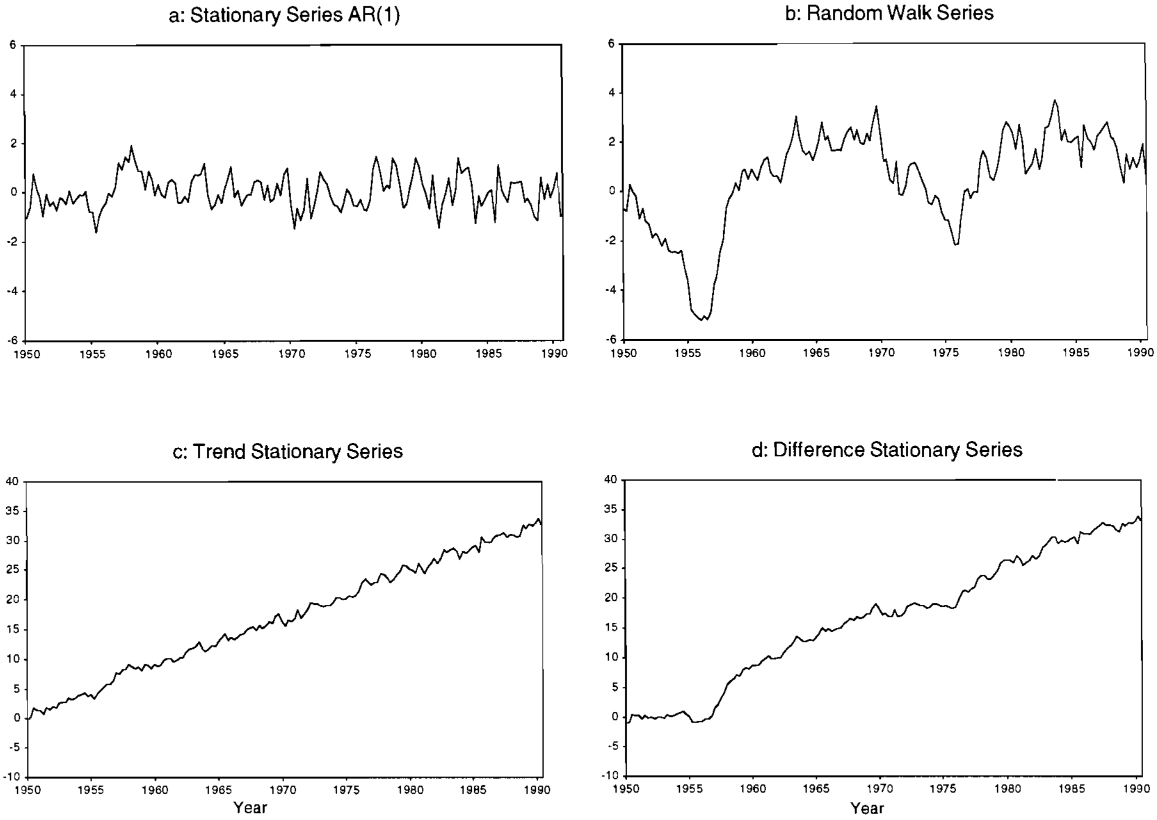

Fig. 1: Four artificial series generated from the same white noise ε_t (t is the time term trend).
a : Stationary : $X_t = 0.5X_{t-1} + \varepsilon_t$
b : Random walk : $X_t = X_{t-1} + \varepsilon_t$
c : Trend Stationary : $X_t = 0.1T + 0.5X_{t-1} + \varepsilon_t$
d : Difference Stationary : $X_t = 0.2 + X_{t-1} + \varepsilon_t$

1.2. Stationary and non-stationary seasonal component

Oceanographic data, particularly series such as SST, are characterized by their strong seasonality. In the oceanographic literature, seasonal components are usually estimated by taking monthly means or by fitting one or several harmonics to the data. Another method, more recently advocated, to deseasonalize monthly oceanographic time series is to transform the series to 12th-differences (Bakun, 1996, p. 165). Each of these two deseasonalizing methods suppose very different seasonal processes. The first one assumes that the seasonal component is deterministic and stationary, while the second one assumes a stochastic and non stationary seasonal component. To use a method in an inappropriate case will lead to spurious results. Prior to any deseasonalization or to any study of the seasonal pattern, it is then important to be able to decide which seasonal process is suitable for the observed time series. Some testing procedures have been recently developed for that purpose.

The concept of seasonality is, unless we have a precise and formal definition, as vague as that of a trend. Yet finding a precise definition for seasonality is not as simple as it appears. Despite a long history in analyzing seasonality, there is no generally agreed upon definition, nor is there a widely accepted view about how seasonality should be treated in empirical work. The main definitions offered by the literature (see for example Hylleberg *et al.*, 1990; Franses, 1996) are:

- A *deterministic seasonal process* : This seasonal process is stationary with a mean that varies by season. It is modeled by a regression on seasonal dummy variables such as the following quarterly series : $Y_t = m_0 + m_1 S_{1t} + m_2 S_{2t} + m_3 S_{3t} + \varepsilon_t$ where ε_t is stationary. Seasonal dummy models imply a regular and non-changing seasonal pattern which can be perfectly forecast though some changes in phase and amplitude may appear in raw series due to the error process and to the existence of an autoregressive structure.
- A *stationary stochastic seasonal process* is a process generated by an equation such as : $\varphi\ (B)\ y_t = \varepsilon_t$ where ε_t are independent and identically distributed with all the roots of $\varphi\ (B) = 0$ lying outside the unit circle and with peaks in its spectrum at seasonal frequencies, as for example: $Y_t = \mathrm{p}Y_{t-s} + \varepsilon_t$ with $|\mathrm{p}|<1$. The mean of such series does not differ across seasons; however, if the initial values are seasonally different and the degree of serial correlation is high, such series may become very similar to the previous one. In such cases, a practical way to remove seasonality in stationary seasonal time series is to regress the series on seasonal dummy variables.
- A *non-stationary stochastic (or integrated) seasonal process* is generated by an autoregressive process like $\varphi(B)y_t = \varepsilon_t$ with one or several unit roots at some seasonal frequencies and ε_t stationary. As for example: $Y_t = -Y_{t-2} + \varepsilon_t$ for a quarterly time series seasonally integrated at one cycle per year. Such process describes changing seasonal patterns where sometimes 'spring' becomes 'summer'. The means in each season are not well-defined, they are an accumulation of all the past random shocks. These shocks which last forever may change permanently the seasonal pattern.
- A *periodic process* is generated by an autoregressive process such as:

  $$y_t = \mu_s + \sum_{i=1}^{p} \varphi_{is} y_{t-i} + \varepsilon_t$$

  where μ_s and φ_{is} are parameters that may vary across the seasons and ε_t are independent and identically distributed. These processes with periodically varying parameters describe a time series which has different properties in different seasons. A periodic process is non-stationary since the autocovariance function is not constant over time. Unit roots can also be present in a periodic process which nests the integrated seasonal model mentioned above.

This classification into deterministic and non-stationary stochastic seasonality parallels the trend classification already presented. The seasonal counterpart to treat with deterministic or integrated process will be to regress the series on seasonal dummy variables if the seasonality is assumed to be deterministic and/or stationary; and to difference the series with the appropriate $(1 - B^s)$ operator, where **s** is the number of seasons, if the seasonality is assumed to be integrated. The dynamics of the seasonal component, however, is more complex than that of a trend component. If we assume we have quarterly data (s=4), and examine the appropriate differencing operator, it can be factored into a product of backshift operators at smaller time lags as:

$$(1-B^4)y_t = (1-B)(1+B+B^2+B^3)y_t = (1-B)(1+B)(1-iB)(1+iB)y_t = (1-B)S(B)y_t \qquad (7)$$

The term $(1 - B)$ removes the longer-run trend while $S(B) = (1 + B + B^2 + B^3)$ removes the seasonal structure. This operator has four roots with modulus one, (1, -1, i, -i), which correspond respectively to zero frequency ("long-run" or non seasonal), 1/2 cycle per quarter or 2 cycles per year (Π) and 1/4 cycle or 3/4 cycle per quarter or one cycle per year ($\Pi/2$) for the pair of conjugate complex roots which cannot be distinguished. When monthly data are involved, the factored backshift operator ($1 - B^{12}$) contains many more roots than does Equation 7.

When modelling seasonality in empirical work, the key question is therefore to firstly establish if the data exhibit more evidence of seasonal dummies or seasonal unit roots. However, the choice of the proper model is not so direct and requires further care. The seasonal differencing operator removes unit roots at all frequencies although unit roots may exist only at some of the seasonal frequencies. In this case, the Δ_S differencing filter induces an over-differencing which further introduces unit roots in the moving average part of the series. In observed non-stationary time series deterministic and stochastic components are often both present. The seasonal pattern can be a combination of stationary deterministic part (seasonal dummies) and of non-stationary stochastic part (seasonal unit roots). All these configurations have to be taken in account when testing for seasonal roots, leading to many possible combinations of tests.

Deterministic, periodic and stochastic seasonal processes generate very different seasonal behaviors but, as with the trend component, over a relatively short time period, they can look very similar when examined visually (Fig. 2).

- The Fig. 2a series is a deterministic seasonal time series governed by four (in this case of quarterly data) alternating linear trends with identical slopes. The 'average' seasonal pattern remains constant. This series has been generated from a white noise and a very slight trend in the mean has been also added. The fluctuations that can be noted in this series are due to the perturbations of the error process.
- The Fig. 2b series is a periodic series where the trends vary with the season producing a changing seasonal pattern.
- The Fig. 2c series is an integrated seasonal series which yields four circularly merged random walks with identical drift, implying persistent and unpredictable changes in the seasonal pattern.
- The Fig. 2d series is the observed SST time series off the Canary Current at 30-32°N reduced to quarterly data. Comparing this last SST series to the three previous seasonal models highlights the difficulties that exists in attributing the observed changes to any type of seasonal process and to disentangle seasonal changes from trend changes when these changes are slow.

Although they can appear similar on small sample, deterministic, periodic and integrated seasonal processes have fundamentally different statistical properties which have to be taken in account when detecting and interpreting seasonal changes. A deterministic seasonal process is a stationary process. Some shifts or fluctuations due to exogenous shocks can appear but these changes will not persist in the seasonal pattern. When a seasonal time series is proven to be seasonally deterministic, each observed change in the seasonal component can be attributed to an exogenous cause that can therefore be investigated. The changing seasonal patterns in periodic processes are more difficult to interpret. The observed changes in the seasonal pattern of a periodic series are endogenous but may also be caused by some external sources. An integrated seasonal process allows a very changing seasonal pattern. The existence of a unit root in the seasonal component, as in the non-seasonal component, implies that a short-lived shock will perturbate definitively the pattern of season and the best prediction we can make of its future shape is always its present one.

For mathematical convenience, most analytical methods assume that the seasonal component is deterministic and unchanging, except for relatively small independent errors around the mean seasonal cycle. Our experience with the ocean is otherwise. Timing of events, such as the spring transition, in upwelling periods, shift over decades in a non-random manner. The intensity of upwelling may increase or decrease over quite a few years, without a corresponding change during the non-upwelling period. This 'trend' which is only during spring (or winter, or summer, etc.) is actually a change in the seasonal component. It seems then that the seasonal pattern in oceanographic variables is not constant over time and also that seasonal and non-seasonal variations are not independent.

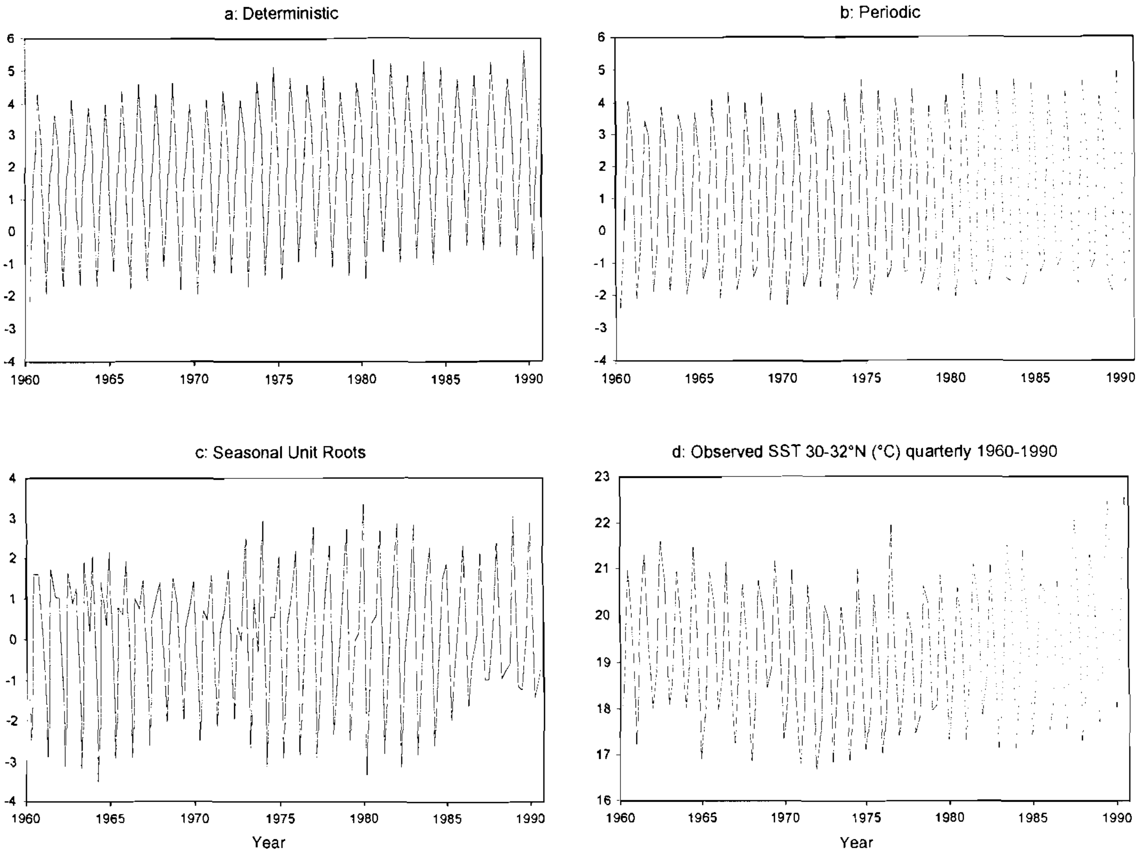

Fig. 2 : Deterministic, periodic and integrated seasonal time series generated from the same white noise ε_t and the observed SST series off the Canary Current at 30-32°N (T is the time term trend).

a : Deterministic : $X_t = 2D_1 - 3D_2 - D_3 + 3D_4 + 0.001T + \varepsilon_t$

b :Periodic : $X_t = 2D_1 - 3D_2 - D_3 + 3D_4 + ((0.01 + 0.001T)D_1 + (0.05 + 0.005T)D_2 - (0.1 + 0.006T)D_3 + (0.04 + 0.007T)D_4)Y_{t-1} + \varepsilon_t$

c : Integrated : $X_t = -X_{t-1} - X_{t-2} - X_{t-3} + \varepsilon_t$

1.3. Change in the variance of a series

A random walk (see Section 1.1) is a time series whose variance is a function of time, in that case a simple linear function of time. There are other cases where the underlying variance evolves with time in a non-linear fashion. For example, the variance can be a step function of time, it changes at a given time period and remains at its new level over a period of time. It is important when analyzing changes in a time series, and particularly when studying climatic changes, to be able to model the evolution process of the variability of the series. These type of non-linear time series processes with changing variance in the residuals are referred to as autoregressive conditional heteroscedastic process (ARCH) in the econometric literature (see Engle, 1982 and Bollerslev, 1986 for the first models), and as red noise in physics (see Steele, 1984 and Bakun, 1996, for reference in oceanography). ARCH or red noise process means that the conditional variance of a series is a function of time. It seems that these non-linear dynamics are frequent in the oceans where waters masses inertia produce endogeneous cycles. In fish catch time series it is often noted that the variability increases with the mean. This is also a conditional heteroscedasticity phenomenon which has to be represented with the appropriate models. More generally when a time series does not follow normal laws, the usual ARMA linear models are not suitable and it is necessary when forecasting or simulating such a series to refer to a class of non-linear time series models. A red noise process can be expressed as:

$$\begin{array}{ll} Y_t = \varepsilon_{t-1}^2 \varepsilon_t & \text{Where } \varepsilon_t \rightarrow N(0,\sigma^2) \\ E(Y_t) = 0 & E(Y_t / \underline{Y_{t-1}}) = 0 \\ V(Y_t) = 3\sigma^6 & V(Y_t / \underline{Y_{t-1}}) = \sigma^2 \varepsilon_{t-1}^4 \end{array} \qquad (8)$$

$\underline{Y_{t-1}}$ define the set of all the past values of Y_t. This process is stationary since the marginal mean and variance are constant and so do not depend upon time but the conditional variance is function of the history of the series.

Along with conditional heteroscedasticity, a time series can also contain deterministic trends or unit roots at some frequencies. All these features can be combined in more complex classes of ARCH models. Bollerslev and Ghysels (1996) have recently proposed a seasonal ARCH model with a periodic structure. A simple example of ARCH(1) process may be given by :

$$\begin{array}{ll} Y_t = (\alpha_0 + \alpha_1 Y_{t-1}^2)^{1/2} \varepsilon_t & \text{Where } \varepsilon_t \rightarrow N(0,1) \\ E(Y_t) = 0 & E(Y_t / \underline{Y_{t-1}}) = 0 \\ V(Y_t) = \alpha_0 / (1 - \alpha_1) & V(Y_t / \underline{Y_{t-1}}) = \alpha_0 + \alpha_1 Y_{t-1}^2 \end{array} \qquad (9)$$

Two examples of such ARCH(1) time series are shown in Figure 3. These are SST times series off the Canary Current at 28-30 and 30-32°N (Fig. 3a and Fig. 3d). They have been decomposed into trend, seasonal and residual components by the STL algorithm (Cleveland *et al.*, 1990). It can be noticed, both on the original series and on the residual series, that once the trend and the seasonality have been removed, the variability of the series is much greater before 1962 and after 1979 for the first 28-30°N SST series and greater before 1962 for the 30-32°N SST series.

These changes, which do not pertain to the trend nor to the seasonal component, have to be taken into account. Interpreting an observed change in a time series requires to be able to disentangle correctly the different components of the series if we want to attribute correctly which part comes from a change in the global mean (trend), in the seasonal cycle or from the behavior of the variance.

2. DETECTING AND MODELING CHANGES

Oceanographical data are generally considered as stationary or having a deterministic trend although it is a question whether freak events such as El Niños do not have lasting effect on the dynamics of the ocean. It is then important to be

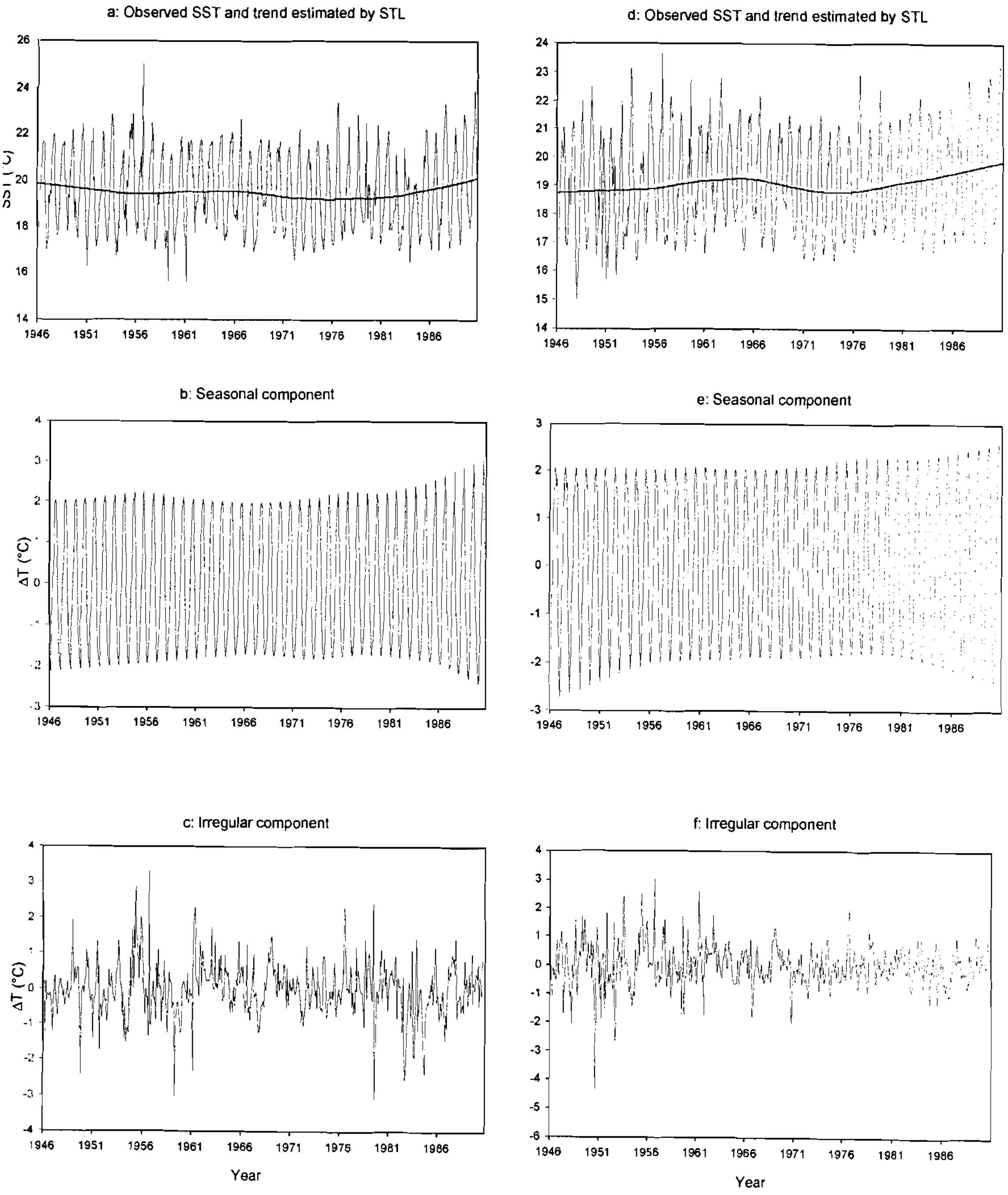

Fig. 3: Decomposition trough STL of two SST observed series off Canary Current at 28-30 (left panels) and 30-32°N (right panels).

able to identify what sort of non-stationarity, deterministic or stochastic, is operating in a series. There is no single method that will correctly model all of these possibilities for non-stationary behavior in a time series. However, several methods have been developed over the last decade that begin to deal with some of these issues, and thereby extend our ability to analyze the past behavior of oceanographic and biological time series. In the next sections, we discuss two possible approaches. Random walk, unit root, integrated series are all terms referring to stochastic trends. An integrated series is a series which has a unit root at some frequency in its autoregressive part. Analyzing the non-stationarity of a series will be then testing for unit root at any of its seasonal or non-seasonal frequencies. An other approach, allowing to avoid a delicate testing procedure, is to decompose a series in its unobservable components using a structural class of models developed by Harvey (1989). These models which treat seasonality as an unobserved component and separate non-seasonal from seasonal factors, are particularly adapted for series with a slowly changing seasonal pattern.

2.1. Testing for unit roots

Searching for unit roots at the zero frequency consists of testing the null hypothesis H_0: $\rho=1$ in a regression equation such as:

$$Y_t = \rho Y_{t-1} + \varepsilon_t \qquad (10)$$

where ε_t are independent and distributed as $N(0,\sigma^2)$. In order to whiten the residuals, autoregressive terms have to be added. The usual test regression is:

$$\Delta Y_t = \alpha + \beta t + \varphi Y_{t-1} + \sum_{i=1}^{q} a_i \Delta Y_{t-i} + \varepsilon_t \qquad (11)$$

The null hypothesis is now $\boldsymbol{H_0}$: $\varphi = 0$, since with the transformation to first difference, $\varphi = 1\text{-}\rho$. If the series has additional deterministic components, such as a deterministic trend for example, they have to be added to the regression test $(\alpha + \beta t)$, along with the autoregressive structure $\sum_{i=1}^{q} a_i \Delta Y_{t-i}$

When $\varphi=0$, the problem examined is no more in a stationary framework. The ordinary least square (OLS) estimates of φ are not distributed as the usual regression test statistics. Instead, the appropriate t-statistics of φ are functions of Brownian motions. The asymptotic distributions of the test statistics will then depend on the different parameters included (constant, linear or quadratic trends). Because the statistical tests change depending on the model, testing for unit root must be done with care. Whatever may be the regression test, the null hypothesis is always the same. A procedure that sequentially tests reduced models is then highly recommended. These tests do not discriminate well between trend stationary and difference stationary series. This is still an open question and new tests are under discussion (see Cochrane, 1988, 1991; Hwang and Schmidt, 1996; Kwiatkowiski *et al.*, 1992; Leybourne and McCabe, 1994; Perron, 1989; Schmidt and Phillips, 1992). Critical values for the test statistics can be found in Fuller (1976) and Dickey and Fuller (1981) or in the above-cited literature for modified tests. Results of these tests may vary with the number of lags included in the model. To avoid this problem, Phillips and Perron (1988) has proposed a non-parametric test where the ε_t may be autocorrelated. Unit root tests have been revised by Kim and Schmidt (1993) in the case of conditional heteroscedastic errors.

Searching for unit roots at seasonal frequencies is a little more complicated and will depend on the periodicity of the series, either quarterly or monthly. As noted earlier a quarterly seasonal integrated process may have four unit roots (1, -1, i, -i) at the frequencies 0, 1/4, 1/2, 3/4. (see Section 1.2). A monthly seasonal integrated process may have 12 unit roots. The testing procedure for unit roots in the seasonal component at their different frequencies has been established for quarterly data by Hylleberg *et al.* (1990) and for monthly data by Beaulieu and Miron (1993). These authors have proven that the autoregressive polynomial of a quarterly seasonal series $\varphi(B)y_t = \varepsilon_t$ can be decomposed as:

$$\varphi(B) = -\pi_1 B(1+B+B^2+B^3) - \pi_2(-B)(1-B+B^2-B^3) - (\pi_4 + \pi_3 B)(-B)(1-B^2) + \varphi^*(B)(1-B^4)$$

Then the deseasonalized y_t series can be decomposed as:

$$\varphi^*(B)y_{4t} = \pi_1 y_{1t-1} + \pi_2 y_{2t-1} + \pi_3 y_{3t-2} + \pi_4 y_{3t-1} + \varepsilon_t \qquad (12)$$

Where:

$y_{1t} = (1 + B + B^2 + B^3)y_t = S(B)\, y_t$ removes the seasonal unit roots at the frequency 1/4, 1/2, 3/4, while keeping the unit root at the zero frequency
$y_{2t} = (1 - B + B^2 + B^3)y_t$ removes the seasonal frequencies 0, 1/4, 3/4, while maintaining the unit root at the semi-annual frequency.
$y_{3t} = (1 - B^2)y_t$ removes the seasonal unit roots at the frequency 0, 1/2, while maintaining the annual frequency.
$y_{4t} = (1 - B^4)y_t$ is the deseasonalized series.

Under the null hypothesis of stochastic seasonality, all the π_i are zero. Testing that the autoregressive polynomial has a root of 1 is equivalent to testing $\pi_1 = 0$, testing that it has a unit root at the semi-annual frequency, root -1, is equivalent to testing $\pi_2 = 0$ and a joint test $\pi_3 = \pi_4 = 0$ will test for a unit root at the annual frequency. Intercept, trend and seasonal dummies have to be added to the regression equation (12), giving the model deterministic as well as stochastic components. This allows the possibility to discriminate between deterministic and stochastic trend model. Autoregressive terms must be added if the errors are not accepted as being a white noise process. As we are no more in a stationary framework, the test statistics do not follow anymore the usual laws. For different configurations of the test regression, critical values are provided by Hylleberg *et al.* (1990) for quarterly data and by Miron and Beaulieu (1993) for monthly data (see Frances and Hobijn (1994) for a detailed revue of critical values). Testing for seasonal unit root is more delicate than testing for the long-term unit root. Discussions of this test procedure and alternative are proposed by Canova and Hansen (1995), Franses (1996), Ghysels *et al.* (1994), Harvey and Scott (1994), Hylleberg (1995), Barthelemy and Lubrano (1996), Osborn *et al.* (1988). Franses (1994) has proposed a test for periodic integration which nests the usual seasonal unit root tests.

2.2. Decomposition of a time series

A simple starting point for modeling an observed time series Y_t such that the series can exhibit some of the more complex behavior of the previous section is to assume that the observed series is additively composed of independent components:

$$y_t = T_t + S_t + I_t + e_t \qquad t=1,T \qquad (13)$$

where T_t is the unobserved time-dependent mean-level (trend) at time t, S_t is the seasonal component at time t, I_t is the irregular term (stationary but autocorrelated) at time t, and e_t is the stationary, uncorrelated component at time t, which here can be viewed as 'observation' or 'measurement' error.

The model (Eq. 13) states mathematically the assumed form of the observed time series, but leaves open the question of the form of each component and how to estimate the component series from the observed data. The components could be modeled parametrically - the trend by a polynomial of a given order, the seasonal by harmonics, for example, but this approach is very limited in handling series with the types of dynamics discussed above. Ideally the components would be defined as flexibly as possible while allowing the model to be estimated. One way to achieve this is to put a constraint on the 'smoothness' (in this case through time) of the component. In the case of continuous functions of time, this implies constraining the derivatives of the function to be estimated. When time is discrete, the equivalent would be to put a smoothness constraint on the differences of the components, or other relevant linear combinations through time.

The use of such piecewise continuous 'smoothing splines' to estimate unobserved components dates back to Thiele (1880), see Lauritzen (1981), and in the more modern era to a paper by Whittaker (1923). Shiller (1973) modeled the distributed lag (impulse response) relationship between the input and output of a time series under difference equation 'smoothness' constraints on the distributed lags. He termed these constraints 'smoothness priors', but did not offer an objective method of choosing the smoothing parameter. Akaike (1979) developed a Bayesian interpretation of the model and used maximum likelihood to estimate the smoothness parameter. Brotherton and Gersch (1981) showed how the Kalman filter and maximum likelihood could be used to solve the smoothing problem. Kitagawa and Gersch (1984, 1985, 1988), in a series of papers, extended the Kalman filter-maximum likelihood approach to a variety of nonstationary problems, and Harvey (1989) developed similar models under the title « structural time series models ».

2.3. Smoothness priors and the trend component

How a smoothness constraint can allow for both a flexible and for a well-defined model can be most clearly understood in terms of estimating a 'smooth' but unknown function which has been observed with 'noise', that is data of the form:

$$y_t = f_t + e_t \qquad (14)$$

where the y_t are the observed data, f_t is an unknown smooth function and e_t are independent gaussian errors. In this model there is no seasonal component and no autoregressive component. Whittaker (1923) suggested that the solution should balance fidelity to the data with fidelity to constraint on the smoothness of the unknown function f_t:

$$\left[\sum_{t=1}^{T} (y_t - f_t)^2 + \mu^2 \sum_{t=1}^{T} (\nabla^k f_t)^2 \right] \qquad (15)$$

Equation 15 is equivalent to solving the least-squares problem subject to a constraint on the differences of the unknown function, using Lagrangean multipliers. The first term in Equation 15 is the usual sum-of-squares criterion, while the second term constrains the k-th order finite differences of the unknown function (the discrete equivalent of splines where the k-th order derivatives are constrained). The two parts are balanced by the 'smoothness parameter' μ. As μ goes to zero, the smoothness constraint disappears, and the estimate of the unknown function exactly interpolates the data. As μ approaches infinity, the sum-of-squares term becomes negligible, and the solution is the appropriate k-th order polynomial of time (e.g., linear for k=1, quadratic for k=2, etc.)

Equation 15 leaves unanswered the crucial question of how to estimate the smoothness parameter μ. Akaike (1979) gave the problem a Bayesian interpretation. He viewed the constraint as a stochastic, zero mean difference equation, that is:

$$\nabla^k f_t \to N(0,\sigma^2) \tag{16}$$

where the notation $N(0,\sigma^2)$ denotes a normal random variate with mean zero and variance σ^2, and where $\mu^2 = 1/\sigma^2$ (which can be interpreted as a signal-to-noise-ratio), is a hyperparameter that can be estimated using maximum likelihood methods. (See the reference above for a demonstration that for a fixed value of μ, the Bayesian model is equivalent to Equation 15). Akaike termed this a 'smoothness prior', because the smoothness constraint is given a prior distribution and is then estimated by likelihood methods.

The 'local trend' fit by the smoothness priors approach can be shown to be a linear smoother — for a given value of the smoothness parameter the estimate of the unknown function at any time period is linear in the data — that is it can be calculated as a weighted linear combination of the observed time series. This estimate differs from a running mean, for example, which is also a linear smoother, in that the window used to smooth the data can vary as can the weights (see Hastie and Tibshirani, 1990). Though the smoothing spline fit by this model is more complex than a running mean, the basic idea is the same: estimate the unobserved component by a linear smoother. We will return to this idea in order to model the seasonal component.

The 'smoothness prior' formulation clarifies the connection between the methods of this section and those of the next section. When k=1, Equation 16 reduces to:

$$y_t - y_{t-1} \to N(0,\sigma^2) \tag{17}$$

which is the same as Equation 2 if ε_t is assumed to be a normal random variable. The two methods are different approaches to dealing with the same problem.

2.4. Smoothness priors and the seasonal component

In Section 2.3, the trend was modeled by placing a prior distribution on low-order differences of the data, which constrains the smoothness of the trend component. This smoothness constraint yields a solution that is a linear smoother of the time series. If we have a time series that is known to have only a seasonal component plus noise, a similar idea can be used by constraining the seasonal differences of the time series (c.f. Eq. 7) as:

$$S_t - S_{t-s} \to N(0,\sigma^2{}_s) \qquad t=1,T \tag{18}$$

where s is the relevant number of periods in a year. If the series were monthly data, Equation 18 would be the same as individually fitting a trend to each monthly difference series, except now there is the added constraint that the amount of smoothing allowed must be the same for each month. Thus the calculated 'trend' for each monthly difference series is suboptimal if considered apart from the rest of the data. As with the trend term, the value of $\sigma^2{}_s$ determines if the differences have no trend, leading to a deterministic seasonal cycle, or a stochastic trend.

Constraining the seasonal differences is not the only way to define a sensible seasonal component. Assuming a series with no trend and a strictly deterministic seasonal component of periods (say, for example, a cosine curve with a period of 12 months), then the seasonal component has the property of having a zero mean if we average over the s-periods, and zero difference if we calculate the difference y_t-y_{t-s} (for example taking 12th differences for monthly data). The equivalent constraint would be to want the s-period running sum to have a mean of zero, but to allow it to vary, that is a constraint of the form:

$$\sum_{i=0}^{s-1} S(t-i) \rightarrow N(0,\sigma^2{}_s) \qquad t=1,T \qquad (19)$$

If $\sigma^2{}_s$ is zero, then the result is a deterministic seasonal cycle, in fact the mean for that season, while if $\sigma^2{}_s$ goes to infinity, then the seasonal component interpolates the data. In between, the estimate of the seasonal component is a smoothing spline, a linear smoother of the observed seasonal time series.

The smoothness constraint of Equation 18 explicitly smoothes the s-differenced time series and thereby implicitly smooths the s-period running sum. Similarly, the smoothness prior of Equation 18 explicitly smoothes the s period sums and thereby implicitly smoothes the time trends.

2.5. Combining trend and seasonal components

The previous examples have considered series that are composed of either a trend component plus noise or a seasonal component plus noise. Most oceanographic and biological time series are likely to have both components present, so the problem arises of simultaneously estimating the trend and the seasonal component. (The discussion that follows is not the algorithm actually used, which is given in Appendix A and which estimates all components simultaneously. However, the backfitting type algorithm described here could be used, and makes the ideas clearer). Start with initial estimates of the trend and seasonal components, say the mean of the series and the monthly means of the demeaned series. Then define the partial residuals as:

$$\begin{aligned} y_{1,t} &= y_t - \hat{S}_t \\ y_{2,t} &= y_t - \hat{T}_t \end{aligned} \qquad (20)$$

where S_t, T_t are respectively the present estimates of the seasonal component and of the trend. Each partial residual series is simply the observed series less the present estimate of the other component. Then iteratively, to get a new estimate for the trend, we calculate $y_{1,t}$ and use the approach of Section 2.3 to estimate the trend term for the partial residual series. The estimated trend in the partial residual series is then used as the new estimate of the trend component T. This new value of T is then used to calculate the partial residual $y_{2,t}$ and the methods of Section 2.4 are used to estimate the seasonal component for this partial residual series. The estimated seasonal component is then used as the new estimate of S and the process is iterated until convergence.

The algorithm can be viewed as iteratively fitting smoothing splines to the partial residuals of the series until convergence is achieved. In the examples (Section 4) we examine the original series and the partial residual series with the components to help understand output of the algorithm. This type of algorithm is not limited to using smoothing splines as the smoother. Cleveland *et al.* (1990) use a similar procedure and the LOWESS smoother in the STL algorithm for time series decomposition. If an autoregressive component (i.e., I_t) is also included in the model, then three partial residuals could be defined, and at each iteration a maximum likelihood estimate of the autoregression parameters would be estimated.

The actual algorithm used (Appendix A) sets up the entire model in state-space form and uses a combination of the Kalman filter and the EM algorithm (Dempster *et al.*, 1977) to calculate the maximum likelihood estimates of the parameters. Given the final estimates of the parameters, the Kalman smoother gives the minimum mean-square error estimates of the different components.

3. MULTIVARIATE ANALYSIS: COINTEGRATION

3.1. Cointegration

The existence of unit roots in a time series is not only important in understanding which type of trends is affecting the behavior of the series and its pattern of seasonality, but also has interesting consequences when several time series are modeled jointly (Granger, 1986, 1988a,, 1988b). For a general survey see Hatanaka (1996), Lütkepohl (1991) and Dolado *et al.* (1990).

All linear combinations of zero order integrated series will also be integrated of zero order. Likewise a linear combination of a group of I(d) series will generally be an I(d) series also. But sometimes it is possible to find a particular linear combination of non-stationary series which produces a new series which is integrated of lower order and which can be stationary. This particular linear combination of the series removes some or all the trends from some or all the series. These series are said to have 'common trends' or to be cointegrated. Ignoring cointegration in a group of series can lead to misspecified models. Since co-movements among time series indicate the existence of common components, this implies a more parsimonious and informative structure in a joint model (Engle and Yoo, 1987; Johansen, 1988).

The term 'integrated series' refers explicitly to unit roots or stochastic trends in a series and 'cointegration' to the existence of common trends in a group of integrated series. These ideas have been extended to a more general framework that tests for the presence of some 'feature' in a time series and whether this feature is common to a group of series. 'Features' are data properties such as serial correlation, trends, seasonality, heterocedasticity, autoregressive conditional heteroscedasticity and excess kurtosis. The idea is the same, if a linear combination of featured variables does not possess the feature any more, the featured variables will be said to have a 'common feature' (Engle and Kozicki, 1993; Vahid and Engle, 1993; Escribano and Pena, 1994).

For notational and presentational convenience, we will only present the case of order-1 integrated series. Let Y_t denote a n-vector of I(1) variables whose first difference is autoregressive.

$$\Phi(B)\Delta Y_t = \Theta(B)\varepsilon_t \qquad (21)$$

where Δ=(1-B) and ε_t is white noise. The stationary process ΔY_t has a moving average representation and can be rewritten as:

$$\Delta Y_t = \Phi^{-1}(B)\Theta(B)\varepsilon_t = H(B)\varepsilon_t \qquad (22)$$

H(B) is a polynomial matrix in B, and may be decomposed as $H(B) = H(1) + (1 - B) H^*(B)$ (see Engle and Granger, 1987). Integrating (taking the integrand of) both sides of equation 22 to solve for ΔY_t yields :

$$Y_t = H(1)\frac{\varepsilon_t}{(1-B)} + H^*(B)\varepsilon_t = H(1)\sum_{s=0}^{\infty}\varepsilon_{t-s} + H^*(B)\varepsilon_t \qquad (23)$$

which shows that an I(1) process is a sum of a random walk and a stationary process. Similarly, an I(d) process can be decomposed as a sum of d-1 random walks of order d, d-1, d-2, ...1, plus a stationary process.

If we can find a n-vector α_i such that $\alpha'_i H(1) = 0$, meaning that the matrix H(1) is not of full rank. Pre-multiplying Y_t by α'_i will cancel-out the random walk part of Yt and $\alpha'_i Y_t = \alpha'_i H^*(B)\varepsilon_t$ will be stationary. In that case, the multivariate process Y_t is said integrated order 1, cointegrated order 1, denoted C(1,1), and α_i is a cointegration vector stationarizing the process. There can exist r (r<n), linearly independent cointegration vectors, meaning that r different subsets of the variables in the

multivariate process Y_t are linked in stationary fashion. The collection of all linearly independent cointegration vectors form the (n,r) matrix α where $\alpha' Y_t$ is I(0). The existence of cointegration vectors implies that the rank of H(1) is n-r, so that testing for cointegration is equivalent to testing the rank of the matrix of H(1). This test is known as 'Johansen's test' (see for details Johansen and Juselius, 1990; Johansen, 1991; Phillips and Ouliaris, 1990 and Stock and Watson, 1988, for similar approach). Procedure and critical value are available in most of the econometric packages like E-Views, PC-Give or RATS.

Engle and Granger (1987) have presented several equivalent representations of cointegrated series. The most interesting one is the 'error-correction representation':

$$A(B)\Delta Y_t = -\gamma z_{t-1} + d(B)\varepsilon_t \qquad (24)$$

where $z_{t-1} = \alpha' Y_{t-1}$ and d(B) is a scalar polynomial in B. The series z_t is a random stationary process that measures the deviations or errors around the so called 'equilibrium relationship' defined by $\alpha' Y_{t-1}$ which is assumed to be null when realised. Stationarity in a linear combination of variables can be intuitively associated with the static notion of a long-term equilibrium relationship between these variables. This error-correction representation shows clearly a system directed by a 'long-term relationship' around with short-term variations adjust for the deviations at the equilibrium which have occurred at the previous period. Non-stationary series when cointegrated can never diverge far from each other over time. They are linked by a steady-state relationship that keeps them close in the long-term.

The presence of both deterministic and stochastic trends in a time series changes the distributional properties of the cointegration test as well as the form of the error-correction model. The appropriate modified procedures must be used in this instance.

The model considered here is linear and with time-invariant parameters. It can be generalized by allowing for time-varying parameters (see for example Granger,1986). The concept of cointegrated system has also been extended to the cases of seasonally integrated series by Hylleberg *et al.* (1990).

3.2. Seasonal cointegration

Seasonal cointegration occurs when a group of time series with changing seasonal pattern exhibit a 'parallel movement' in their seasonal component.

Assume that Y_t is an n-vector of zero mean quarterly variables which are all I(1) at the frequencies Θ=0, 1/4, 1/2, 3/4. The autoregressive-moving average representation of Y_t is:

$$(1 - B^4)Y_t = C(B)\varepsilon_t \qquad (25)$$

where the ε_t are independant random n-vectors identically distributed as NID(0,Ω) and C(B) is an (n,n) matrix of lag polynomials. As in the previous univariate case (Section 1.4), the polynomial matrix C(B) can be expanded as:

$$C(B) = \Psi_1\left[1 + B + B^2 + B^3\right] + \Psi_2\left[1 - B + B^2 - B^3\right] + (\Psi_3 + \Psi_4 B)\left[1 - B^2\right] + C^*(B)(1 - B^4) \quad (26)$$

where $\Psi_1 = \frac{C(1)}{4}, \Psi_2 = \frac{C(-1)}{4}, \Psi_3 = \frac{\mathrm{Re}\left[C(i)\right]}{2}, \Psi_4 = \frac{\mathrm{Im}\left[C(i)\right]}{2}$.

To examine a group of series for seasonal cointegration requires analyzing the properties of the model:

$$(1-B^4)\alpha' Y_t = \alpha' C(B)\varepsilon_t \qquad (27)$$

Seasonal cointegration exists when :

- The existence of an (n,r_1) matrix α_1, with $r_1<n$, such that $\alpha'_1 \Psi_1 = \alpha'_1 C(1) = 0$ implies cointegration at the zero frequency.
- The existence of an (n,r_2) matrix α_2, with $r_2<n$, such that $\alpha'_2 \Psi_2 = \alpha'_2 C(-1) = 0$ implies cointegration at the 1/2 frequency.
- The existence of an (n,r_3) matrix α, $r_3<n$, such that $\alpha'(\Psi_3 + \Psi_4 B) = \alpha' C(i) = 0$. Implies cointegration at the 1/4 and 3/4 frequencies without being distinguishable.

The columns in α_1 and α_2 form the cointegrating vectors at the zero and 1/2 frequencies. Columns in α will be called "polynomial cointegrating vectors" since they are of the form $\alpha(B) = \alpha_3 + \alpha_4 B$.

There is an error correction representation for seasonal cointegration which varies with the number and frequencies of unit roots which are canceled out by the cointegrating vectors α's (see example in Hylleberg *et al.*, 1990).

Testing for seasonal cointegration is still in an early age of development. The critical values for seasonal cointegration based on unit root test are already available for quarterly data (Engle *et al.*, 1993) but not for monthly data. Furthermore, the only procedure presently available for estimating the cointegration vectors and error correction representation is the two-step procedure similar to that of Engle and Granger (1987) and developed by Engle *et al.* (1993). Unfortunately this procedure works only in the bivariate case. A new method has been recently developed by Franses (1994) in order to test for seasonal unit roots. This method consists of a multivariate decomposition of a univariate time series into its different seasonal components allowing to use the Johansen's test procedure. This approach could be fruitfully extended in order to test for seasonal cointegration but will necessitate huge sample sizes.

Deseasonalizing time series by using a seasonal difference operator, which a priori assumes a changing seasonal pattern, has been increasingly preferred to diseasonalizing the series by a regression on seasonal dummy variables which assumes a deterministic seasonality. However, if the time series are seasonaly integrated and cointegrated at some frequencies, then both methods would lead to incorrect results. The appropriate method would be to use seasonally unadjusted data and jointly model the series.

4. APPLICATIONS

4.1. Interpretation of cointegration in oceanography

Cointegration models have a meaningful economic interpretation explaining why such an approach is burgeoning in economics. Economic theory postulates that economic variables will eventually reach an 'equilibrium relationship'. These 'target equilibrium' are generally not observed but there is strong belief that these variables should not diverge from equilibrium by too great an extent. Most of the time an economy is in disequilibrium, but market mechanisms and other economic forces bring about a dynamic adjustment of the variables towards their equilibrium.

Considered in a spatial context, theses new techniques in time series analysis could be usefully applied to oceanographic data. Identifying and estimating trends in oceanographic time series which are common to an entire region (global change) and separating these from stationary cyclical swings or non-stationary components which are unique to a local area (local dynamics) is an important problem in the studies of climatic change in oceanography. For example, if we can show that SST series at different adjacent latitudes are both integrated (i.e., non-stationary) either in their seasonal component or in the mean, as well as cointegrated either in their trend or seasonal component, then the estimated common trends can be viewed as 'global changes' since they affect all the SST series in the same manner over the region. The remaining variations of each individual SST series around these common trends can be viewed as 'local changes'. Identifying over a large region which group of SST series enter or do not enter in cointegration relationships, can also allow to better determine and characterize transition zones in the ocean's dynamic.

Since seasonality is driven by broad processes in the ocean, and if seasonal integration explain the varying and changing structure of seasonal pattern in oceanographical data, then seasonal cointegration should not be uncommon.

4.2. Decomposition of time series: examples

To illustrate the consequencies of misusing the different detrending and deseasonalizing methods previously exposed, they have been applied to the SST time series off the Canary Current at 22-24°N. Results obtained can be compared on Figure 4. This series have been tested for unit roots at long-term and seasonal frequencies. When deterministic term are included in the regression equation, the series appears to be deterministic although the results seem ambiguous for the zero frequency. To accept the hypothesis of a deterministic series (absence of unit roots at all frequencies) implies that the 12-difference operator must not be used to deseasonalize the series. A deterministic trend and season have been therefore estimated (Fig. 4d and 4e). Trend, although small, is significantly negative. Most of variations remain in the errors process. The error process is non-stationary which testify for a wrong decomposition of the series (Fig. 4f).

Decomposing the series through the STL algorithm, the behavior of the trend appears quite different, decreasing from 19.92°C in 1946 to 19.26°C in 1972 and increasing regularly again after this date (Fig. 4a). Without having seasonal unit roots, the seasonal pattern appear quite changing. This series has time varying parameters in the season (Fig. 4b). The irregular term is stationary yet proved to be conditionally heteroscedastic after being tested. This time series is non linear with time varying parameters and it could be modeled by a periodic conditionnally heteroscedastic model.

Changes in the series, both in the trend (inter-year changes) and in the season (intra-year changes) can be easily seen and interpreted with the results issued of the STL decomposition of the series. Although this series can be accepted as deterministic, it is in fact non linear and to estimate a deterministic trend and season will lead to spurious results and to the incapacity to really detect changes.

Two other examples will help to clarify some of these ideas. We calculate the decomposition for SST and the north-south component of the wind stress at 36-38°N, an area off the California coast between Monterey and San Francisco. SST in this region displays relatively little variation as compared to the mean level. If the overall series mean is removed from the SST series, then the residuals over the entire time period are less than three degrees in absolute value, compared to a mean level of roughly 14 degrees. So the trend likely to dominate any other component SST in this region is also highly seasonal and strongly autocorrelated. The seasonal component may vary to a degree, but winters are colder than summers etc. so that the basic pattern will be fairly deterministic. Wind stress, in contrast, is highly variable, with the variability around the overall mean

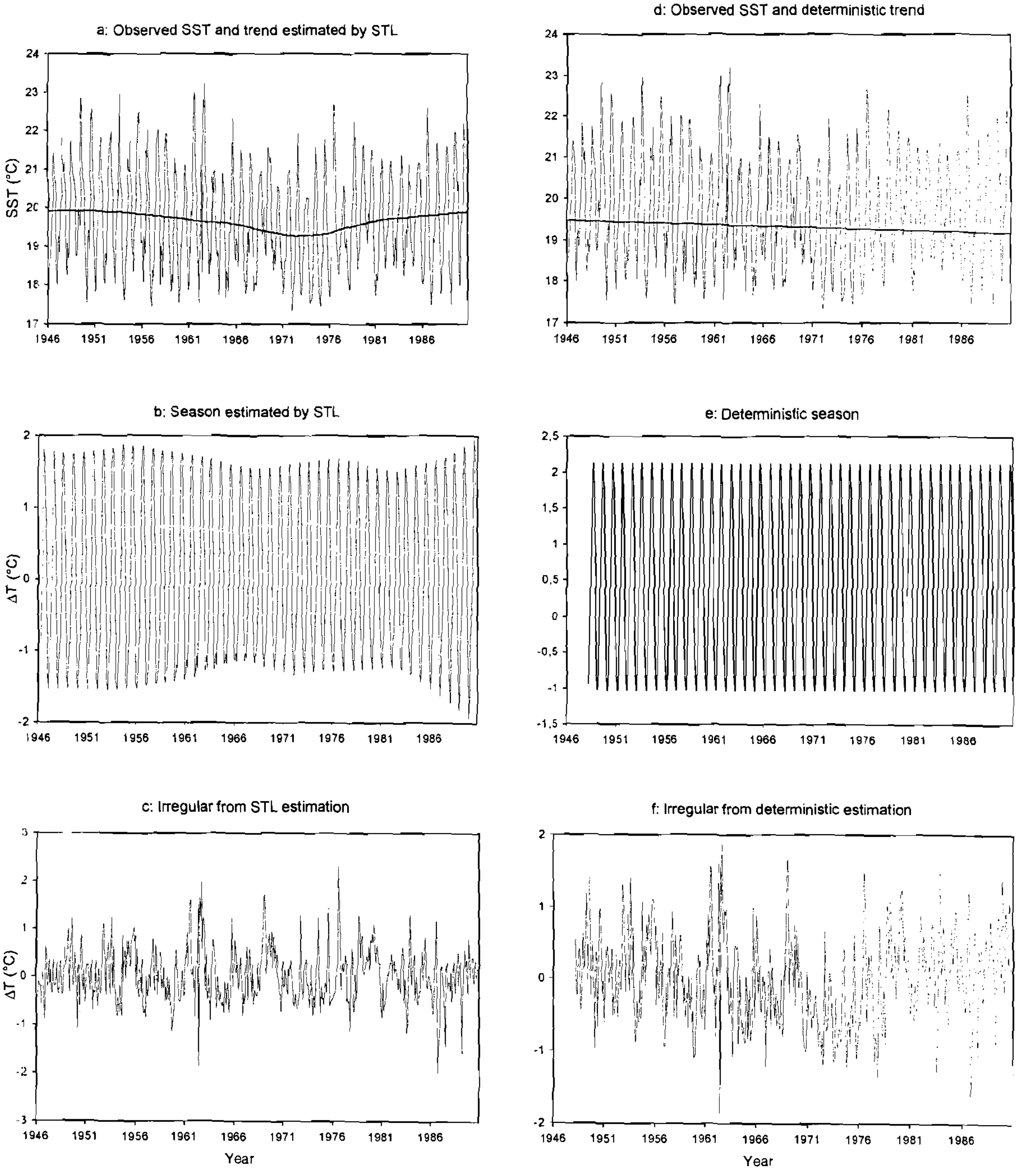

Fig. 4: SST time series off the Canary Current at 22-24°N. Decomposition in trend, season and irregular components through the STL algorithm (a,b,c), estimation of a deterministic trend (d), a deterministic seasonal (e), and irregular (f).

larger than the mean itself. Wind stress is not highly seasonal and with a low degree of autocorrelation, particularly when compared to SST. A reasonable procedure should at minimum reproduce these features of the ocean in this region.

The raw SST series and the estimated components (Fig. 5a-e) have the desired characteristics. The seasonal component is nearly deterministic and only varies by 3 degrees. The autoregressive term is nearly as large as the seasonal component, while the noise component is very small, less than 0.25 degree Celsius in absolute value.

When the estimated trend is plotted against the raw series (Fig. 6a), some of the features of the trend term are apparent in the raw time series, but others are more obscure. When the estimated seasonal component is removed (Fig. 6b), the estimated trend is clear in the partial residual series, and it is evident that the trend component is a smoother of the partial residual. When both the seasonal and the AR components are removed (Fig. 6c), the estimated trend differs from the partial residual series only by the relatively small noise series.

The estimated SST seasonal component (Fig. 7a) is a mean zero series (as desired, so that the trend component has at least one desired property), and when compared to the detrended series differs from it by roughly the AR component. The SST component can be seen to smooth the resulting partial residual series. The basic features of the series are deterministic, but the component series does vary, such as in the timing of the occurrence of the spring transition and other secondary maximum and minimum. Variations in the timing of such events can have significant implications for fish stocks, and would not be as easily identified if a purely deterministic model were used. Note that if the AR and trend components are removed, then the seasonal component differs from the partial residual series only by the amount of the noise series.

When both the estimated SST trend and seasonal components are removed, the resulting series is highly autocorrelated (Fig. 8a) and very close to the estimated AR component. The interplay of the three components and how each smoothes the appropriate partial residual series can be seen clearly in this example.

If we look at a similar sequence of graphs for north-south pseudo-stress in this region (Fig. 9, 10, 11), the seasonal component is closer to the trend in absolute value, while the AR component is very small and the uncorrelated noise series is as large in value as any of the other components. The trend is not as obvious from the data and the seasonal component is more variable.

These examples demonstrate the consistency of the procedure, how the different components interact in forming the estimates of the other components. Also, this example illustrates that the decomposition can estimate components that are consistent with what was known a priori, and which have very different dynamics.

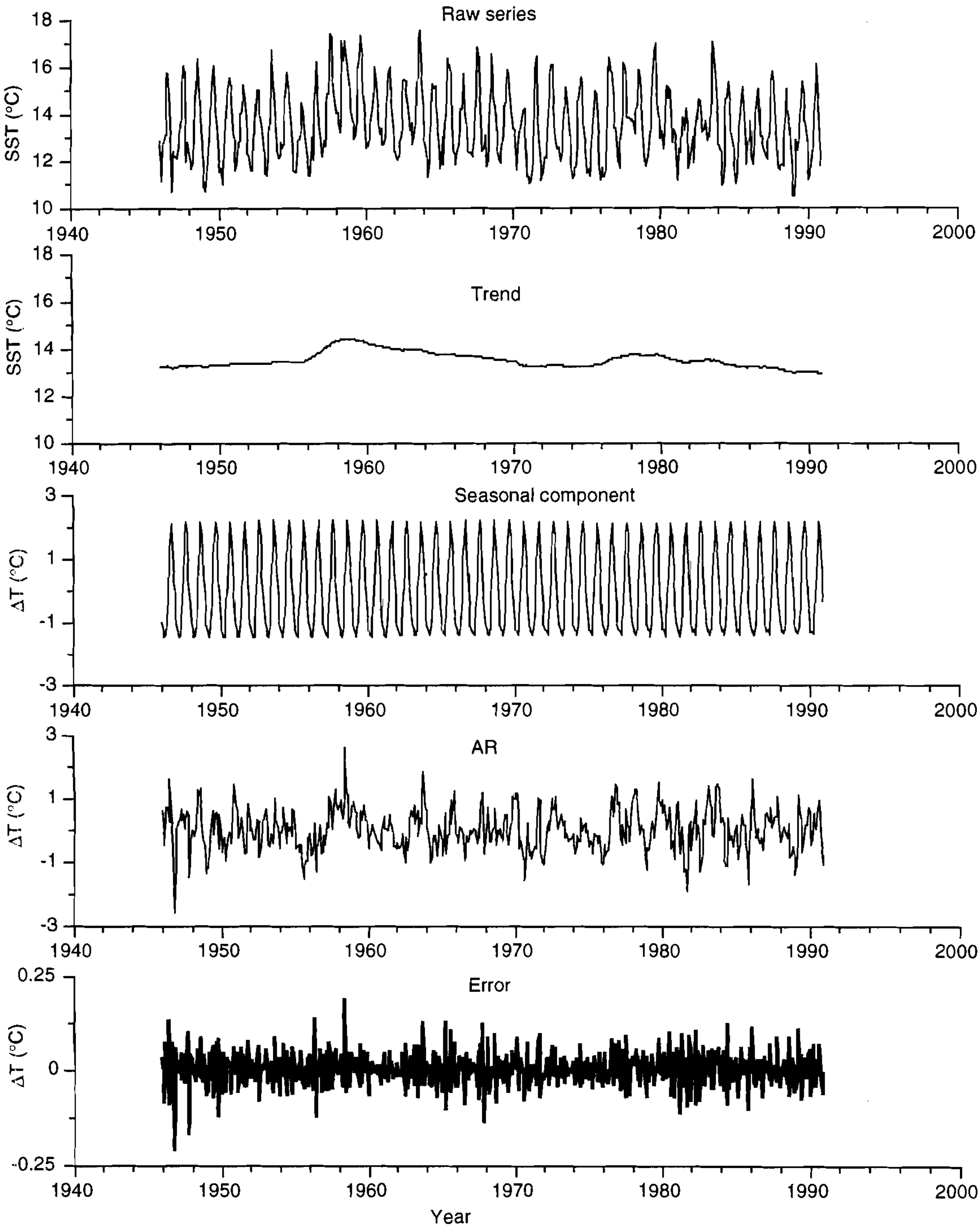

Fig. 5: Time series of SST (°C) off the California coast (36-38°N) and its decomposition into a non-parametric trend (°C); a non stationary seasonal component (ΔT; °C); and an autoregressive component (ΔT; °C); and an error term.

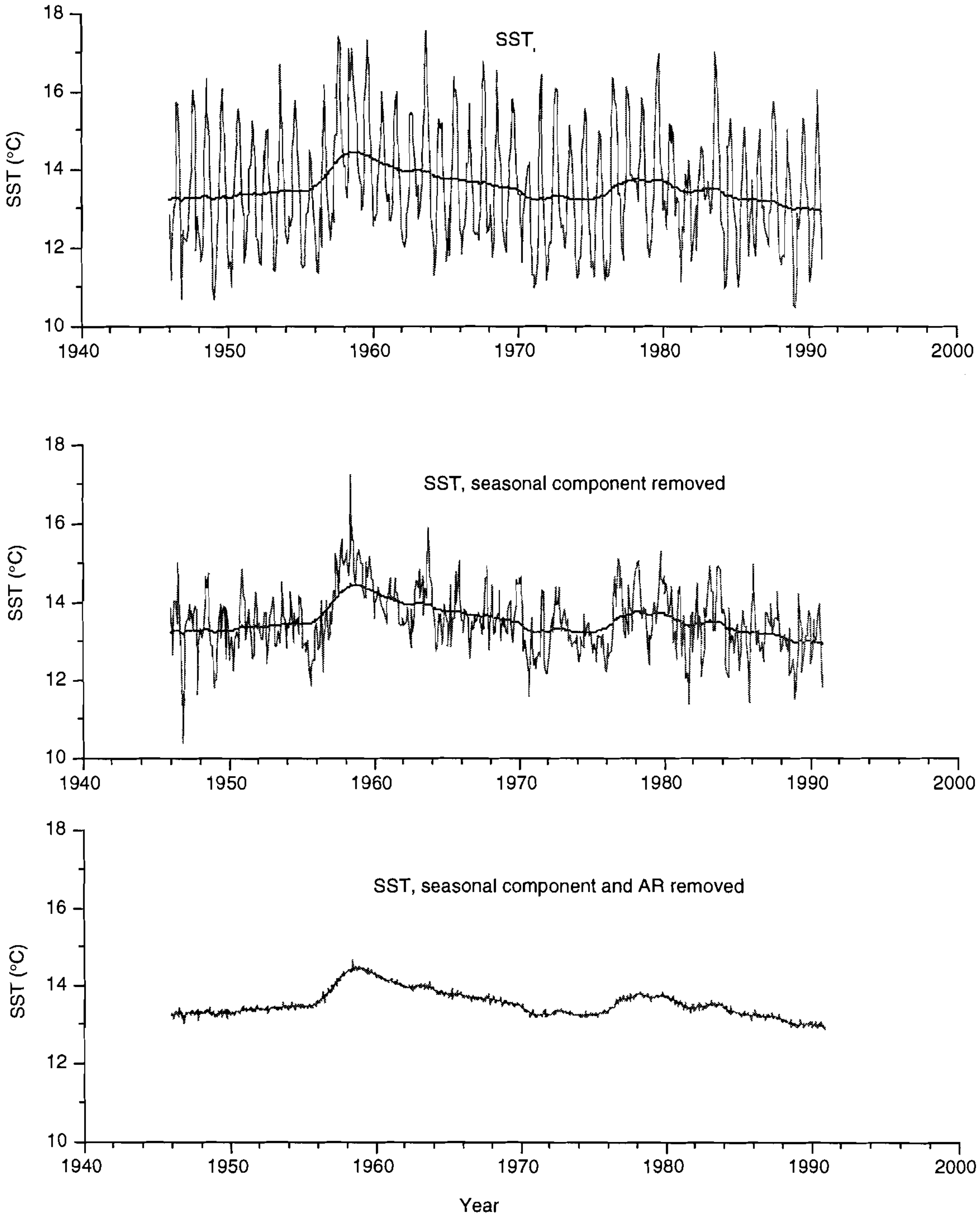

Fig. 6: California Current SST (°C) time series at 36-38°N : calculation of the trend from the partial residuals . The top panel shows the trend versus the original series; the middle panel the trend versus the original series minus the estimated seasonal component; the bottom panel the trend versus the original series minus both the estimated seasonal and the autoregressive components.

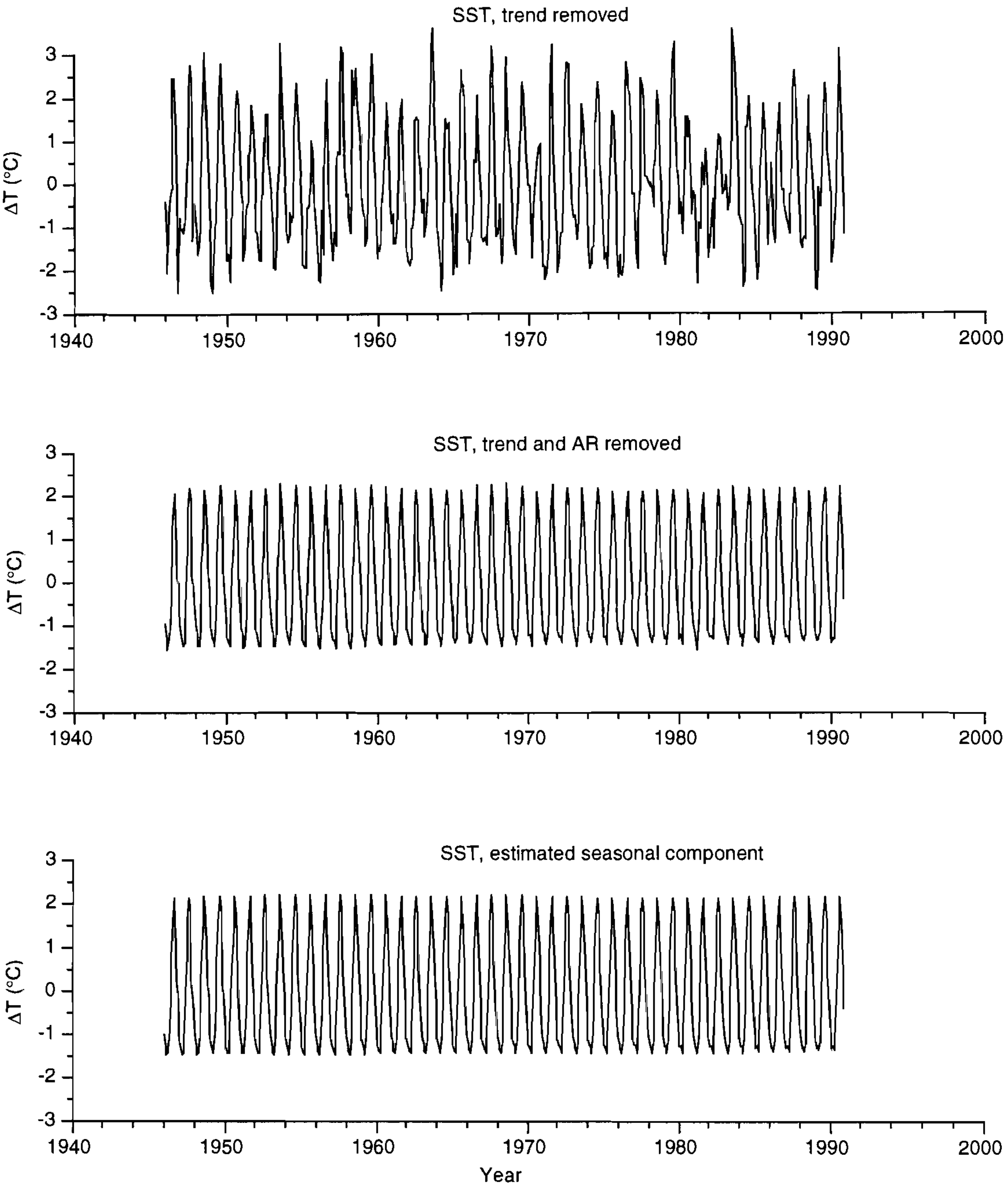

Fig. 7: California Current SST time series at 36-38°N: calculation of the seasonal component (ΔT; °C) from the partial residual series. The upper panel shows the detrended series; the middle panel shows the original series minus the trend and autoregressive components; the bottom panel shows the estimated seasonal component versus the original series, with the trend and AR components removed.

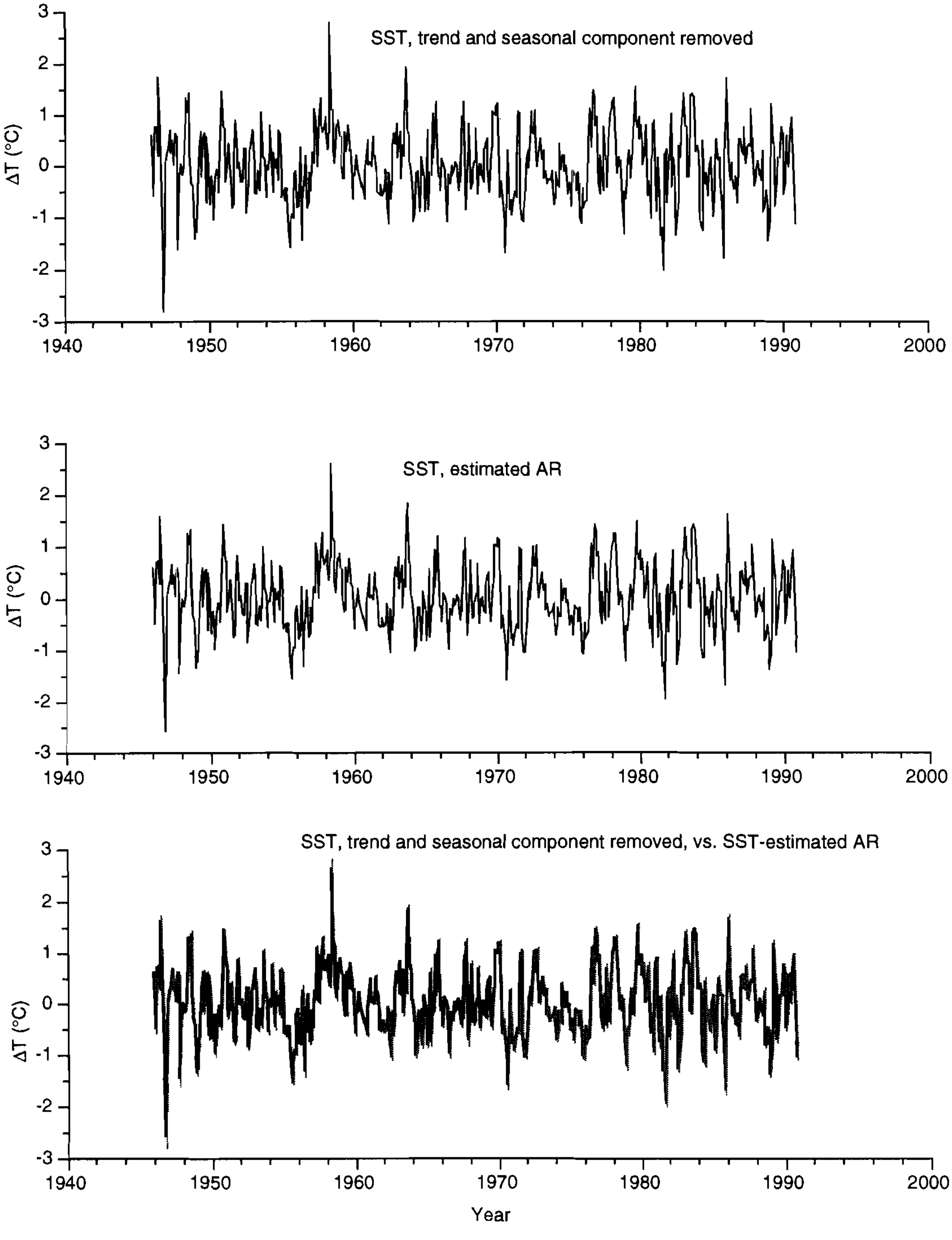

Fig. 8: California Current SST time series at 36-38°N: calculation of the AR component from the partial residual series (ΔT; °C). The upper panel shows the original series with the trend and seasonal component removed; the middle panel shows the estimated AR components; and the bottom panel shows the estimated AR component versus the original series with the trend and seasonal component removed.

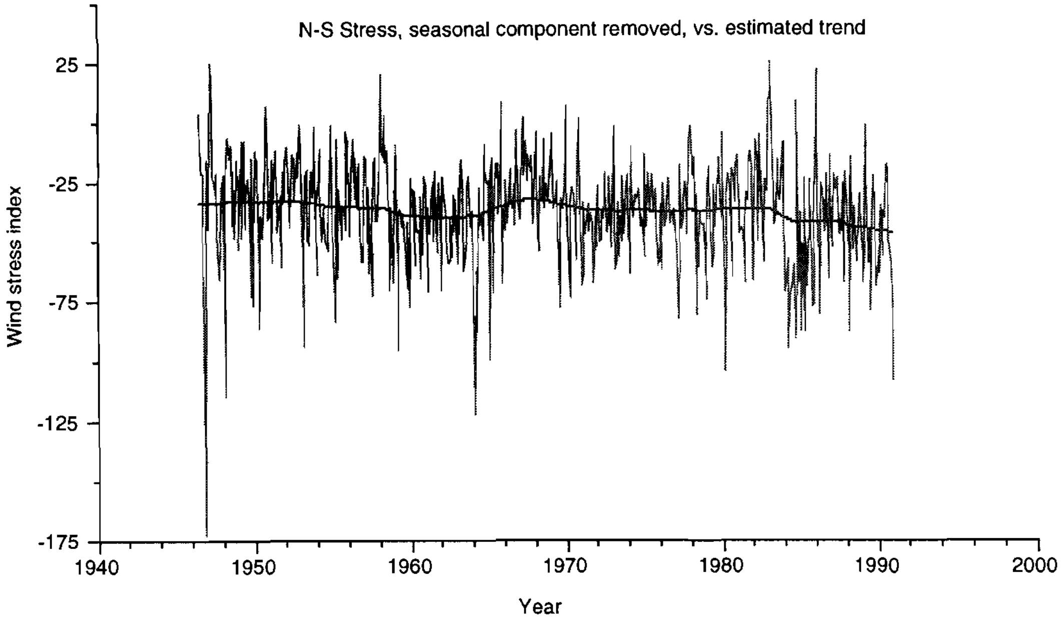

Fig. 9: California Current north-south wind stress time series at 36-38°N: calculation of the trend from the partial residuals. The panel shows the trend versus the original series minus the estimated seasonal component.

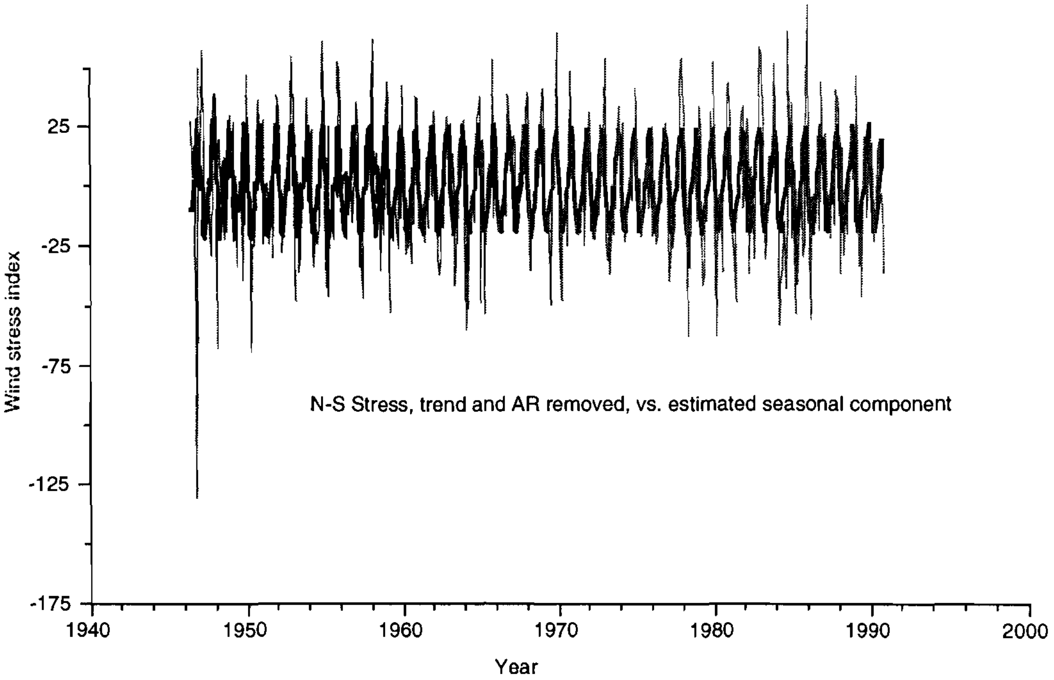

Fig. 10: California Current north-south wind stress time series at 36-38°N: calculation of the seasonal component from the partial residual series. The panel shows the estimated seasonal component versus the original series, with the trend and AR components removed.

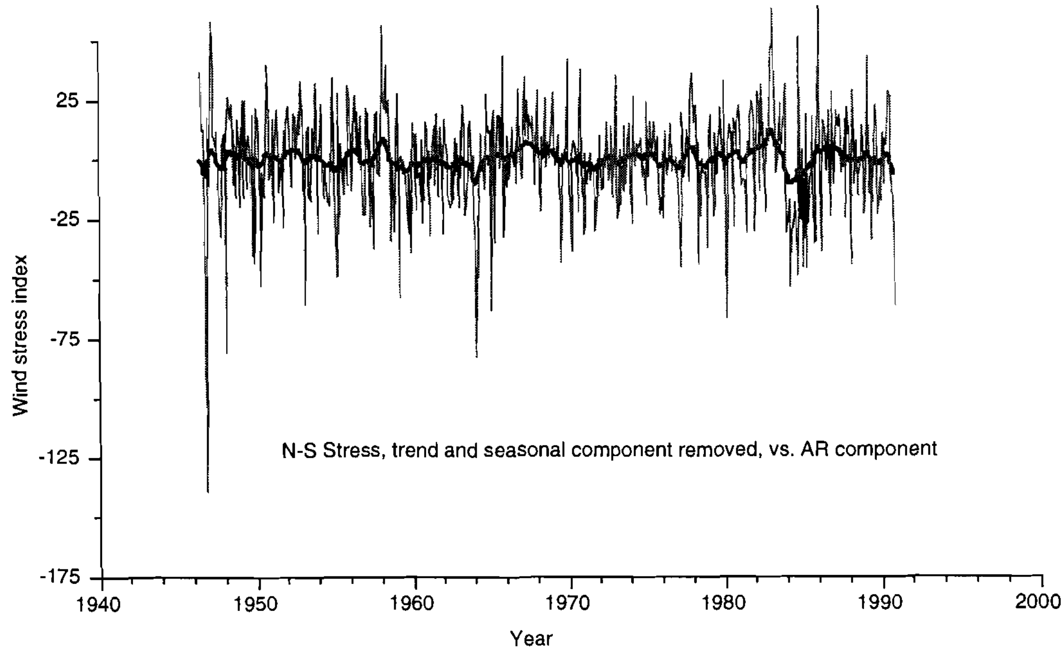

Fig. 11: California Current north-south wind stress time series at 36-38°N: calculation of the AR component from the partial residual series. The panel shows the estimated AR component versus the original series with the trend and seasonal components removed.

APPENDIX A: STATE-SPACE DECOMPOSITION OF TIME SERIES

The linear state-space model that is amenable to the Kalman filter takes the form:

$$y_t = A_t x_t + \upsilon_t \tag{28a}$$

$$x_t = \Phi x_{t-1} + \omega_t \tag{28b}$$

where the *observation equation* (Eq. 28a) has y_t a *q*x1-vector of the observed data (in this case $q=1$), A_t is a *qxp* matrix which relates the data to the unobserved components x_t, which is a vector of dimension *p*x1, and v_t is a qx1-vector of independent, identically distributed gaussian random variables with $Ev_t = 0$ and noise covariance matrix:

$$R = E(\upsilon_t \upsilon_t') \tag{29}$$

The evolution of the unobserved components or states x_t is governed by the initial value x_0 and the *state equation* (Eq. 28b). The matrix $\mathbf{\Phi}$ is a *pxp transition matrix* and the *p*x1-vector ω_t is another independent, identically distributed gaussian random variable with $E(\omega_t) = 0$ and:

$$Q = E\left(\omega_t \omega_t'\right) \tag{30}$$

The specification of the model is completed by assuming that X_0 is also gaussian with $E(x_0) = \mu$ and:

$$\Sigma = E(x_0 - \mu)(x_0 - \mu)' \tag{31}$$

See Shumway (1988, Section 3.4) for further details on the state-space model. Kitagawa and Gersch (1984) show how to put the smoothness priors assumptions of Equations 17-19 into state-space form. The model for k=1, and with a first order autoregression will be given. The model for other values follows analogously. The vector y_t is a scalar, the observed value of the time series at time t. The state vector x_t is of dimension 13 and is of the form:

$$x_t' = (T_t, S_t, \ldots, S_{t-11}, I_t) \tag{32}$$

and the transition matrix $\mathbf{\Phi}$ is given by

$$\begin{pmatrix} 1 & 0 & 0 & \cdots & 0 & 0 \\ 0 & -1 & -1 & \cdots & -1 & 0 \\ 0 & 1 & 0 & \cdots & 0 & 0 \\ 0 & 0 & 1 & \cdots & 0 & 0 \\ \vdots & \vdots & \vdots & \ddots & \vdots & \vdots \\ 0 & 0 & 0 & \cdots & 1 & 0 \\ 0 & 0 & 0 & \cdots & 0 & \phi \end{pmatrix} \tag{33}$$

where ϕ is the autoregressive parameter which is to be estimated. The observation matrix (from Eq. 13) is given by :

$$A = \begin{pmatrix} 1 & 1 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 1 \end{pmatrix} \tag{34}$$

The specification is complete by setting the observation error covariance matrix equal to $R = \sigma^2_e$ and by setting the state noise covariance matrix equal to:

$$\begin{pmatrix} \sigma^2_T & 0 & 0 & \cdots & 0 & 0 \\ 0 & \sigma^2_S & 0 & \cdots & 0 & 0 \\ 0 & 0 & 0 & \cdots & 0 & 0 \\ \vdots & \vdots & \vdots & \vdots & \vdots & \vdots \\ 0 & 0 & 0 & \cdots & 0 & \sigma^2_I \end{pmatrix} \tag{35}$$

For given values of the vector of parameters $\Theta = (\phi, \sigma^2_T, \sigma^2_S, \sigma^2_I, \sigma^2_e)$, the minimum mean-square-error estimates of each of the components of the state vector can be estimated using the Kalman filter and smoother. A particularly efficient form of the algorithm was developed independently by Ansley and Kohn (1985, 1990), Kohn and Ansley (1987) and De Jong (1989, 1990, 1991). Both algorithms include the case where $\Sigma \rightarrow \infty$, a diffuse or noninformative prior (see above references).

Let $X_{t|\tau}$ denote the expected value of the state vector given the data up to and including time τ, let $P_{t|\tau}$ denote the covariance matrix of the state vector conditional on the data up to and including time τ. Let r_t be a vector of dimension *p*, and R_t a *pxp* matrix. Then the filter and smoothing steps proceed as follows:

FILTERING:
Initialize:

$$\begin{aligned} x_0 &= \mu \\ P_0 &= \Sigma \end{aligned} \tag{36}$$

Iterate for t=1,T:

$$\begin{aligned} e_t &= y_t - Ax_{t/t-1} \\ D_t &= AP_{t/t-1}A + R \\ K_t &= \Phi P_{t/t-1}A' D_t^{-1} \\ x_{t+1/t} &= \Phi x_{t/t-1} + K_t e_t \\ L_t &= \Phi - K_t A \\ P_{t+1/t} &= \Phi P_{t/t-1} L'_t + Q \end{aligned} \tag{37}$$

SMOOTHING
Initialize:

$$\begin{aligned} r_T &= 0 \\ R_T &= 0 \end{aligned} \tag{38}$$

Iterate for t=T-1,0:

$$\begin{aligned} r_{t-1} &= A' D_t^{-1} e_t + L'_t r_t \\ R_{t-1} &= A' D_t^{-1} A + L'_t R_t L_t \\ x_{t/T} &= x_{t/t-1} + P_{t/t-1} r_{t-1} \\ P_{t/T} &= P_{t/t-1} + P_{t/t-1} R_{t-1} P_{t/t-1} \end{aligned} \tag{39}$$

The log-likelihood $L(Y;\Theta)$ given all the data Y and the parameter vector Θ is given by (see for example Shumway, 1988, page 178):

$$\ln L(Y;\Theta) = -\frac{1}{2}\sum_{t=1}^{T} \ln|D_t| - \frac{1}{2}\sum_{t=1}^{T} e'_t D_t^{-1} e_t \tag{40}$$

In order to use the EM algorithm (Dempster *et al.*, 1977) it is necessary to derive the complete data likelihood; here the components x_t are viewed as unobserved or "missing". After some manipulation, this can be shown to be (Shumway 1988, page 179):

$$\begin{aligned}
&-\frac{1}{2}\ln|\Sigma|-\frac{1}{2}tr\left\{\Sigma^{-1}\left[P_{0/T}+(x_{0/T}-\mu)(x_{0/T}-\mu)'\right]\right\}\\
&-\frac{T}{2}|\ln Q|\\
&-\frac{1}{2}tr\left\{Q^{-1}\left[S_t(0)-S_t(1)\Phi'-\Phi S_t(1)'+\Phi S_{t-1}\Phi'\right]\right\}\\
&-\frac{T}{2}\ln|R|\\
&-\frac{1}{2}tr\left\{R^{-1}\sum_{t=1}^{T}\left[(y_t-Ax_{t/T})(y_t-Ax_{t/T})'+AP_{t/T}A'\right]\right\}
\end{aligned} \tag{41}$$

where the terms $S_t(0)$, $S_t(1)$, and $S_{t-1}(0)$ are defined as:

$$\begin{aligned}
S_t(0)&=\sum_{t=1}^{T}\left(P_{t/T}+x_{t/T}x'_{t/T}\right)\\
S_{t-1}(0)&=\sum_{t=0}^{T-1}\left(P_{t-1/T}+x_{t/T}x'_{t/T}\right)\\
S_t(1)&=\sum_{t=1}^{T}\left(P_{t,t-1/T}+x_{t/T}x'_{t-1/T}\right)
\end{aligned} \tag{42}$$

and:

$$P_{t,t-1/T}=E\left[(x_t-x_{t/T})(x_{t-1}-x_{t-1/T})'/y_1,y_2,\dots,y_T\right] \tag{43}$$

A recursion for $P_{t,t-1|T}$ is given in Shumway and Stoffer (1982) and De Jong (1990). The complete data likelihood is maximized by setting:

$$\begin{aligned}
\Phi&=S_t(1)\left[S_{t-1}(0)\right]^{-1}\\
Q&=T^{-1}\left[S_t(0)-S_t(1)\Phi'-\Phi S_t(1)'+\Phi S_{t-1}(0)\Phi'\right]\\
R&=T^{-1}\sum_{t=1}^{T}\left[(y_t-Ax_{t/T})(y_t-Ax_{t/T})'+AP_{t/T}A'\right]
\end{aligned} \tag{44}$$

In the model of this paper, since most of Φ is fixed, the new estimate of Φ is the (13,13) element of Φ, and since most of Q is fixed to zero, the new estimates of Q are the (1,1), (2,2) and (13,13) elements of the above matrix, with all other elements set to zero. Here R is a scalar. The complete algorithm then consists to

1. Choose initial values for x_0, Σ and Φ;
2. Calculate the Kalman filter and smoother for the given parameter values;
3. Update the parameters by Equations 42;
4. Iterate until convergence.

The Kalman smoothers, calculated at the final parameter estimates, produce the component time series.

REFERENCES CITED

Akaike H. 1980. Likelihood and the Bayes procedure. *In*: J.M. Bernardo, M.H. DeGroot, D.V. Lindley and A.F.M. Smith (eds.), *Bayesian statistics*. Univ. Press, Valencia: 143-166.

Ansley C.F. and R. Kohn.1985. Estimation, filtering and smoothing in state space models with incompletely specified initial conditions. *Ann. Stat.*, 13:1286-1316.

Ansley C.F. and R. Kohn. 1990. Filtering and smoothing in state space models with partially diffuse initial conditions. *Time Series Anal.*, 11:275-293.

Bakun A. 1990. Global climate change and intensification of coastal ocean upwelling. *Science*, 247: 198-201.

Bakun A. 1996. *Patterns in the Ocean: ocean processes and marine population dynamics*. Sea Grant College Syst., Univ of Calif., La Jolla, 323p.

Barthelemy F. and M. Lubrano. 1996. Unit root tests and SARIMA models. *Econ. Lett.*, 50:147-154.

Beaulieu J.J. and J.A. Miron. 1993. Seasonal unit roots in aggregate U.S. data. *J. Econometrics*, 55: 305-328.

Bollerslev T. 1986. Generalized autoregressive conditional heteroscedasticity. *J. Econometrics*, 31:307-327.

Bollerslev T. and E. Ghysels. 1996. Periodic autoregressive conditional heteroscedasticity. *J. Bus. Econ. Stat.*, 14 (2): 139-151.

Brotherton T. and W. Gersch. 1981. A data analytic approach to the smoothing problem and some of its variations. *Proc. of the 20th IEEE Conference on Decision and Control*: 1061-1069.

Canova F. and B.E. Hansen. 1995. Are seasonal patterns constant over time ? a test for seasonal stability. *J. Bus. Econ. Stat.*, 13(3): 237-252.

Cleveland R.B., W.S. Cleveland, J.E. McRae and I.J. Terpenning. 1990. STL: A seasonal trend decomposition procedure based on Loess. *J. Official Stat.*, 6:3-73.

Cochrane J.H. 1988. How big is the random walk in GNP? *J. Polit. Econ.*, 95 :893-920.

Cochrane J.H. 1991. A critique of the application of unit root tests. *J. Econ. Dyn. Contr.*, 15 :275-284.

De Jong P. 1989. Smoothing and interpolation with the state-space model. *J. Am. Stat. Assoc.*, 84: 1085-1088.

De Jong P. 1990. Stable algorithms for the state space model., *J. Time Series Anal.*, 12:143-157.

De Jong P. 1991. The diffuse Kalman filter. *Ann. Stat.*, 19:1073-1083.

Dempster A.P., N.M. Laird and D.B. Rubin. 1977. Maximum likelihood from incomplete data via the EM algorithm. *J. Roy. Stat. Soc.*, Ser.B., 39:1-38.

Dickey D.A. and W.A. Fuller. 1981. Likelihood ratio statistics for autoregressive time series with a unit root., *Econometrica*, 49: 1057-1072.

Dolado J.J., T. Jenkinson and S. Sosvilla-Riveros.1990. Cointegration and unit roots. *J. Econ. Surveys*, 4: 249-273.

Engle R.F. and C.W.J. Granger. 1987. Cointegration and error correction representation, estimation and testing. *Econometrica*, 55: 251-276.

Engle R.F. and B.S. Yoo. 1987. Forecasting and testing in cointegrated systems. J. *Econometrics*, 35: 143-159.

Engle R.F. and S. Kozicki. 1993. Testing for common features. *J. Bus. Econ. Stat.*, 11: 369-395.

Engle R.F., C.W.J. Granger, S. Hylleberg and H.S. Lee. 1993. Seasonal cointegration, the Japanese consumption function. *J. Econometrics*, 55: 275-298.

Escribano A. and D. Pena. 1994. Cointegration and common factors. *J. Time Series Anal.*, 15: 577-586.

Franses P.H. 1994. A multivariate approach to modelling univariate seasonal time series. *J. Econometrics*, 63: 133-151.

Franses P.H. and B. Hobijn. 1994. *Critical values for unit root tests in seasonal time series*, Erasmus Univ. Rotterdam, Rep. 9462/A, 25p.

Franses P.H. 1996. Recent advances in modelling seasonality, *J. Econ. Survey*, 10(3): 299-344.

Fuller W.A. 1976. *Introduction to statistical time series*. Wiley, New-york.

Ghysels E., H.S. Lee and J. Noh. 1994. Testing for unit roots in seasonal time series. *J. Econometrics*, 62: 415-442.

Granger C.W.J. 1986. Development in the study of cointegrated economic variables. *Oxford Bull. Econ. Stat.*, 48: 213-228.

Granger C.W.J. 1988a. Some recent development in a concept of causality. *J. Econometrics*, 39: 199-211.

Granger C.W.J. 1988b. Causality,cointegration and control. *J. Econ. Dyn. Contr.*, 12: 551-559.

Harvey A.C. 1989. *Forecasting Structural Time Series Models and the Kalman Filter.* Cambridge Univ. Press, Cambridge, 554p.

Harvey A.C. and A. Scott. 1994. Seasonality in dynamic regression models. *Econ. J.*, 104: 1324-1345.

Hastie T.J. and R.J. Tibshirani. 1990. Generalized additive models. Monographs on Statistics and applied Probability, 43, Chapman and Hall, 335p.

Hatanaka M. 1996. *Time-series-based Econometrics, unit-roots and cointegration*, Oxford Univ. Press, 294p.

Hylleberg S. 1995. Tests for seasonal unit roots, general to specific or specific to general ? *J. Econometrics*,69: 5-25.

Hylleberg S., R.F. Engle, C.W.J. Granger and B.S. Yoo. 1990. Seasonal integration and cointegration, *J. Econometrics*, 44: 215-238.

Hwang J. and P. Schmidt. 1996. Alternative methods of detrending and the power of unit root tests, *J. Econometrics*, 71: 227-248.

Johansen S. K. 1988. Statistical analysis of cointegration vectors. *J. Econ. Dyn. Contr.*, 12: 231-254.

Johansen S.K. and S. Juselius. 1990. Maximum likelihood estimation and inference on cointegration with applications to the demand for money., Oxford Bull. Econ.Stat., 52: 169-210.

Johansen S.K.1991. Estimation and hypothesis testing of cointegration vectors in gaussian vector autoregressive models. *Econometrica*, 59: 1551-1580.

Kim K. and P. Schmidt. 1993. Unit root tests with conditional heteroscedasticity. *J. Econometrics*, 59: 287-300.

Kitagawa G. and W. Gersch. 1984. A smooothness priors - state space modeling of time series with trend and seasonality. *J. Am. Stat. Assoc.*, 79: 378-389.

Kitagawa G. and W. Gersch. 1985. *A smoothness priors time varying AR coefficient modeling of nonstationary time series.* IEEE Trans. Automat. Contr., AC-30: 48-56.

Kitagawa G. and W. Gersch. 1988. Smoothness priors in time series. *In*: J. Spall (ed.). Bayesian analysis of time series and dynamic models. Marcel Dekker, N.Y.

Kohn R. and C.F. Ansley. 1987. A new algorithm for spline smoothing and interpolation based on smoothing a stochastic process. *SIAM J. Sci. Stat. Comput.*, 8:33-48.

Kwiatkowiski D., P.C.B. Phillips, P. Schmidt and Y. Shin. 1992. Testing the null hypothesis of stationarity against the alternative of a unit root. *J. Econometrics*, 54: 159-178.

Lauritzen S.L. 1981. Time series analysis in 1880: A discussion of contributions made by T.N. Thiele., *Int. Statist. Rev.*, 49: 319-331.

Leybourne S.J., B.P.M. McCabe. 1994. A consistent test for unit root, *J. Bus. Econ. Stat.*, 12 (2): 157-166.

Lütkepohl H. 1991. *Introduction to multiple time series analysis.* Springer-Verlag, 545p.

Osborn D.R., A.P.L. Chui, J.P. Smith and C.R. Birchenhall. 1988. Seasonality and the order of integration for consumption. *Oxford Bull. Econ. Stat.*, 50: 361-377.

Perron P. 1989. The great crash, the oil price shock and the unit root hypothesis. *Econometrica*, 57: 1361-1401.

Perron P. 1990. Testing for unit root in a time series with changing mean. *J. Bus. Econ. Stat.*, 8 (2): 153-162.

Phillips P.C.B. and P. Perron. 1988. Testing for a unit root in a time series regression. *Biometrika*, 75: 335-346.

Phillips P.C.B. and S. Ouliaris. 1990. Asymptotic properties of residual based tests for cointegration. *Econometrica*, 58: 165-193.

Shiller J.Y. 1988. Interpreting cointegrated models. *J. Econ.Dyn. Contr.*, 12: 505-522.

Shiller R. 1973. A distributed lag estimator derived from smoothness priors. *Econometrica*, 41: 775-778.

Schmidt P. and P.C.B. Phillips. 1992. LM tests a unit root in the presence of deterministic trends. *Oxford Bull. Econ. Stat.*, 54: 257-287.

Shumway R.H. 1988. *Applied statistical time series analysis.* Prentice-Hall, Englewood Cliffs, 379p.

Shumway R.H. and D.S. Stoffer. 1982. An approach to time series smoothing and forecasting using the EM algorithm. *J. Time Series Anal.*, 3: 253-264.

Steele J.H. 1984. Kinds of variability and uncertainty affecting fisheries. *In*: R.M. May (ed.). *Exploitation of marine communities*. Dahlem Konferenzen, Springer-Verlag: 245-263.

Stock J.H. and M.W. Watson. 1988. Testing for common trends. *J. Am. Stat. Assoc.*, 83: 1097-1107.

Thiele T.N. 1880. Om Anvedelse af Mindste Kvadraters Methode i Nogle Tilfaelde, Hvor en Komlikation af Visse Slags Uensartede Tilfaeldige Fejlkilder Giver Fejlene en 'Systematisk' Karakter, Vidensk. Selsk. (French Translation: Sur la compensation de quelques erreurs quasisystématiques par la méthode des moindres carrés. Kobenhaven: Rietzel, 1880. Vidensk. Selsk. Skr. 5. rk., Naturvid og Mat. Afd, 12: 381-408.).

Vahid F. and R.F. Engle. 1993. Common trends and common cycles. *J. Appl. Econom.*, 8: 341-360.

Wecker W.E. and C.R. Ansley. 1983. The signal extraction approach to nonlinear regression and spline smoothing, *J. Am. Stat. Assoc.*, 78:81-89.

Whittaker E.T. 1923. On a new method of graduation. *Proc. Edinborough Math.Assoc.*, 78: 81-89.

Long-term Variability in the Seasonality of Eastern Boundary Current (EBC) Systems: an Example of Increased Upwelling from the California Current

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ABSTRACT

State-space statistical models are applied to long environmental time series of monthly northward wind stress, sea surface temperature (SST), coastal salinity (SSS) and coastal sea level (SL) from the west coast of North America. We describe the models, which use a combination of Kalman filtering and maximum likelihood methods to estimate a non-parametric non-linear trend, a non-stationary and statistically non-deterministic seasonal signal, and an autoregressive term. The models effectively separate the seasonal signals from the long-term trends.

The seasonal series are examined for behavior consistent with increasing coastal upwelling during April--July, the 'upwelling season'. We test the A. Bakun's hypothesis that equatorward wind stress, hence upwelling, has been increasing in eastern boundary current systems over the past several decades, presumably in response to a pattern of long-term global warming. Over a region of the California Current System (CCS) where coastal upwelling is a dominant process (32-40°N), wind stress,

SST, salinity and sea level all show strong evidence of a systematic intensification of upwelling during April-July. Equatorward stress and salinity display a strong linearly increasing tendency over time, while SST and sea level decrease significantly. The four parameters are significantly correlated in a manner consistent with increased upwelling as well; SST and sea level have decreased, and salinity has increased, coincident with strengthening equatorward stress.

To check that these results are unique to the seasonal model components, time series of April-July averages from the monthly observations and model trend series were examined. The trends in the region 32-40°N suggest a linear tendency for increasing equatorward stress (in agreement with the seasonal tendency), but warmer SST (opposite the seasonal and the expectation of greater upwelling), and closely match the tendencies in the observations. The linear tendencies of the SST and stress trends are generally an order of magnitude greater than in the seasonal tendencies. Thus the long-term trend in SST masks the cooling effect of increased seasonal upwelling, and the trend in equatorward stress suggests an artificially large seasonal increase in the observed spring and summer stress. A key to identifying these patterns has been the ability to separate the long-term non-linear trend, using the state-space models, which mask the signal of increased upwelling in the observations.

RÉSUMÉ

Des modèles Espace-Etat sont appliqués à des séries environnementales de la côte ouest de l'Amérique du Nord : tension méridienne du vent, température de surface (SST), salinité côtière (SSS) et niveau de la mer (SL). Ces modèles estiment de façon non paramétrique une tendance non linéaire, un signal saisonnier non stationnaire et statistiquement non déterministe et un terme autorégressif par la méthode du filtre de Kalman et du maximum de vraisemblance. Il est ainsi possible séparer les signaux saisonniers des tendances de long terme.

D'après A. Bakun, la tension méridienne du vent dans les écosystèmes d'upwelling aurait augmenté durant les dernières décennies probablement à cause de la tendance au réchauffement global. Le comportement de diverses séries saisonnières pendant la saison d'upwelling a été examiné dans la région de l'écosystème du courant de Californie où l'upwelling côtier est un processus dominant (32-40 °N). L'évolution de la tension du vent, de la température de surface, de la salinité et du niveau de la mer montre que durant la saison d'upwelling d'avril à juillet, il y a une intensification systématique de l'upwelling. La tension méridienne du vent et la salinité présentent une forte augmentation dans le temps tandis que la température de surface et le niveau de la mer diminuent significativement. Le sens de ces évolutions correspond bien à une intensification de l'upwelling.

Pour vérifier que ces résultats sont bien spécifiques de la composante saisonnière du modèle, la composante tendancielle et la moyenne des observations mensuelles sur la période avril-juillet ont également été examinées. Pour ce qui concerne la tension méridienne du vent, la tendance à long terme, tout comme la tendance saisonnière, vont dans le sens d'une augmentation. Par contre, la composante tendancielle et les observations sur la période avril-juillet de la température de surface montrent l'existence d'un réchauffement à long terme alors que c'est un refroidissement qui est constaté dans la composante saisonnière des températures de surface. Que ce soit pour la tension méridienne du vent ou pour la température de surface, l'ordre de magnitude des variations est plus grand pour la tendance à long terme que pour la tendance saisonnière. Ainsi, la tendance au réchauffement à long terme de la température de surface masque l'existence d'un refroidissement accru durant la saison d'upwelling. De même, la tendance à l'augmentation à long terme de la tension méridienne du vent suggère que la croissance observée durant la saison d'upwelling soit en partie artificielle. Elle relève pour partie d'un phénomène plus général et non pas d'un phénomène saisonnier. Les modèles Espace-Etat qui permettent d'extraire préalablement des données observées les tendances à long terme sont un instrument clé pour pouvoir identifier correctement l'évolution des phénomènes saisonniers.

INTRODUCTION

Climate variability on very large time (century) and space (global) scales impacts – or has the potential to impact – marine ecosystems at a variety of smaller scales. A number of recent papers have explored the patterns and dynamics of fluctuations embedded within the long-term, globally-integrated tendency commonly referred to as climate change ((Trenberth, 1990; Mann and Park, 1993, 1994; Graham, 1994; Miller *et al.*, 1994; Roemmich, 1992; Trenberth and Hurrell, 1994; Ware, 1995) to name but a few). However these studies have concentrated on large-scale temporal oscillations, generally on decadal scales; fewer examples (cf. Parrish *et al.*, 1981) describe variability on sub-basin (i.e., 100-1000 km) space scales.

In a particularly striking example of how global climate change may be affecting ocean conditions on smaller scales, Bakun (1990) postulates that under the scenario of global warming, continental air masses will warm more rapidly than oceanic air masses, leading to an intensified summer continental atmospheric low, a greater cross-margin pressure gradient between the continental low and higher pressure over the cooler ocean, stronger equatorward wind stress and increased coastal upwelling along eastern ocean boundaries. The effect on eastern boundary current (EBC) systems could be significant, because of the highly productive nature of these ecosystems and their potentially important role in the global CO_2 budget.

Upwelling is not a temporally continuous or spatially uniform process, but displays periods of favorable conditions for upwelling and downwelling (as well as substantial interannual variability), and has a distribution that suggests certain geographical sites as being more conducive to upwelling (Rosenfeld *et al.*, 1994). Empirical studies of upwelling and its effects on biological production suggest that optimal fisheries production occurs within a limited range of wind speeds; at speeds greater than about 5-7 m/s the biomass of small pelagic fish decreases (Cury and Roy, 1989). This has resulted in an ecosystem that is tuned to these variations. Any long-term changes in the seasonal patterns of upwelling, their intensity or the duration of upwelling events could have dramatic implications to EBC ecosystems and their living marine resources.

In this and in a companion paper (Schwing *et al.*, this vol.), we take advantage of a unique data set of long (multi-decadal) coastal environmental time series from along the west coast of North America, to evaluate changes in both the long-term trend and in the seasonal variability of EBC atmospheric forcing and the oceanic response. We were able to perform this evaluation by applying state-space models (Shumway, 1988, Chapter 3; Harvey, 1989; and Durand and Mendelssohn, this vol.) to separate the seasonal component from the long-term trend in a variety of California Current System (CCS) environmental time series.

Here we examine the variability in the seasonal component on climate (decadal and longer) scales, and in particular we test the hypothesis of Bakun (1990) that equatorward wind stress in spring and summer, hence upwelling, has been increasing in EBCs over the past several decades, presumably in response to a long-term global warming trend.

1. METHODS

1.1. Time series

The monthly-averaged time series described here were generated from a variety of sources. The primary data base was the Comprehensive Ocean-Atmosphere Data Set (COADS). The COADS contains almost 100 million reports of ocean surface conditions, mostly taken by ships-of-opportunity. The data have been collected, quality-controlled and put into common formats and units (Slutz *et al.*, 1985; Woodruff *et al.*, 1987). Data were extracted using the CD-Rom-based version of COADS and the CODE extraction program described in Mendelssohn and Roy (1996). The CD-Rom version contains Release 1 of COADS for the period 1854-1979 and the Interim release for 1980-1990, in CMR5 format. The wind data are marked as estimated, for winds approximated using the Beaufort scale; as measured, for anemometer or buoy measurements; or as unknown, when the measurement method and device were not known. Only wind data marked as estimated or unknown were used in forming the mean series, to avoid as much as possible the known bias in the data due to an increase over time in the use of anemometers to measure the wind (Cardone *et al.*, 1990; Isemer, 1992; Wu and Newell, 1992). Based on statistics from the data set, each observation for each parameter has been flagged as to the 'quality' of the observation (Slutz *et al.*, 1985). Poleward (northward) pseudo-stress, henceforth referred to as wind stress, was derived by squaring the northward wind component from each record extracted prior to monthly averaging. Spatial regions approximately two degree latitude by four degree longitude were defined based on a combination of ecological and oceanographic features as well as data density, and time series of poleward wind stress and sea surface temperature (SST) were calculated for each region (Fig. 1, Table 1) from the monthly means of each variable. To exclude possibly erroneous observations, all COADS data outside of their 'wide interval' (roughly equal to three standard deviations) were excluded from the averaging. These geographic boxes are referred to in terms of their central latitude (e.g., 23°N refers to the 22-24°N COADS box). The time period of extraction is 1946-90.

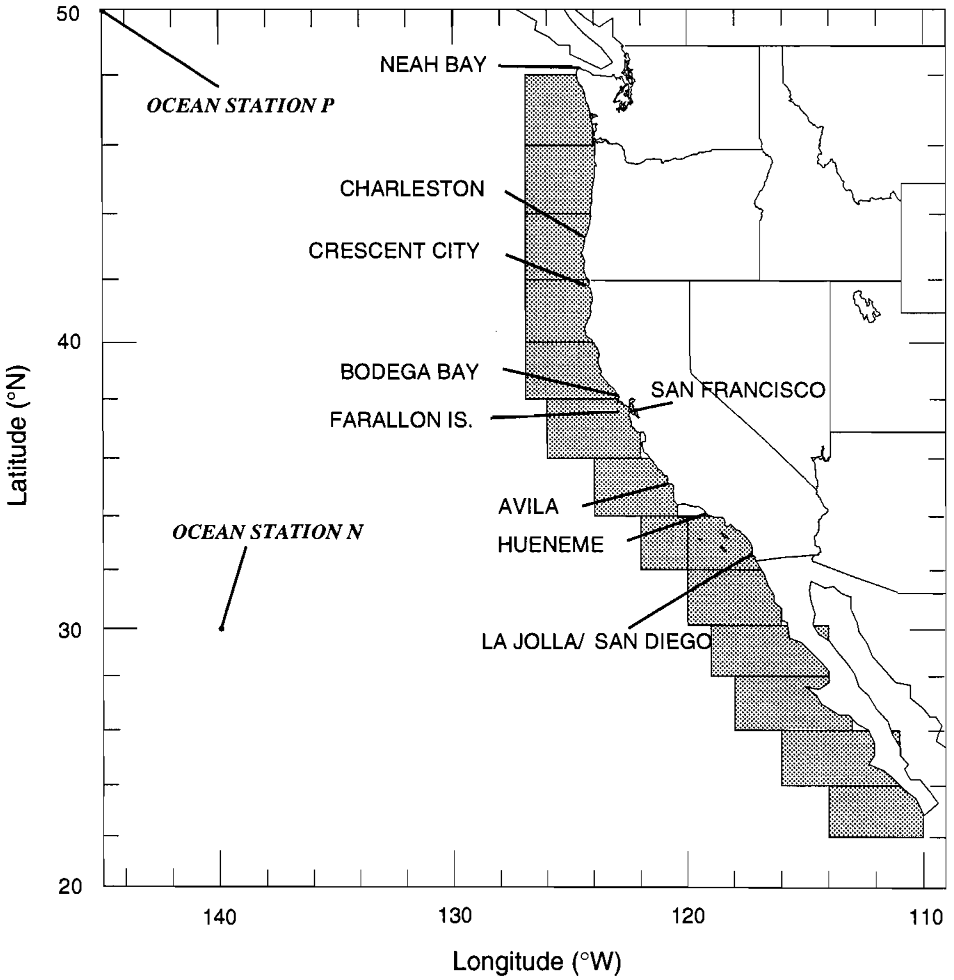

Fig. 1: Locations of COADS 2° boxes (shaded), and coastal stations from which monthly time series were generated. Locations of Ocean Stations P and N also are shown.

COADS LAT. (°N)	COADS LONG. (°W)	SHORE & OCEAN STATIONS (°N)	SST	SSS	SL
46-48	124 - 127	Neah Bay (48°22')	1935-92	1936-92	1934-92
44-46	123.5- 127	—	—	—	—
42-44	124 - 127	Charleston (43°21')	1966-92	—	—
40-42	123 - 127	Crescent City (41°45')	1933-92	1934-92	1933-92
38-40	122 - 127	Bodega Bay (38°19')	1957-92	1975-92	—
36-38	122 - 126	Farallon (37°25')	1925-92	1925-92	1915-92
34-36	120.5- 124	Avila (35°10')	1945-92	1945-79	—
S.C. Bight	116 - 120	Hueneme (34°09')	1919-87	1919-63	—
		La Jolla (32°52')	1916-92	1926-92	1915-92
30-32	116 - 120	—	—	—	—
28-30	114 - 119	—	—	—	—
26-28	113 - 118	—	—	—	—
24-26	111 - 116	—	—	—	—
22-24	110 - 114	—	—	—	—
—	—	Station P (50°N,145°W)	1950-92	1956-92	—
—	—	Station N (30°N,140°W)	1954-74	—	—

Table 1: Dimensions of COADS boxes containing derived monthly averaged equatorward wind stress and SST (for period 1946-1990), and selected shore stations within the COADS boxes. Years for monthly averaged time series of coastal SST, coastal salinity (SSS) and sea level (SL) shown.

Shore-based monthly SST and salinity (SSS) time series were averaged from daily observations made by volunteers, which were sent to the Marine Life Research Group, Scripps Institution of Oceanography (Walker *et al.*, 1993). SSTs were reported to the nearest 0.1°C at most sites. The observations are accurate to about ±0.2°C. Salinities were determined at Scripps from daily sea water samples using an inductive salinometer. Daily observations were quality controlled prior to the monthly-averaging. The number of daily values varied from 15-20/month (and as little as 10/month during winter months) at some of the northern stations (e.g., Farallon, Crescent City), to nearly complete coverage (e.g., La Jolla). Since 1979, NOAA/NOS has measured density with a hydrometer at Neah Bay and Crescent City. Salinities were back-calculated from these monthly-averaged densities. The locations of shore stations are shown in Fig. 1 and Table 1.

Monthly-averaged time series of sea level (SL) were supplied by NOAA/NOS, some through the Pacific Climate (PACLIM) data base (Cayan *et al.*, 1988). Long SL series are available at four sites (Fig. 1, Table 1). With a few exceptions, missing values in the shore time series were sparse and of only one to a few months duration. The time- and space-averaging for the COADS series were selected to ensure no missing observations while maximizing resolution. Months with no data were included in the analysis; the model fits through periods of missing data.

1.2. State-space statistical model

To estimate a time-varying (i.e., nonstationary) seasonal component for each observed time series, we assume that each observation y(t) is the sum of four components

$$y(t) = T(t) + S(t) + I(t) + e(t),\ t=1,T \quad (1)$$

where, at time t, $T(t)$ is the unobserved time-dependent mean-level (trend), $S(t)$ is the seasonal component, $I(t)$ is the irregular term (stationary but autocorrelated), and $e(t)$ is the stationary, uncorrelated component which here can be viewed as "observation" or "measurement" error.

As given, the model in Equation (1) is not uniquely specified, so meaningful solutions are not possible. To obtain a meaningful solution some constraints must be placed on the 'smoothness' of each component in the decomposition. Several methods for constraining the components have been suggested in the literature, related to 'smoothing spline' estimation of unknown functions. (The methodology is discussed in some detail in Durand and Mendelssohn, this vol.). For our analysis, we constrain the first differences of the trend component (the discrete equivalent of the first derivative) to be normal random variables with a mean of zero and unknown variance, that is:

$$\nabla^k T(t) \sim N(0, \sigma^2_T) \qquad (2)$$

The seasonal component is defined by constraining the running sum of the seasonal component to be a normal random variable with a mean of zero and unknown variance, that is (assuming s periods in a season; e.g., $s=12$ for monthly data, $s=4$ for quarterly data)

$$\sum_{i=0}^{s-1} S(t-i) \sim N(0, \sigma^2_S) \qquad (3)$$

The irregular term $I(t)$ is assumed to be a p-th order autoregression, that is

$$I(t) \sim \sum_{i=1}^{p} \phi_i I(t-i) + \varepsilon(t) \qquad (4)$$

$$\varepsilon(\tau) \sim N(0, \sigma^2_I) \qquad (5)$$

and the observation errors are assumed to be zero mean, independent, identically distributed as

$$e(t) \sim N(0, \sigma^2_e),\ t=1,T. \qquad (6)$$

In our analysis, a first order autoregressive model is used throughout for the irregular term. The entire model can be written in state-space format and solved using a combination of Kalman filtering and maximum likelihood (see Durand and Mendelssohn, this vol., for details).

The flexibility of this parameterization can be understood best by examining the limits of the trend and seasonal components at the extreme values of their variances (zero and infinity) when the other components have been removed (the partial residual series). If the seasonal and irregular terms were somehow known, then the algorithm would estimate a smoothed version of the observed series minus the seasonal and irregular components. When the trend variance (σ^2_T) is zero, this smoother is simply a linear least-squares fit to the partial residual series. When the trend variance approaches infinity, then the smoother simply interpolates the partial residual series.

If the trend and irregular were removed from the data, then the algorithm calculates for the seasonal component given by

Equation (3), a smoothed version of the *s*-period running sums of the partial residual series, where the amount of smoothing applied is the same throughout the series. (This implicitly will smooth the s-period differences also.) When the seasonal variance (σ^2_s) is zero, the result is the monthly means of the partial residual series. When the seasonal variance approaches infinity, then the result again interpolates the partial residual series.

Likewise, if the trend and seasonal components were known, then the irregular term estimates a *p*-th order autoregressive model to the partial residual series after the trend and the seasonal were removed. While the algorithm used in this paper estimates the components simultaneously, this 'backfitting' type approach of recursively smoothing the partial residual series could be used with other smoothing algorithms. Examples of the partial residual series and the estimated components for several series are given in Durand and Mendelssohn (this vol.).

The means of the monthly seasonal model time series for April-July (the upwelling 'season') were calculated in each year to produce the time series analyzed and described below (i.e., each annual value represents the average of the April-July period in that year). These series will henceforth be referred to as the upwelling time series.

2. RESULTS

2.1. Upwelling time series

The mean wind stress and SST for April-July (the upwelling 'season') were calculated in each year from the seasonal model series for the COADS 2° boxes. Plots of these upwelling time series are shown in Fig. 2. In most boxes, there is a close positive correlation between stress and SST. This is reflected in the linear correlations between these variables (Fig. 3, Table 2). There also is considerable consistency in stress and SST between adjacent boxes.

Seasonal series over most of the CCS region south of about 40°N display a fairly linear tendency of increasing equatorward (more negative) stress and decreasing SST over time. Both tendencies reverse north of 40°N, although stress again becomes more equatorward over time north of 44°N. The strong positive correlation between stress and SST also decreases in this northern region (Fig. 2, Table 2), and is actually significantly negative ($p<0.01$) over 44-48°N. South of 30°N the pattern of decreasing stress and SST changes gradually from a 'bowl-shaped' series to a linear increasing trend, similar to that noted north of 40°N.

In summary, upwelling wind stress has become more strongly equatorward over time in the region 32-40°N and north of 44°N. SST has become significantly cooler during the upwelling season between 30 and 40°N. The linear correlation between stress and SST is statistically significant and positive south of 40°N. Over the region 32-40°N, from about the U.S.-Mexico border to Cape Mendocino (shaded region in Fig. 3), the linear relationship between stress, SST and time are all consistent with increased upwelling.

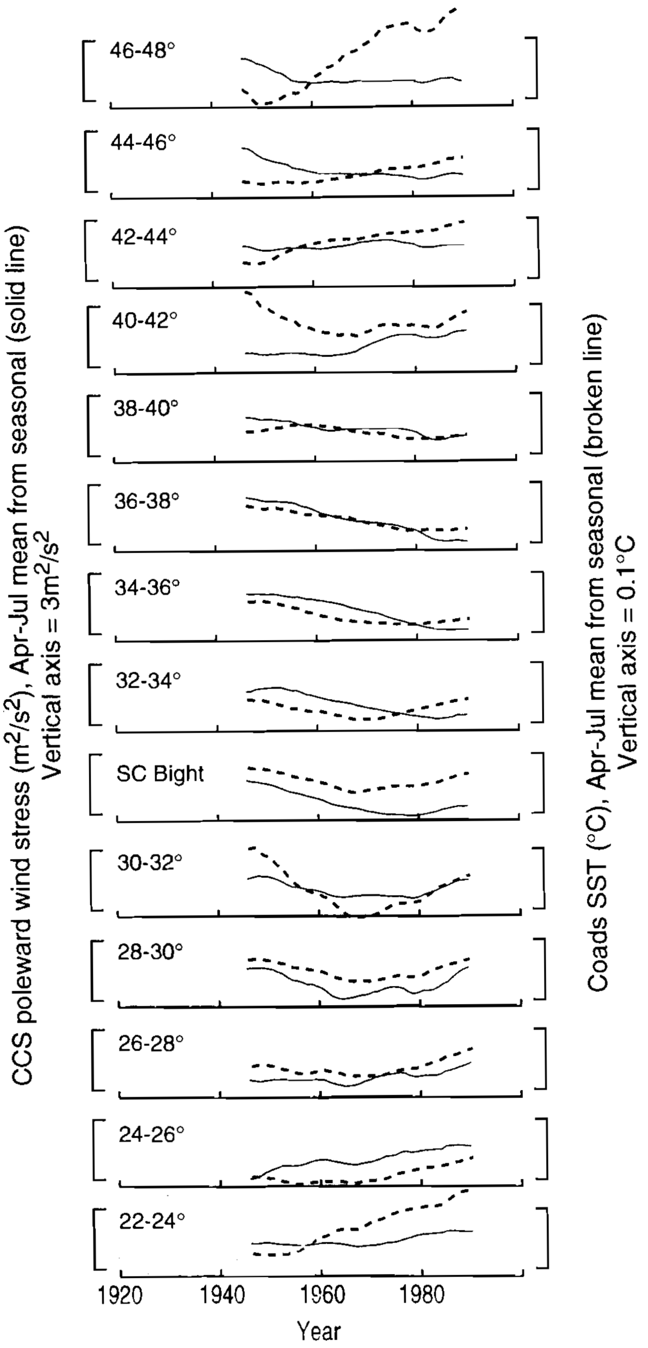

Fig. 2: Time series plots of 'upwelling' series (April-July averages from seasonal model components) for poleward wind stress (solid lines) and SST (dashed lines), for COADS 2° boxes. Vertical axes denote $3m^2/s^2$ and 0.1°, respectively.

LATITUDE	τ vs. YEAR (Apr-Jun)			SST vs. YEAR (Apr-Jun)			SST vs. τ (Apr-Jun)			SST vs. τ (Oct-Jan)		
	r	b(10^{-2})	±99%CI	r	b(10^{-3})	±99%CI	r	b(10^{-2})	±99%CI	r	b(10^{-2})	±99%CI
46-48	**-.670**	-1.805 ±	.785	.966	3.865 ±	.405	-.602	-8.937 ±	4.659	.315	1.016 ±	1.215
44-46	**-.834**	-2.625	.681	.958	.968	.144	-.646	-2.073	.963	**.922**	1.172	.196
42-44	.469	.500	.370	.969	1.427	.142	**.484**	6.682	4.748	-.570	-1.781	1.020
40-42	.897	3.061	.592	-.380	-.256	.247	-.037	-.073	.783	.371	6.596	6.564
38-40	**-.923**	-2.271	.372	**-.791**	-.489	.149	**.631**	1.587	.266	**.472**	2.252	.167
36-38	**-.992**	-5.556	.284	**-.975**	-1.126	.100	**.958**	1.976	.231	-.720	-2.661	1.019
34-36	**-.986**	-5.130	.343	**-.852**	-.894	.216	**.814**	1.642	.461	-.294	-5.270	6.800
Bight	**-.850**	-3.686	.897	**-.436**	-.414	.335	**.819**	1.790	.493	.092	.671	2.902
30-32	-.378	-1.053	1.014	**-.433**	-1.100	.900	**.945**	8.605	1.175	-.147	-1.040	2.786
28-30	-.338	-1.296	1.416	-.275	-.264	.140	**.950**	2.374	.306	.334	.446	.501
26-28	.710	1.399	.545	.507	.461	.308	**.789**	3.644	1.113	.257	.935	1.399
24-26	.953	3.263	.406	.801	.794	.233	**.780**	2.261	.712	**.602**	1.200	.633
22-24	.809	1.627	.465	.992	2.658	.130	**.803**	10.700	3.116	**.816**	4.129	1.161

Table 2: Correlations (r) and slopes (b) of linear fits (y = a + bx) of averaged April-July upwelling series values for northward wind stress (t) (m^2/s^2) against year, SST (°C) against year, and SST against northward wind stress, and SST against northward stress for October-January series, for period 1946-90 for 2° COADS data. Dependent (y) variable listed first. The 99% confidence intervals are given. The .01 (.05) significance level on r is .397 (.302), n=45 for Apr-Jul series; .402 (.306), n=44 for Oct-Jan series. Bold values of r denote linear regression is significant at .01 level, and of the sign consistent with increased upwelling (decreasing τ, SST over time; decreasing SST vs. τ). Bold latitudes denote regions where all three linear regressions are significant and of the sign consistent with increased upwelling.

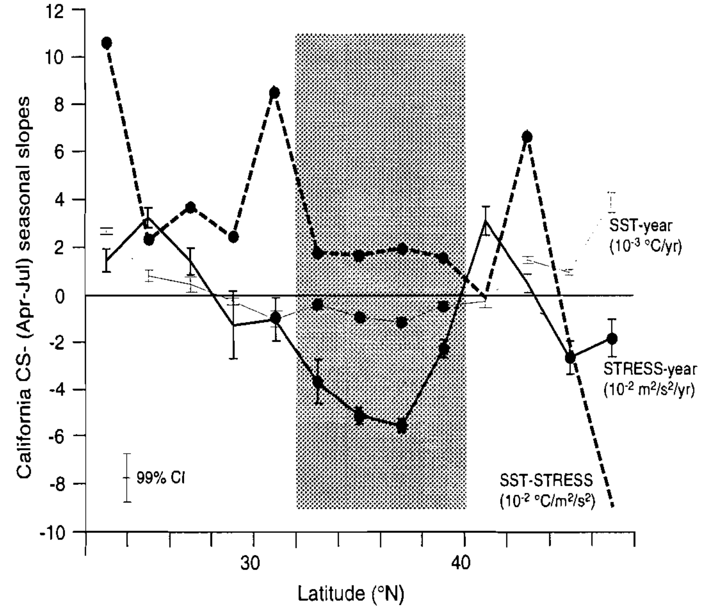

Fig. 3: Slopes (*b*) of linear fits (*y* = *a* + *bx*) of averaged April-July upwelling series values for northward wind stress (τ) (m^2/s^2) against year (bold solid line), SST (°C) against year (light solid line), and SST against northward wind stress (dashed line), for period 1946-90 for 2° COADS data. The 99% confidence intervals are shown. Solid circles denote linear regression is significant at .05 level. Shading denotes region where all three linear regressions for a COADS box are significant and of the sign consistent with increased upwelling. Horizontal axis is 10^{-3} m^2/s^2/yr for stress vs. time, 10^{-3} ° for SST vs. time, and 10^{-2} °C/ m^2/s^2 for SST vs. stress.

2.2. A comparison of shore-based seasonal series to the COADS series

All coastal upwelling (April-July seasonal) SST and sea level series decreased over time and all SSS series increased over time, implying an increase in upwelling (Fig. 4, Table 4). The magnitude of their changes corresponds to about 0.07-0.14°C, 0.01-0.1 ppt, and 0.1-0.7cm over the past 45 years. Correlations versus time are all highly significant ($p < .01$). Except for Crescent City, where the adjacent COADS stress (41N) shows an increasing seasonal trend, SST and sea level (SSS) are highly positively (negatively) correlated with local wind stress (Table 3). The patterns occurring during the period covered by the COADS data (1946-90) are consistent with those seen in the full-length shore series (57-78 years) (Table 5). Regressions between coastal SST, SSS and sea level (the series shown in Fig. 4) are highly significant and of the sign consistent with that expected if upwelling is the controlling process (Tables 3, 6). This is consistent with the fact that upwelling is a dominant process off much of the west coast during April-July.

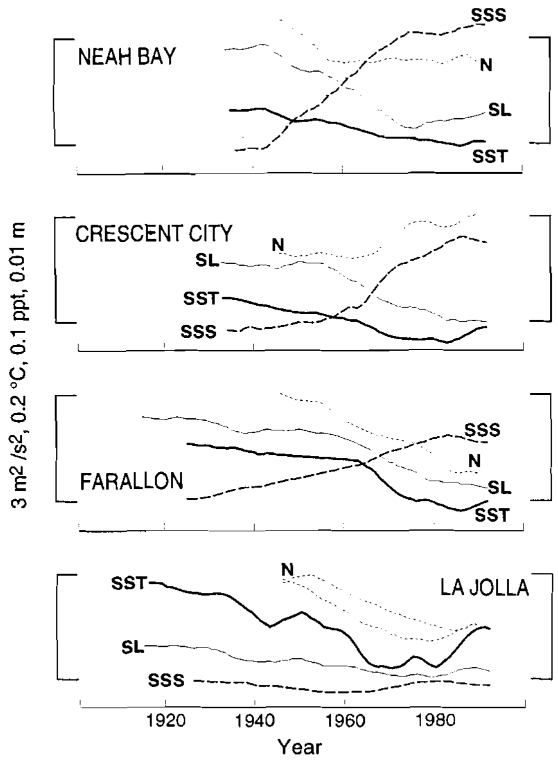

Fig. 4: Time series plots of 'upwelling' series (April-July averages from seasonal model components) for shore SST (bold solid lines), sea level (SL, light solid lines), surface salinity (SSS, bold dashed lines), and COADS poleward wind stress (τ), light dotted lines), for Neah Bay, WA (vs. 46-48°N τ), Crescent City, CA (vs. 40-42°N τ), Farallon, CA (vs. 36-38°N τ), and La Jolla, CA (vs. Southern California Bight τ). Vertical axes denote 0.2°, 0.1 ppt, 0.01m, and 3 m^2/s^2, respectively. Refer to Fig. 1 for location of shore stations.

STATION	SST vs. τ		SSS vs. τ		SL vs. τ	
	r	b (10^{-2})	r	b (10^{-3})	r	b (10^{-3})
NEAH BAY	**.656**	3.415±1.542	**-.764**	-72.178±23.951	**.715**	4.601±1.766
CRESCENT	-.827	-4.047±1.082	.936	64.961±9.596	-.890	-4.200±.844
FARALLON	**.944**	11.28±2.729	**-.966**	-1.920±.202	**.971**	2.638±.256
LA JOLLA	**.892**	5.777±1.150	**-.645**	-4.264±1.983	**.966**	.918±.097

Table 3: Correlations (r) and slopes (b) of linear fits of averaged April-July upwelling series values for coastal SST (°C), salinity (SSS) (ppt), and sea level (SL) (m) against northward wind stress (τ) (m^2/s^2) in adjacent 2° COADS regions, for period 1946-90. Dependent (y) variable listed first. Results shown for Neah Bay, WA (vs. 46-48°N τ), Crescent City, CA (vs. 40-42°N τ), Farallon, CA (vs. 36-38°N τ), and La Jolla, CA (vs. So. Cal. Bight τ). The 99% confidence intervals are given. The .05 (.01) significance level on r is .302 (.397), n=45. Bold values of r denote linear regression is significant at .05 level, and of the sign consistent with increased upwelling (increasing SST and SL, decreasing SSS, vs. τ). Bold stations denote locations where all three linear regressions are significant and of the sign consistent with increased upwelling.

STATION	SST vs. YEAR		SSS vs. YEAR		SL vs. YEAR	
	r	b (10^{-3})	r	b (10^{-4})	r	b (10^{-4})
NEAH BAY	**-.972**	-1.362±.129	**.959**	24.416±2.820	**-.919**	-1.591±.269
CRESCENT	**-.898**	-1.500±.289	**.981**	23.235±1.794	**-.974**	-1.568±.143
FARALLON	**-.958**	-3.009±.355	**.976**	10.870±.955	**-.981**	-1.493±.116
LA JOLLA	**-.566**	-1.589±.910	**.775**	2.219±.712	**-.728**	- .300±.111

Table 4: Correlations (r) and slopes (b) of linear fits of averaged April-July upwelling series values for Neah Bay, Crescent City, Farallon, and La Jolla SST (°C), SSS (ppt), and sea level (m) against year, or period 1946-90 for 2° COADS data. Dependent (y) variable listed first. The 99% confidence intervals are given. The .05 (.01) significance level on r is .302 (.397), n=45. Bold values of r denote linear regression is significant at .05 level, and of the sign consistent with increased upwelling (decreasing SST and SL, increasing SSS over time). All three linear regressions are significant and of the sign consistent with increased upwelling at all four locations.

An examination of the April-July seasonal averages at other coastal stations reveals very similar patterns (Fig. 5). Note the high degree of visual correlation between coastal SST series in adjacent boxes and along the entire coast. Several stations along the central and southern California coast (e.g., Avila, Bodega), over the 32-40°N range of increased upwelling suggested by the COADS data, feature decreasing SST and increasing SSS. These time series agree quantitatively with the other coastal sites discussed previously, both in the linear tendency and the decadal period fluctuations. Upwelling SST and SSS series generated for coastal stations north of 50°N (e.g., Cape St. James, British Columbia; Seward, Alaska) display no statistical change during April-July, suggesting the patterns of increased upwelling noted in the center of the CCS are not evident in the subarctic Pacific region influenced by the Alaskan Gyre.

The correlations between COADS and coastal SST are significant, although the slopes of the linear regressions between shore-based SST and COADS stress series are larger than with the COADS SST (Tables 3, 6); i.e., shore SST changes are

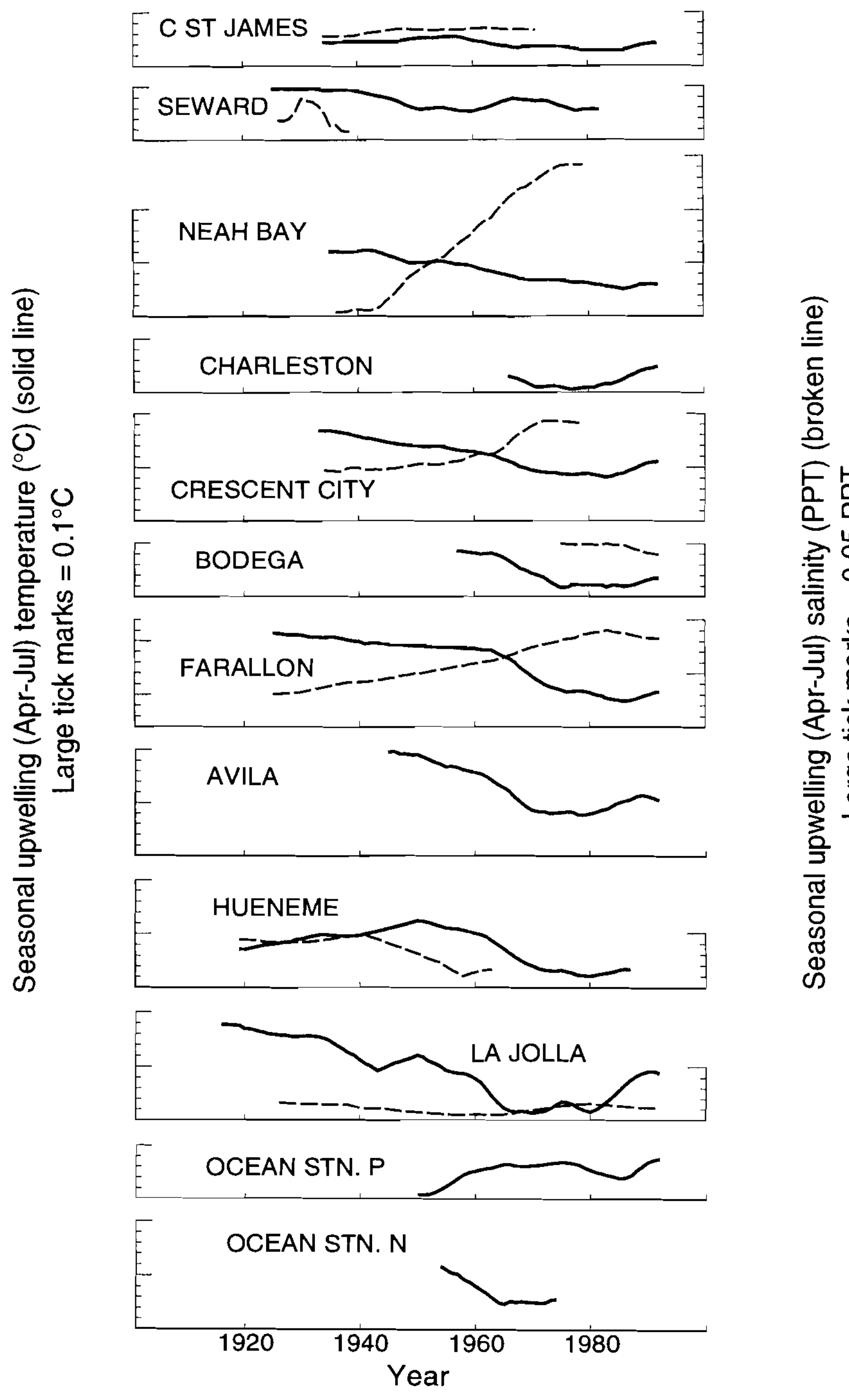

Fig. 5: Time series plots of 'upwelling' series (April-July averages from seasonal model components) for shore SST (solid lines) and SSS (dashed lines), for representative shore stations along the North American coast, and Ocean Stations N and P. Large tick marks on vertical axes denote 0.1°C and 0.05 ppt, respectively. Refer to Fig. 1 and Table 1 for location of shore stations.

greater than COADS SST changes. One exception is the negative correlation between the COADS and coastal SST at Neah Bay. The differences between the linear slopes of SST at the coast and COADS SST, which integrates SST over a large offshore area, probably are due to the dilution of coastal upwelling in the offshore domain of the COADS boxes.

To test whether these tendencies in the seasonal series are a coastal phenomenon, or possibly basin-wide, upwelling series were constructed from the seasonal model components of time series of SST and SSS at Ocean Station P (OSP), and SST at Ocean Station N (OSN) (Fig. 1, Table 1). The upwelling series at OSP (Fig. 5), located in the West Wind Drift, an eastward current that separates into the California Current and the Aleutian Current, reflect an increasing SST and SSS over time (Table 5), implying an increase in the contribution of subtropical water. This pattern does not reconcile with that seen in the CCS downstream of this ocean site, thus it is not likely linked with the COADS results.

SST at OSN, located in the subtropical North Pacific well to the west of the CCS, displays a clear cooling tendency of the same magnitude as the coastal sites, and looks quite similar to coastal SST series over its relatively short (21 years) record length (Fig. 5). Its position rules out changes in coastal upwelling as an explanation for this pattern. However changes in the wind curl over the eastern Pacific, which could lead to an intensification in Ekman pumping at locations remote from the coast, are a possibility. The hypothesized intensification of the thermal continental low in summer, which would contribute to increased coastal upwelling, could lead to changes in the wind gradients in the region of OSN as well. While an investigation of this possibility is beyond the scope of this paper, it is nevertheless an intriguing question, given the similarity between the coastal and OSN SST upwelling series. Closer analysis may suggest mechanisms by which long-term basin-scale forcing variability may impact upper ocean circulation patterns, and possibly coastal upwelling processes.

While the majority of the upwelling series display a highly linear tendency over time, some series exhibit considerable variability on decadal scales that is consistent within adjacent areas. For example, shore SSTs shift suddenly to more rapid cooling in early 1960s, to a slower rate of decreasing SST a few years later, and appears to reverse around 1980 (Fig. 5); SSS shows the opposite pattern. Non-linear upwelling series should not be construed as lacking a climate signal. Climate variability is not monotonic (e.g., the dramatic 1976 climate shift over the north Pacific (Trenberth, 1990; Graham, 1994; Trenberth and Hurrell, 1994)). Many of the series have variability such that truncating their length by even a few years leads to substantially different linear tendencies. A key result here is their consistency within geographical regions, such as the 32-40°N area dominated by coastal upwelling.

STATION	SST vs. YEAR		SSS vs. YEAR		SL vs. YEAR	
	r	b (10^{-3})	r	b (10^{-4})	r	b (10^{-4})
NB	**-.976**	-1.378±.105(58)	**.993**	38.379±1.798(44)	**-.943**	-1.569±.189(59)
CC	**-.926**	-1.473±.204(60)	**.928**	11.942±1.867(46)	**-.949**	-1.205±.135(60)
FAR	**-.942**	-2.124±.240(68)	**.985**	9.760±.540(68)	**-.949**	-.953±.093(78)
LJ	**-.853**	-2.028±.369(77)	-.068	-.131±.615(67)	**-.920**	-.403±.051(78)
OSP	.581	.859±.484(43)	**.844**	1.173±.325(37)	—	—
OSN	**-.881**	-3.285±1.043(21)	—	—	—	—

Table 5: As above, for entire series (n shown in parentheses next to 95% CI).

3. DISCUSSION

Strong evidence of a systematic intensification of upwelling during April--July is seen along the west coast of North America between 32-40°N (Fig. 3, Table 2). This region corresponds with an area where coastal upwelling predominates during spring and summer (Parrish *et al.*, 1981). It is offset slightly south of the primary upwelling region (Point Conception CA-Cape Blanco OR), suggesting that southward advection may account for the distribution of some of the cooling tendencies in COADS SSTs. This is consistent with the small negative SST-stress slope at 41°N, at the northern edge of the upwelling region, as well as the relatively large positive slope at 31°N, the southern boundary of upwelling (Fig. 3). Another large positive slope is seen at 23°N, south of an upwelling center off Baja California (Bakun and Nelson, 1977).

SST during the upwelling season has increased north and south of this region of intensified upwelling. However a corresponding decrease in equatorward stress, implying decreased coastal upwelling, only occurs south of 28°N. Stress is negatively correlated with SST north of 40°N, suggesting that seasonal changes in wind stress are not reflected in SST through coastal upwelling. This is not surprising since this region is at the northern extent of predominantly meridional wind associated with the pressure gradient between the continental low over the western U.S. and the North Pacific High, and is more influenced by predominantly zonal wind stress in the gradient between the High and the Aleutian Low (Bakun and Nelson, 1991). Offshore-directed Ekman surface transport during spring and summer is greatly reduced north of 40°N as well (Parrish *et al.*, 1983), further demonstrating the reduced role of coastal upwelling at northern latitudes.

Regions north of 40°N and south of 32°N are away from the influence of the continental low as well. Bakun (1992) points out that the Gulf of California occupies the area corresponding to the continental interior at higher latitudes. Therefore these areas are less susceptible to any increase in upwelling that would be associated with the intensification of the summer continental low and the subsequent strengthening of equatorward wind stress. Finally, anticyclonic curl dominates in the northern and southern regions, in contrast to strong cyclonic curl off California (Bakun and Nelson, 1991). Anticyclonic curl leads to Ekman convergence and downwelling, countering the effect of offshore Ekman transport and possibly explaining the limited geographical extent of the increased coastal upwelling over the past several decades.

The coastal stations corroborate these results. Four shore stations –Neah Bay, Crescent City, Farallon and La Jolla– have long series of SST, SSS and SL for comparison to the COADS wind (Fig. 4). Farallon is located in the center of the upwelling region on an island about 45 km west of San Francisco (SL for this location was measured at San Francisco). This site is frequently bathed by recently upwelled water from the north (Schwing *et al.*, 1991). An increasing equatorward wind stress corresponds with decreasing SST and SL, and increasing SSS at this location, all consistent with a systematic intensification of upwelling over the past several decades.

The tendencies at Neah Bay are similar to those at Farallon. The same is true at La Jolla; however the rate of change in the series over time is reduced. Coastal upwelling may be increasing in the Bight, but it is either a relatively small change or may be partially masked by other factors that impact the seasonality of the dynamics controlling the Bight's oceanic conditions. At Crescent City, the oceanic variables change in a manner consistent with increased upwelling, despite the fact that wind stress at this latitude has become increasingly poleward. The COADS winds may not be truly representative of the nearshore winds that drive coastal upwelling. Another possibility is that ocean conditions off northern California are controlled by non-local forcing which advects upwelled water south from the Cape Blanco upwelling region. Crescent City is near the divergence point of both the mean wind stress and the tendency of the COADS upwelling series. Ongoing analysis of wind and SST trends suggests further that the area's wind and SST fields are extremely heterogeneous on space scales of $O(100\ km)$ at time scales of years-decades (R. Parrish, pers. comm.), which suggest a combination of non-local forcing and complex circulation may be responsible for the seasonal tendencies seen at Crescent City.

Are the seasonal tendencies in wind stress and SST truly limited to the upwelling season, or are they representative of a pattern that occurs throughout the year? The former should be the case, since non-seasonal tendencies will be incorporated into the trend model component. Time series were constructed from the October-January means of the seasonal model series. The slopes of the linear fits of COADS SST to wind stress for these winter seasonal series (Table 2) show a very different pattern from the upwelling season. Only a few isolated COADS boxes reflect a significant positive correlation between SST and stress. Of these, a positive correlation was found for only one box within the 32-40°N upwelling area (39°N), and this was associated with an increasing (reduced upwelling) SST and stress tendencies. From this it can be concluded that the patterns consistent with increasing upwelling limited to the spring and summer. Other physical processes are controlling the seasonal wind and SST tendencies at other times of the year.

Are the regression statistics described above unique to the seasonal model components? The analysis was repeated by examining time series constructed from the April-July averages of the model trends and the monthly observations (raw data). The series constructed from the observations are analogous to those analyzed by Bakun (1990). The wind stress trend series display an increasing equatorward tendency south of 42°N and poleward north of 42°N, a pattern matched by the April-July observations (Fig. 6). The tendencies of the observed and trend series are negative, consistent with the seasonal upwelling series in the region 32-40°N (but at a lower level of significance). However the linear slopes of the trends and observations ($0.1\text{-}0.6\ m^2/\ s^2/yr$) are generally an order of magnitude greater than in the seasonal tendencies ($0.01\text{-}0.05\ m^2/\ s^2/yr$), reflecting the strong bias of the April-July observations toward the long-term trend. Linear tendencies of the CCS geostrophic wind series constructed by Bakun (1990) for April-September are very similar to the trend and observation tendencies reported here, reflecting the fact that long-term trends were incorporated in the «seasonal» series in his analysis.

The April-July trend and observed series south of 36°N display a general warming pattern (Fig. 7), whereas the seasonal upwelling series show a cooling tendency over the region 28-42°N. The wind and SST trend series are significantly correlated only at 39N, which is also the only location where the SST trends have a statistically significant cooling tendency. As with stress, the linear tendencies of the SST trends are $O(10)$ and greater than the seasonal tendencies, and generally of opposite sign. Again the observation and trend series correspond closely. The linear regressions off much of California and Baja California imply the seasonal SST component has been cooling at a rate of $-0.5\text{-}1.0 \times 10^{-3}\,°C/yr$, while the trends in this area exhibit a warming tendency of greater than $10 \times 10^{-3}\,°C/yr$. Schwing (1994) found consistent results from a similar comparison of the Farallon SST and SSS observed, trend and seasonal series. The long-term warming trend masks seasonal cooling associated with increased upwelling during spring and summer off central and southern California. These comparisons reflect the importance of using a method that separates seasonal and long-term contributions to environmental time series, and argue against looking for changing seasonal patterns in direct extractions from observations without properly accounting for the non-linear climate trend. Otherwise long-term climate patterns may be improperly linked to, and even misidentified as, changes in the seasonal cycle.

Because the dynamical relationship between wind forcing and coastal upwelling is the same at any time scale that is long relative to the inertial period, we expect that the SST model trend series should correspond to stress trends in a manner consistent with Bakun's (1990) hypothesis of increased upwelling (e.g., SST displays a cooling trend at locations where the trend suggests increased equatorward stress). A comparison of linear fits to the stress and SST trends (Fig. 6 and 7) shows the correlation between these trends is positive from about 34-42°N, as Bakun (1990) hypothesizes, but negative off the

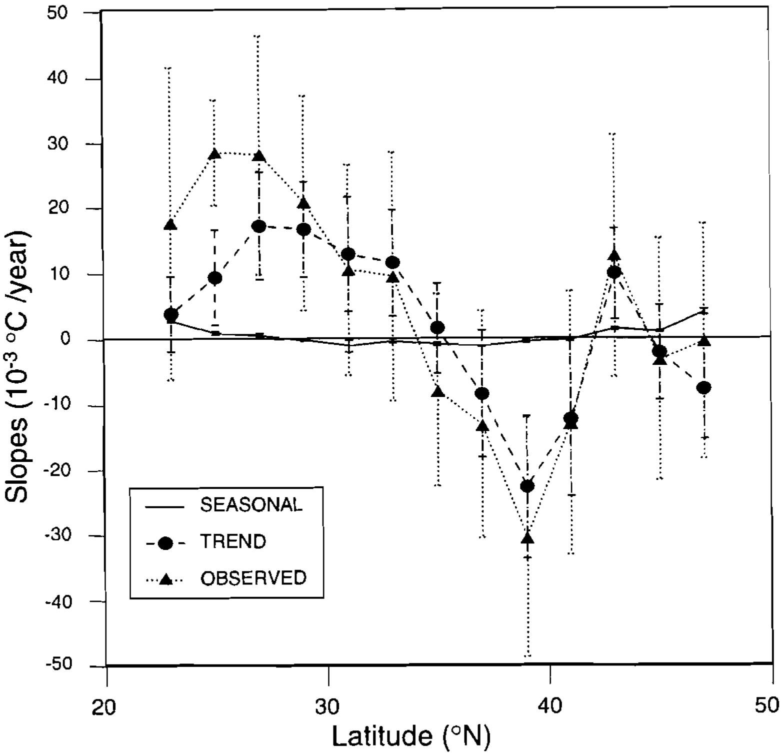

Fig. 6: Slopes (b) of linear fits ($y = a + bx$) of averaged April-July values of 2° COADS data poleward wind stress (m^2/s^2) against year, from monthly observations (dotted line), trend model component (dashed line), and seasonal model component (solid line), for the period 1946-90. The 99% confidence intervals are shown.

northwest U.S., and southern and Baja California. An analysis of the model trends is the focus of another publication (Schwing *et al.*, 1991). It is important however to recognize the difference between changes in the model trend series, which are due to superannual changes over time, and changes in the seasonal series, which are associated with climate variations that favorably affect a certain season or portion of the year. Because wind-driven coastal upwelling is one of several processes that impact SST and other ocean conditions, other factors (e.g., global warming) that may affect upper ocean variability cannot be ignored. The importance of these effects relative to wind forcing differs as a function of time scale. This may account for the different relationship between stress and SST in the trend and seasonal model components. Specifically we conclude that coastal upwelling controls SST in much of the CCS on seasonal scales. Therefore a close relationship exists between the spring/summer seasonal stress and SST series. SST trends, on the other hand, appear less closely linked to changes in local wind stress because factors other than wind forcing contribute significantly to SST variability.

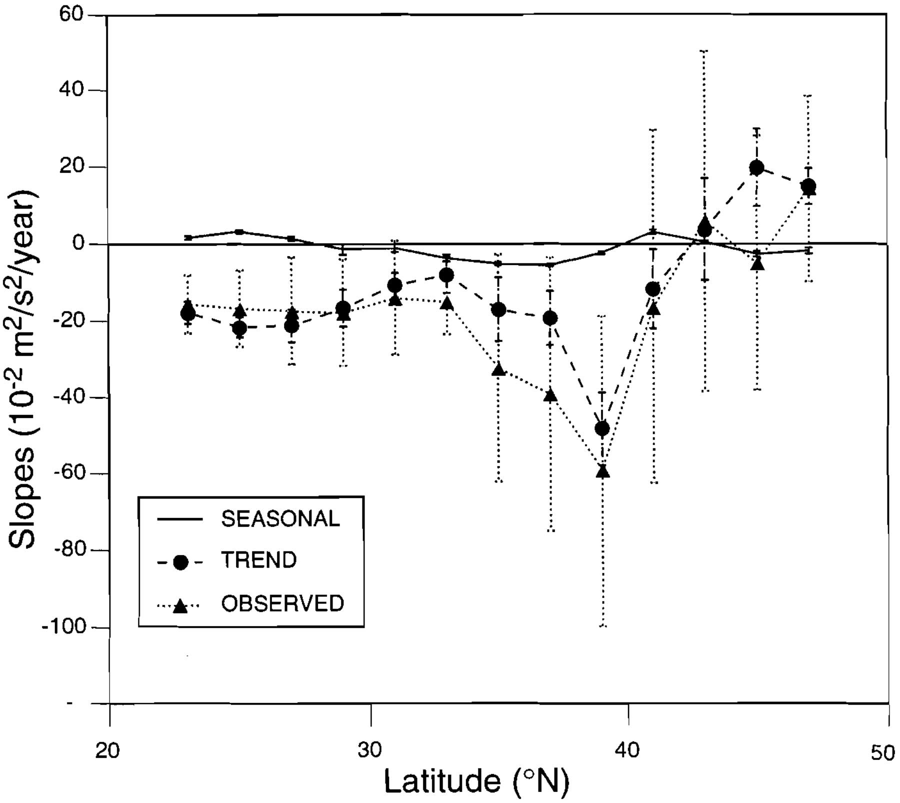

Fig. 7: Slopes (*b*) of linear fits (*y* = *a* + *bx*) of averaged April-July values of 2° COADS SST °C) against year, from monthly observations (dotted line), trend model component (dashed line), and seasonal model component (solid line), for period 1946-90. The 99% confidence intervals are shown.

	CSST vs. SST		SSS vs. SST		SST vs. SL		SSS vs. SL	
	r	b	r	b	r	b	r	b
NEAH	-.963	-2.745±.304	**-.977**	-1.774±.153	**.962**	7.778±.871	**-.985**	-14.464±1.007
CRES	**.497**	.203±.139	**-.933**	-1.323±.200	**.945**	9.809±1.330	**-.988**	-14.540±.881
FAR	**.972**	.357±.034	**-.978**	-.347±.029	**.989**	20.410±1.219	**-.988**	-7.226±.453
LA JOLLA	**.950**	.320±.041	**-.442**	-.045±.036	**.943**	64.292 8.862	**-.602**	-4.190±2.179

Table 6: Correlations (r) and slopes (b) of linear fits of averaged April-July upwelling series values for COADS SST (CSST), coastal SST (°C), SSS (ppt), and sea level (m), for period 1946-90. Dependent (y) variable listed first. Results shown for Neah Bay, WA (vs. 46-48°N CSST), Crescent City, CA (vs. 40-42°N CSST), Farallon, CA (vs. 36-38°N CSST), and La Jolla, CA (vs. So. Cal. Bight CSST). The 99% confidence intervals are given. The .05 (.01) significance level on r is .302 (.397), n=45. Bold values of r denote linear regression is significant at .05 level, and of the sign consistent with increased upwelling (decreasing CSST, SST and sea level, increasing SSS).

LATITUDE (°N)	SEASONAL τ vs. YEAR		TREND τ vs. YEAR		OBSERVED τ vs. YEAR	
	r	b (10^{-2}) ±99%CI	r	b (10^{-2}) ±99%CI	r	b (10^{-2}) ±99%CI
46-48	**-.670**	-1.805±.785	.781	14.892±4.682	.228	14.362±24.148
44-46	**-.834**	-2.625±.681	.614	19.718±9.961	-.060	-5.050±33.003
42-44	.469	.500±.370	.112	3.760±13.142	.053	5.974±44.337
40-42	.897	3.061±.592	**-.409**	-11.703±10.268	-.140	-16.557±46.009
38-40	**-.923**	-2.271±.372	**-.893**	-48.468±9.605	**-.499**	-59.258± 40.476
36-38	**-.992**	-5.556±.284	**-.730**	-19.280±7.103	-.396	-39.169±35.689
34-36	**-.986**	-5.130±.343	**-.627**	-17.002±8.288	-.394	-32.457±29.702
Bight	**-.850**	-3.686±.897	**-.562**	-8.026±4.641	**-.570**	-15.043±8.523
30-32	-.378	-1.053±1.014	**-.792**	-10.649±3.227	-.347	-14.007±14.871
28-30	-.338	-1.296±1.416	**-.803**	-16.611±4.850	**-.450**	-17.839±13.892
26-28	.710	1.399±.545	**-.888**	-21.280±4.340	**-.438**	-17.428±14.051
24-26	.953	3.263±.406	**-.956**	-21.663±2.615	**-.551**	-16.765±9.982
22-24	.809	1.627±.465	**-.922**	-17.776±2.940	**-.629**	-15.598±7.577

Table 7: Correlations (r) and slopes (b) of linear fits ($y = a + bx$) of averaged April-July upwelling series values for northward wind stress (τ) (m^2/s^2) against year, from seasonal and trend model series, and from monthly observed time series, for period 1946-90 for 2° COADS data. Dependent (y) variable listed first. The 99% confidence intervals are given. The .01 (.05) significance level on r is .397 (.302), n=45. Bold values of r denote linear regression is significant at .01 level, and of the sign consistent with increased upwelling (decreasing τ over time).

CONCLUSION

State-space models are applied to multi-decadal monthly-averaged time series of poleward wind stress, sea surface temperature, coastal salinity, and coastal sea level from the California Current System. The period of analysis is 1946-90. The models estimate a non-stationary non-deterministic seasonal component, a non-parametric non-linear trend, and an AR(1) series for each time series of monthly observations using a combination of Kalman filtering and maximum likelihood methods. Our objective here is to examine the variability of the seasonal patterns of coastal upwelling during spring and summer in the CCS, over climate (long-term) time scales. Specifically we test the hypothesis of Bakun (1990) that a long-term global warming trend has led to increasing equatorward wind stress along the west coast of North America, which has resulted in increased rates of coastal upwelling.

The results show a clear separation of the seasonal signal from the trend for wind stress, SST, salinity and sea level. The utility of estimating non-stationary seasonal patterns –using the state-space models– is demonstrated with the finding of a systematic increase in equatorward wind stress, decrease in SST and sea level, and increase in salinity during spring and summer, evidence that coastal upwelling has been increasing in intensity. Significant regional differences in the seasonal series were found. Evidence of increased upwelling is strongest and most prevalent in areas where seasonal coastal upwelling is a dominant process (e.g., 32-40°N). Shifts in the phase and amplitude of the seasonal cycle over several decades are suggested with this technique as well. This pattern of increasing upwelling intensity over time cannot be discerned in the monthly observations or trend model series. Evidence of increased upwelling is not found in fall-winter, either.

The state-space model appears to be a powerful tool for separating the interannual-to-interdecadal fluctuations in environmental time series from seasonal patterns of variability. The model results help provide a better understanding of the linkages between long-term variations in atmospheric forcing and the coastal ocean's response to this variability, as well as the potential contribution of natural and anthropogenic signals, and regional differences in these effects. The results presented here demonstrate the importance of evaluating temporal and spatial variability over the entire spectrum, rather than simply at global climate scales, when examining long-term environmental fluctuations. They also demonstrate the importance of considering independently the change in seasonal patterns versus changes in the long-term climate trend.

REFERENCES CITED

Bakun A. 1990. Global climate change and intensification of coastal ocean upwelling. *Science*, 247: 198-201.

Bakun A. 1992. Global greenhouse effects, multi-decadal wind trends, and potential impacts on coastal pelagic fish populations. *ICES Mar. Sci. Symp.*, 195: 316-325.

Bakun A. and C.S. Nelson. 1977. Climatology of upwelling related processes off Baja California. *CalCOFI Reports*, 19: 107-127.

Bakun A. and C.S. Nelson. 1991. The seasonal cycle of wind-stress curl in subtropical eastern boundary current regions. *J. Phys. Oceanogr.*, 21: 1815-1834.

Cardone V.J., J.G. Greenwood and M. Cane. 1990. On trends in the historical marine wind data. *J. Climate*, 3: 113-127.

Cayan D.R., D.R. McLain, W.D. Nichols, and J.S. DiLeo-Stevens. 1988. *Monthly climatic time series data from the Pacific Ocean and western Americas.* USGS Open-File Report, 379p.

Cury P. and C. Roy. 1989. Optimal environmental window and pelagic fish recruitment success in upwelling areas. *Can. J. Fish. Aquat. Sci.*, 46: 670-680.

Graham N.E. 1994. Decadal scale variability in the 1970's and 1980's: observations and model results. *Clim. Dyn.*, 10: 60-70.

Harvey A.C. 1989. Forecasting, structural time series models and the Kalman filter. Cambridge University Press, Cambridge, 554p.

Isemer H.-J. 1992. Comparison of estimated and measured marine surface wind speed. *In*: H.F. Diaz, K. Wolter and S.D. Woodruff (eds.). *Proceedings of the International COADS Workshop*, Boulder, Colorado, 13-15 January 1992. U.S. Dept. of Commerce. 142-158.

Mann M.E. and J. Park. 1993. Spatial correlations of interdecadal variation in global surface temperatures. *Geophys. Res. Lett.*, 20: 1055-1058.

Mann M.E. and J. Park. 1994. Global-scale modes of surface temperature variability on interannual to century timescales. *J. Geophys. Res.*, 99: 25819-25833.

Mendelssohn R. and C. Roy. 1996. Comprehensive Ocean Data Extraction. Users Guide, U.S. Dep. comm., NOAA Tech. Memo. NOAA Tech. Rep. NMFS SWFSC, La Jolla, CA., 228, 67p.

Miller A.J., D.R. Cayan, T.P. Barnett, N.E. Graham and J.M. Oberhuber. 1994. Interdecadal variability of the Pacific Ocean: model response to observed heat flux and wind stress anomalies, *Clim. Dyn.*, 9: 287-302.

Parrish R.H., C.S. Nelson and A. Bakun. 1981. Transport mechanisms and reproductive success of fishes in the California Current. *Biol. Oceanogr.*, 1: 175-203.

Parrish R.H., A. Bakun, D.M. Husby and C.S. Nelson. 1983. Comparative climatology of selected environmental processes in relation to eastern boundary current fish production. *FAO Fish Rep.*, 291: 731-778.

Roemmich D. 1992. Ocean warming and sea level rise along the southwest U.S. coast. *Science*, 257: 373-375.

Rosenfeld L.K., F.B. Schwing, N. Garfield and D.E. Tracy. 1994. Bifurcated flow from an upwelling center: a cold water source for Monterey Bay. *Continental Shelf Research*, 14: 931-964.

Schwing F.B. 1994. Long-term and seasonal patterns in coastal temperature and salinity along the North American west coast. *In*: K.T. Redmond and V.L. Tharp (eds.). *Proceedings of the Tenth Annual Pacific Climate (PACLIM) Workshop*. Interagency Ecological Studies Program for the Sacramento-San Joaquin Estuary. Tech. Rep., 36: 129-143.

Schwing F.B., D.M. Husby, N. Garfield and D.E. Tracy. 1991. Mesoscale oceanic response to wind events off central California in spring 1989: CTD surveys and AVHRR imagery. *CalCOFI Reports*, 32: 47-62.

Shumway R.H. 1988. *Applied statistical time series analysis*. Prentice-Hall, Englewood Cliffs, 379p.

Slutz R.J., S.J. Lubker, J.D. Hiscox, S.D. Woodruff, R.L. Jenne, D.H. Joseph, P.M. Steurer and J.D. Elms. 1985. *Comprehensive Ocean-Atmosphere Data Set*. Release 1. NOAA Environmental Research Laboratories, Climate Research Program, Boulder, CO. 268p.

Trenberth K.E. 1990. Recent observed interdecadal climate changes in the northern hemisphere. *Bull. Am. Meteor. Soc.*, 71: 988-993.

Trenberth K.E. and J.W. Hurrell. 1994. Decadal atmospheric-ocean variations in the Pacific. *Clim. Dyn.*, 9: 303-319.

Walker P.M., D.M. Newton and A.W. Mantyla. 1993. *Surface water temperatures, salinities and densities at shore stations, United States West Coast, 1992*. University of California, San Diego, Scripps Institution of Oceanography, La Jolla, CA, SIO Ref. 93-18, 46p.

Ware D.M. 1995. A century and a half change in the climate of the NE Pacific. *Fish. Oceanogr.*, 4: 267-277.

Woodruff S.D., R.J. Slutz, R.L. Jenne and P.M. Steurer. 1987. A Comprehensive Ocean-Atmosphere Data Set. *Bull. Am. Meteor. Soc.*, 68: 1239-1250.

Wu Z. and R.E. Newell. 1992. The wind problem in COADS and its influence on the water balance. *In*: H.F. Diaz, K. Wolter and S.D. Woodruff (eds.). *Proceedings of the International COADS Workshop*, Boulder, Colorado, 13-15 January 1992. U.S. Dept. of Commerce: 189-200.

Recent Trends in the Spatial Structure of Wind Forcing and SST in the California Current System

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ABSTRACT

State-space statistical models are applied to long time series of monthly COADS northward wind stress and sea surface temperature (SST) from the California Current System (CCS) for the period 1946-1990. The models estimate a non-parametric and non-linear trend, a non-stationary and non-deterministic seasonal signal, and an autoregressive (AR) term. They are also applied to long SST time series from selected coastal sites for comparison to the COADS series. SST shows decadal-scale periods of warm and cool anomalies that extend through the entire CCS. Wind stress anomalies are less extensive latitudinally and generally uncorrelated with SST, suggesting that decadal-scale SST variations in the CCS are controlled by fluctuations in the basin- to global-scale pressure and wind fields, rather than local wind forcing.

The CCS can be divided into three distinct geographical regions, which are similar to the system's biological regions. The northern region of the CCS (42-48°N) features a transition from strongly equatorward to poleward stress with distance north. The mean stress north of 44°N is poleward and has become increasingly poleward over time. This region features spatially uniform SST that has cooled over time. Winds south of 42°N are equatorward and can be described in terms of a central and southern region. The central region (34-42°N) exhibits the strongest wind stress in the CCS; equatorward stress has increased over time more than in the northern and southern regions. This region features the greatest interannual to decadal variation in stress and SST as well. Stress in the southern region (22-34°N) has become increasingly equatorward over time in a relatively monotonic pattern. Mean SST decreases consistently with increasing latitude in the central and southern regions. SST off California warms rapidly in response to ENSO events as well as the 1976 regime shift, but much more slowly at other latitudes. While SST along the entire coast has warmed during the past several decades, offshore SST has cooled north of 36°N. This long-term cooling in the northern CCS is linked to large-scale cool anomalies in the central north Pacific rather than changes in local wind forcing. A different complex of processes is responsible for the long-term coastal warming tendency. It also appears that distinct combinations of wind-forced advection, mixing and direct heating lead to significantly different regional responses of the coastal ocean to climate change, which in turn may have substantial consequences for marine populations in eastern boundary current ecosystems.

RÉSUMÉ

Des séries mensuelles de la tension méridienne du vent et de la température de surface du système du courant de Californie, issues de la base de données COADS sur la période 1946-1990, sont décomposées à l'aide de modèles Espace-Etat. Ces modèles estiment de façon non paramétrique une tendance non linéaire, un signal saisonnier non déterministe et non stationnaire, et un terme autorégressif. Pour pouvoir effectuer des comparaisons, des séries de températures de surface provenant de quelques sites côtiers ont également été décomposées par les mêmes méthodes statistiques. On montre qu'il existe pour la température de surface de la mer, des périodes d'anomalies chaudes ou froides à l'échelle décennale sur l'ensemble du système du courant californien. Les anomalies de la tension du vent s'étendent moins en latitude et sont généralement non corrélées avec les anomalies observées dans les températures de surface. Ceci suggère que les variations décennales de température de surface sont contrôlées par des champs de pression et de vent à une échelle globale plutôt que par le forçage local du vent. Le système du courant de Californie peut être divisé en trois régions correspondant à trois écosystèmes différents. La région nord (42-48 °N) est une zone de transition entre des vents dirigés vers l'équateur au sud de cette zone et vers le pôle au nord de 44 °N. Cette orientation vers le pôle a tendance à s'accentuer avec le temps. De même, la température de surface de la mer, relativement homogène dans la région (42°-48 °N), a tendance à diminuer. Au sud de 42 °N, la direction du vent est orientée vers l'équateur, cette latitude détermine la séparation entre la région nord et les régions centrale et sud. C'est dans la région centrale (34°-42 °N) que la tension du vent est la plus forte et que l'augmentation de la composante sud du vent a été la plus importante. C'est aussi dans la région centrale que les variations interannuelles et décennales de la tension de vent et de la température de surface sont les plus grandes. La composante sud du vent augmente régulièrement avec le temps dans la région sud (22°-34 °N). A mesure que l'on augmente en latitude dans les régions centrale et sud, la température de surface moyenne diminue significativement. En réponse aux phénomènes ENSO, mais aussi en raison du changement de régime de 1976, la température de surface augmente rapidement au large de la Californie mais beaucoup plus lentement aux autres latitudes. Alors que la température de surface a augmenté tout le long de la côte durant les dernières décades, elle a diminué au large du 36 °N. Cette tendance longue au refroidissement au nord du système du courant californien est liée aux anomalies froides à grande échelle observées dans le Pacifique nord plutôt qu'à des changements de la direction locale des vents. C'est un ensemble de processus différents qui est responsable de la tendance au réchauffement le long de la côte. Il apparaît également que des combinaisons particulières d'advection dues au forçage du vent, au mélange et à l'échauffement direct provoquent, dans les zones côtières, des réponses régionales aux changements climatiques pouvant être très différentes. Ceci pourrait donc avoir des conséquences importantes sur les populations d'espèces marines dans les écosystèmes d'upwellings côtiers.

INTRODUCTION

In eastern boundary current (EBC) systems, the physical environment is rarely uniform in time. In addition to seasonal and higher frequency variations, ENSOs and other perturbations produce profound anomalies in the atmosphere and ocean on interannual to decadal and century time scales. Analogously, EBCs appear to be spatially heterogeneous. Each system can be separated into several discrete regions, dominated by different physical processes, and presumably different biological structure. These regions may be separated by sharp gradients in physical forcing and characteristics, or by broad transition zones that extend over several degrees of latitude. It is expected that environmental variability in an EBC will impact its ecosystem's components, and may lead to perturbations in plankton and fish abundance, biomass and distribution. The timing of seasonal cycles in each region, as well as the timing and intensity of large-scale events (e.g. ENSOs), may not be coherent throughout an ecosystem.

To understand better how EBC ecosystems might respond to climate change, it is critical to describe their primary scales of spatial and temporal variability, and discern the dynamics responsible for this variance, rather than treat EBCs as spatially homogeneous systems or use seasonally-averaged data to describe their climatology. This background is essential if scientists are to address the likely impact of climate change scenarios on ecosystem structure and the distribution of its populations.

The objective of this paper is to describe the temporal variability in the spatial texture of the California Current System (CCS), a major EBC system, to provide a base from which to evaluate the effect of climate variability in the environment on fisheries - in the recent past, at present, and for the future. Specifically, we will describe the patterns of variability that have occurred over the past 45 years (1946-1990) in the monthly-averaged wind stress and sea surface temperature (SST) fields of the CCS, using state-space statistical models (Schwing and Mendelssohn, this vol.) to separate a non-linear, non-parametric trend for each series from seasonal and other higher frequency variance. It is our hope that the results described here will encourage researchers to look for analogous spatial and temporal patterns in climate variability in other EBCs and relate this variability to fluctuations in marine populations.

1. METHODS

The environmental data used to generate the monthly-averaged time series analyzed here were obtained from a variety of sources. The primary data base was the Comprehensive Ocean-Atmosphere Data Set (COADS). The COADS contains almost 100 million reports of ocean surface conditions, mostly taken by ships-of-opportunity. The data have been collected, quality-controlled and put into common formats and units (Slutz *et al.*, 1985; Woodruff *et al.*, 1987). Data were extracted using the CD-Rom-based version of COADS and the CODE extraction program described in Mendelssohn and Roy (1996). The CD-Rom version contains Release 1 of COADS for the period 1854-1979 and the Interim release for 1980-1990, in CMR5 format.

Only wind data marked as estimated or unknown were used in forming the mean series, to avoid as much as possible the known bias in the data due to an increase in the use of anemometer-wind measurements (Cardone *et al.*, 1990; Isemer, 1992; Wu and Newell, 1992). All COADS observations outside of the wide interval (see Slutz *et al.*, 1985, page D6) were excluded from the summaries as well. Poleward wind pseudo-stress, henceforth referred to as wind stress, was derived by squaring the northward wind component from each record included in the extraction. Spatial regions approximately two-degree latitude by four-degree longitude were defined based on a combination of ecological and oceanographic features as well as on data density, and monthly mean time series of wind stress and sea surface temperature (SST) were calculated for each region (Fig. 1, Table 1). These geographic boxes are referred to in terms of their central latitude (e.g. 23°N refers to the 22-24°N COADS box). The time period of extraction is 1946-1990.

The parameterization of wind stress used here is one of several possibilities found in the scientific literature. It was applied because only the time series of the north wind components were available initially. Winds along the west coast are oriented predominantly north-south. Follow-up analyses using the wind total vector, as well as other stress parameterizations, provide very similar results, suggesting the north wind series described here qualitatively represent the variability in the coastal wind field over the past half-century.

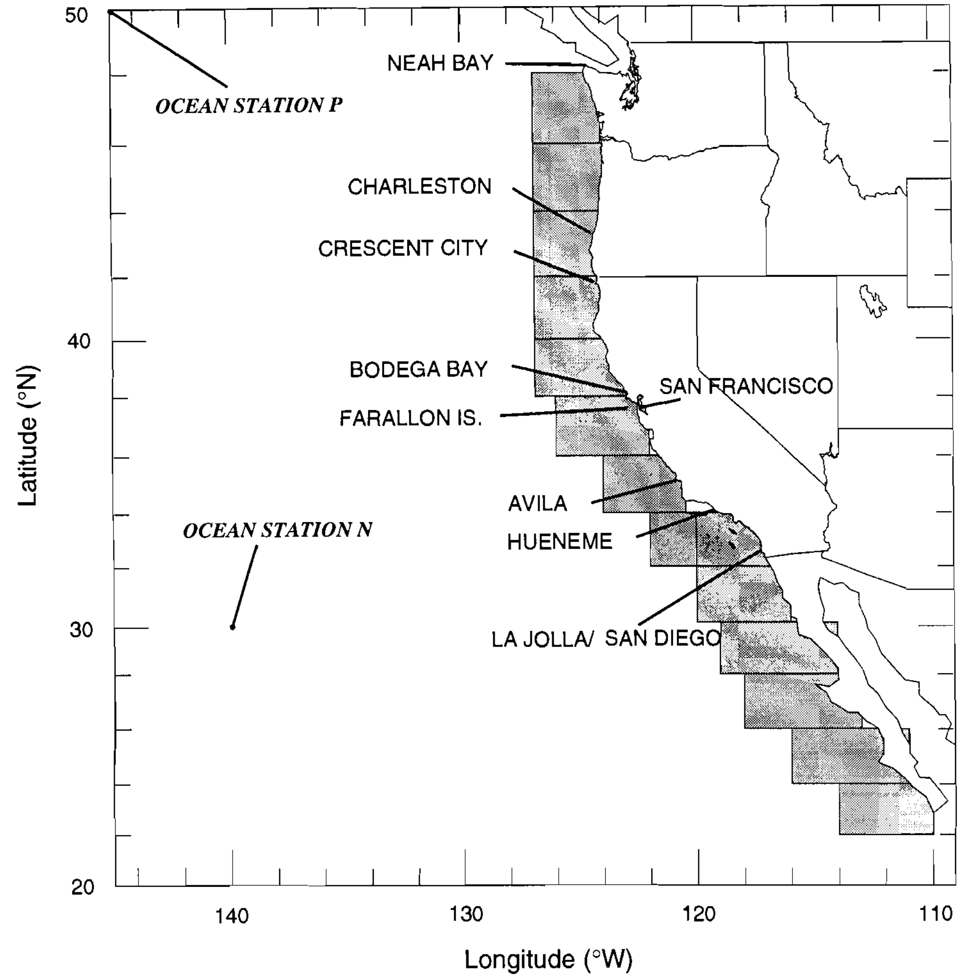

Fig. 1: Locations of COADS 2° boxes, shown as shaded boxes, and coastal stations from which monthly time series were generated. Locations of Ocean Stations P and N also are shown.

Shore-based monthly-averaged sea surface temperature (SST) time series were derived from daily observations made by volunteers, which are sent to the Marine Life Research Group, Scripps Institution of Oceanography (Walker *et al.*, 1993). SSTs were reported to the nearest 0.1°C at most sites and are accurate to about +/-0.2°C. The number of daily samples per month varied from 15-20/month (and as little as 10/month during winter months) at some of the northern stations (e.g. Farallon, Crescent City), to nearly complete coverage (e.g., La Jolla) (Skillman, 1993). The locations of the primary stations are shown in Figure 1 and Table 1.

COADS BOX (°N)	COADS LAT (°N)	COADS LONG (°W)	SHORE & OCEAN STATIONS (°N)	SST
47	46-48	124 - 127	Neah Bay (48°22')	1935-1992
45	44-46	123.5- 127	—	—
43	42-44	124 - 127	Charleston (43°21')	1966-1992
41	40-42	123 - 127	Crescent City (41°45')	1933-1992
39	38-40	122 - 127	Bodega Bay (38°19')	1957-1992
37	36-38	122 - 126	Farallon (37°25')	1925-1992
35	34-36	120.5- 124	Avila (35°10')	1945-1992
33	32-34	120 - 122	—	—
BIGHT	32-34	116 - 120	Hueneme (34°09')	1919-1987
			La Jolla (32°52')	1916-1992
31	30-32	116 - 120	—	—
29	28-30	114 - 119	—	—
27	26-28	113 - 118	—	—
25	24-26	111 - 116	—	—
23	22-24	110 - 114	—	—
—	—	—	Station P (50°N,145°W)	1950-1992
—	—	—	Station N (30°N,140°W)	1954-1974

Table 1: Dimensions of COADS boxes containing derived monthly averaged equatorward wind stress and SST (for period 1946-1990), and selected shore stations within the COADS boxes. Dates for monthly averaged time series of SST, salinity and sea level shown.

To estimate a time-varying (i.e. non-stationary) trend component for each monthly-averaged time series, we assume that each monthly average y(t) is the sum of four components

$$y(t) = T(t) + S(t) + I(t) + e(t), t=1,T \quad (1)$$

where, at time t, T(t) is the unobserved time-dependent mean-level (trend), S(t) is the seasonal component, I(t) is the irregular term (stationary but autocorrelated), and e(t) is the stationary uncorrelated component, which can be viewed as 'observation' or 'measurement' error. A non-parametric and non-linear trend is estimated for the monthly-averaged time series using a state-space model solved by using a combination of the Kalman filter and maximum likelihood methods (Kitagawa and Gersch, 1984, 1988). The trend term in Equation 1 can be viewed as an unknown function of time, and parameterized as

$$\nabla^k T(t) \sim N(0, \sigma^2_T). \quad (2)$$

For $k = 1$ and $\sigma^2_T = 0$, Equation 2 reduces to a linear fit; i.e. $T(t) = a + bt$, rather than the discrete equivalent of a k-th order smoothing spline. Figures 2 and 3 show examples of observed time series of wind and SST, respectively, along with their respective trends from the state-space models. The models work much better in accounting for SST variability; the difference between the SST trend and the residual of the observed, less the seasonal and AR series, (equal to the trend plus model error) is negligible. The errors in the wind stress models are higher, presumably because the response time of SST to atmospheric forcing acts to 'smooth' month-to-month variability occurring in wind forcing. These examples also demonstrate that variability in long-term trends is small relative to that in the seasonal cycles of wind stress and SST, pointing to the need for a method that will extract long-term variability for analysis of climate change. Schwing and Mendelssohn (this vol.) and Durand and Mendelssohn (this vol.) discuss in detail the statistical techniques applied here.

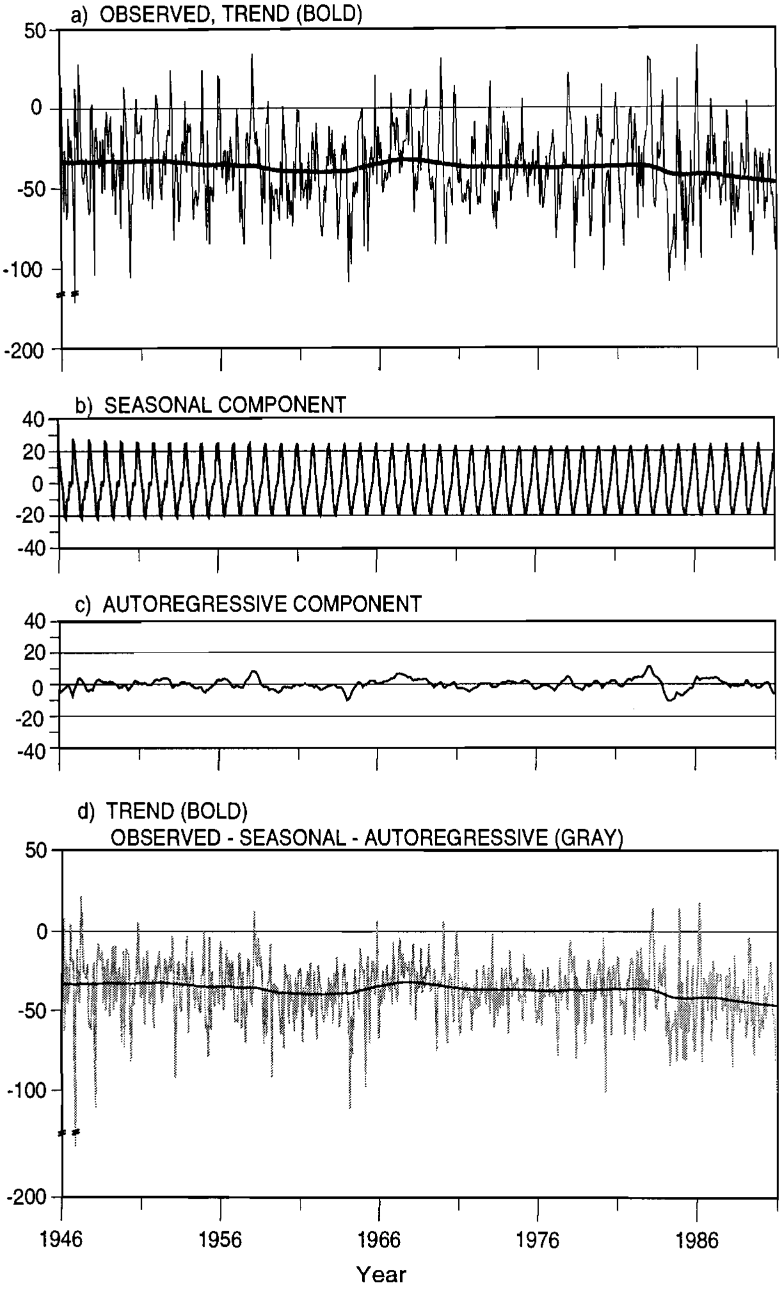

Fig. 2: Comparison of COADS 37°N (36-38°N) poleward wind stress monthly observations to model results, for period 1946-90. a) overlay of trend model component (bold line) and observed monthly series; b) seasonal model component; c) autoregressive (AR) model component; d) overlay of trend model component (bold line) and observed series minus seasonal and AR model components (gray line). The y-axes of panels a) and d) have been condensed to ease presentation of one large negative observation.

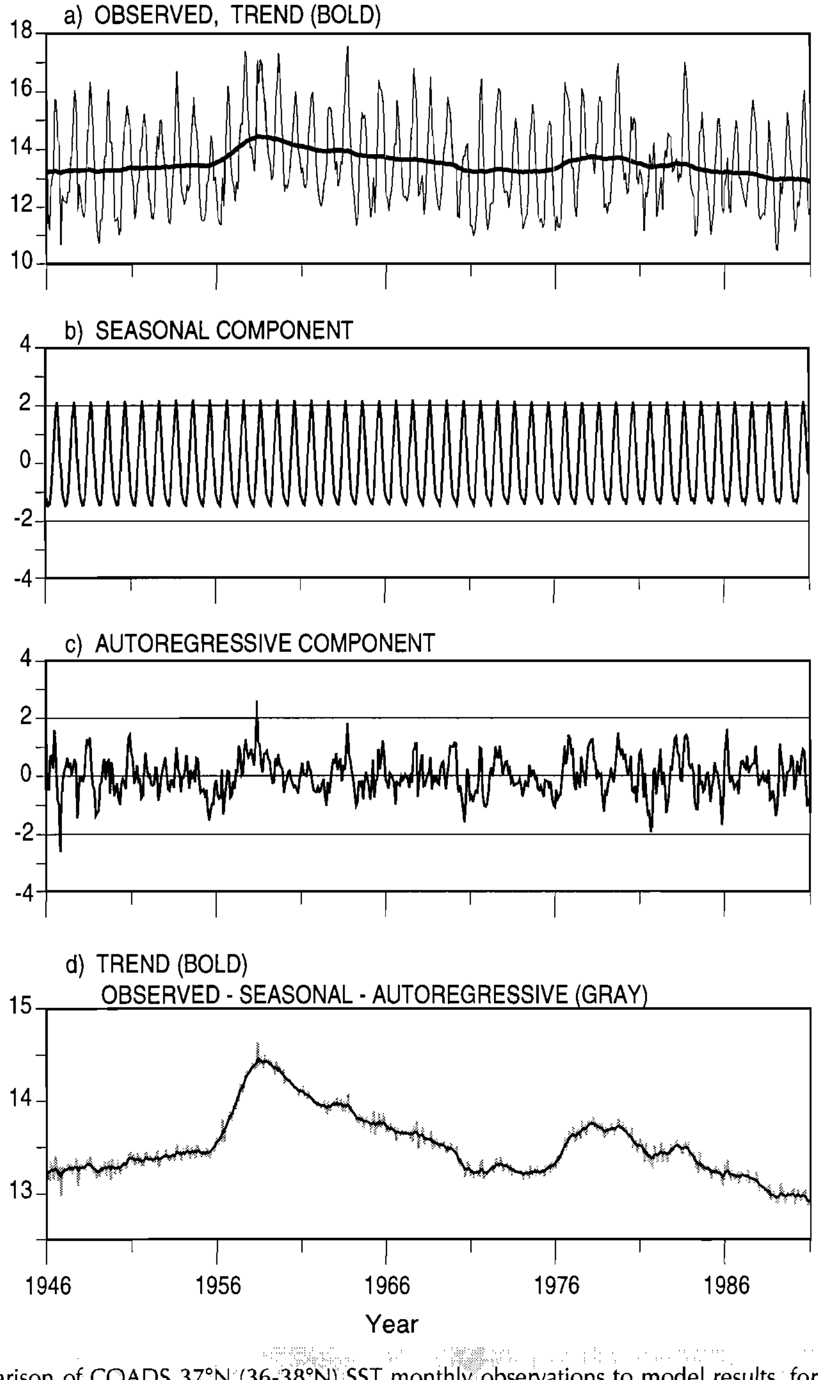

Fig. 3: Comparison of COADS 37°N (36-38°N) SST monthly observations to model results, for period 1946-90. a) overlay of trend model component (bold line) and observed monthly series; b) seasonal model component; c) autoregressive (AR) model component; d) overlay of trend model component (bold line) and observed series minus seasonal and AR model components (gray line). The y-axis of panel D has been expanded for clarity.

2. RESULTS

Time series of poleward wind stress trends for the COADS 2° boxes display the spatial and temporal variability of the CCS wind field (Fig. 4). The wind separates into three distinct geographical regions; 22-32°N (south), 32-40°N (central), and 42-48°N (northern), based on a visual comparison of the time series, and the clustering of statistical correlations between the series (Table 2). Wind stress trends in the southern region (dashed-dotted lines) became increasingly equatorward (negative) over time in a relatively monotonic pattern, as noted by the highly linear fits to the series (Table 3). Stress also strengthened from 22° to 30°, but was weaker in the southern California Bight; local maximum equatorward stress was seen over 26-30°N. The Bight featured weaker stress and more variability on 5-10 year scales, relative to adjacent boxes, and is weakly correlated with the other wind time series in the CCS, particularly those off central California.

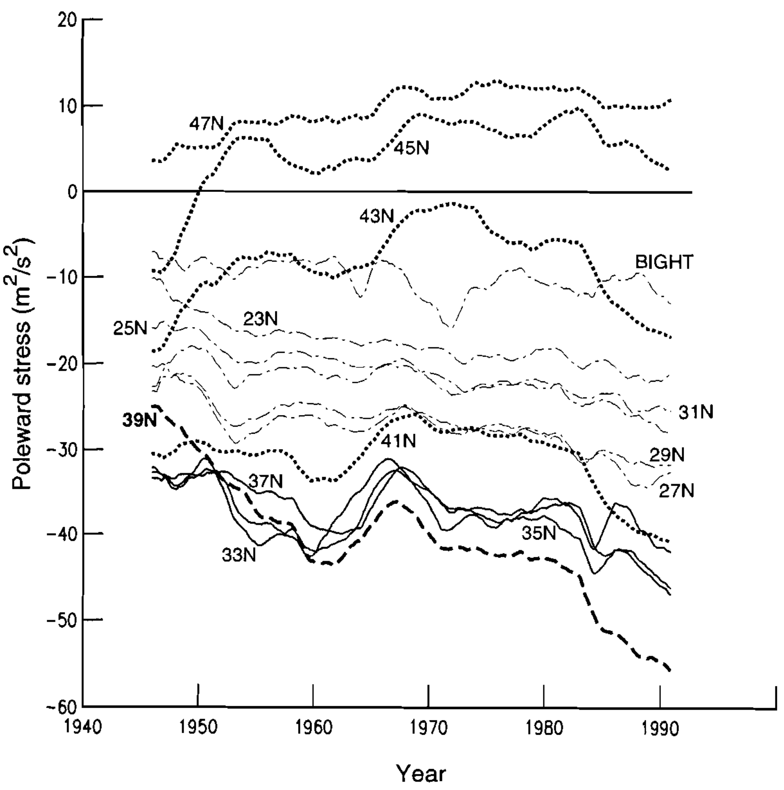

Fig. 4: Time series of poleward wind stress trends for COADS boxes. Dashed-dotted lines represent time series from the southern region (22-32°N). Solid lines represent time series from the central region (32-40°N). Bold dotted lines represent time series from the northern region (40-48°N). Bold dashed line represents the 39°N time series.

	23N	25N	27N	29N	31N	BIGHT	33N	35N	37N	39N	41N	43N	45N	47N
47N	-.80	-.73	-.57	-.59	-.51	-.59	-.34	-.36	-.36	-.62	.05	**.60**	**.84**	
45N	-.71	-.60	-.49	-.61	-.37	-.56	-.29	-.25	-.17	-.53	.13	**.73**		**.94**
43N	-.17	-.01	.17	.01	.16	-.39	.03	.28	.37	.08	.71		**.76**	**.59**
41N	.49	.59	.72	.65	.68	.08	.58	**.83**	**.87**	**.71**		.41	.81	.83
39N	.93	.93	.91	.89	.81	.47	.65	**.86**	**.90**		**.82**	.24	.72	.81
37N	.77	.81	.84	.80	.84	.37	.71	**.93**		**.90**	**.90**	.52	.84	.83
35N	.72	.75	.79	.82	.80	.31	.87		**.84**	**.61**	**.73**	.76	.85	.77
33N	.59	.57	.59	.68	.69	.35		.75	.39	.12	.28	.73	.51	.45
BIGHT	.61	.62	.51	.55	.60		.98	.74	.41	.13	.22	.90	.61	.49
31N	**.80**	**.88**	**.92**	**.88**		**.98**	.89	.78	.43	.11	.28	.90	.63	.50
29N	**.90**	**.91**	**.94**		**.97**	**.95**	.84	.66	.27	-.08	.15	.90	.52	.35
27N	**.90**	**.96**		**.98**	**.96**	**.95**	.79	.67	.33	.00	.19	.95	.59	.41
25N	**.96**		**.96**	**.93**	**.94**	**.93**	.78	.77	.49	.22	.38	.97	.76	.62
23N		**.97**	**.87**	**.83**	**.88**	**.87**	.72	.77	.56	.35	.46	.91	.82	.73

Table 2: Correlation matrix for COADS 2° box trend time series. Upper-left half of matrix shows correlations between poleward wind stress series. Lower-right half shows correlations between SST series. Clusters of correlation values in bold denote subjective groupings of highly coherent series in three geographic regions. Spaces between rows and columns separate regions within CCS, based on subjective examination of time series. The 0.01 level of significance is 0.11 (n=540).

The central region (solid lines) displayed the strongest equatorward stress in the CCS (Fig. 4). Stress trends became increasingly equatorward over time (Table 3), but exhibited much more interannual variation compared to the southern region. The stress series at these latitudes are less correlated with those in the other regions as a result of this interannual variability (Table 2). A period of stronger than normal stress in the 1950s was followed by a period of decreasing equatorward stress in the mid-1960s. The center of this region (39°N, bold dashed line in Fig. 4) featured the greatest change over time (Table 3), shifting from the site of the region's weakest stress in the 1960's to strongest stress in the 1980's. While stress in the Bight appears relatively uncoupled with this region (Fig. 4, Table 2), winds immediately offshore of the Bight (33°N in Fig. 4) are similar to the central region's stress series.

In contrast to wind stress off California and Baja, the region north of 44°N featured a mean poleward stress that strengthened over time (Fig. 4, Table 3). These series are negatively correlated with virtually the rest of the CCS, due to their opposing series-long trend. 40-44°N was a transition area between the central and northern regions; equatorward stress decreased rapidly north of 40°N. In about 1976 the 43°N COADS series shifted from the pattern seen in the northern region to that of the central region. This results in the 43°N winds being poorly correlated with most of the other stress series.

Two temporal phenomena are notable for their absence in the stress trend series. ENSO events (e.g. 1957, 1983) are not apparent in the series. Instead the model allocated their variance into the AR series (Fig. 2c), and model error (difference in gray and black lines in Fig. 2d), presumably because the wind field responds rapidly to a developing and decaying ENSO.

The well-documented regime shift in 1976 (Trenberth, 1990; Ebbesmeyer *et al.*, 1991; Miller *et al.*, 1994, Trenberth and Hurrell, 1994) is not seen in the wind trends either, despite its clear presence in north Pacific atmospheric pressure indices. A likely possibility is that the CCS is out of the region where winds were directly affected by the intensification of the Aleutian Low beginning in 1976. However a substantial increase in equatorward stress did occur in about 1983 in the central region and north to about 44°N. One interpretation of this intensification is that the transition zone between the central and northern regions has broadened south; another is that the area off northern California and Oregon developed its own distinct wind regime after 1983. In either case, the net effect is that the alongshore gradient in poleward stress has strengthened greatly over the last 45 years.

	23N	25N	27N	29N	31N	BIGHT	33N	35N	37N	39N	41N	43N	45N	47N
Stress:SST	-.26	-.41	-.61	-.60	-.34	.07	-.03	-.23	.16	.41	.37	-.04	.16	-.21
Stress:Time	-.92	-.95	-.89	-.80	-.80	-.55	-.33	-.63	-.73	-.89	-.41	.10	.61	.77
slope	-17.7	-21.7	-21.3	-16.5	-10.7	-7.9	-7.9	-17.0	-19.3	-48.3	-11.9	3.3	19.4	14.7
SST:Time	.23	.43	.63	.66	.49	.48	.34	.09	-.33	-.63	-.38	.48	-.13	-.37
slope	3.4	8.9	16.8	16.4	12.6	11.2	8.3	1.5	-8.7	-22.9	-12.6	9.5	-2.3	-7.8

Table 3: Correlation matrix for COADS 2° box trend time series. First line shows correlations between stress and SST series, for each COADS box. Second and third lines show correlation between COADS stress and time, and slope of linear fit between stress and time (linear rate of change, 10^{-2} m^2/s^2/year), respectively. Positive (negative) sign denotes linear trend for increasing poleward (equatorward) stress. Fourth and fifth lines show correlation between SST and time, and slope of linear fit between SST and time (linear rate of change, 10^{-3} °C/year), respectively. Positive (negative) sign denotes warming (cooling) trend. Spaces between columns separate three geographic regions within CCS, based on subjective examination of time series. The 0.01 level of significance is 0.11 (n=540).

Contours of COADS poleward wind stress trend anomalies, relative to the long-term mean at each latitude, reveal additional temporal and spatial patterns in the wind field (Fig. 5). For reference, the zero contour of the stress trends (dashed line) is included. Prior to the mid-1950s, stress anomalies were negative (more equatorward) north of 40°N and positive (less equatorward) south of 40°N. A particularly strong spatial contrast occurs in the 38-44°N region at the beginning of the series. A period of negative stress anomalies north of 30°N began near the onset of the 1957 ENSO and continued into the early 1960s, contrasting with a contemporaneous period of weak positive anomalies south of 30°N. Stress was anomalously strong throughout the entire CCS from about 1964 to 1970. Since 1970, anomalies have become increasingly negative (more equatorward) south of 40°N, and negative at higher latitudes since about 1983.

The COADS SST trends separate visually (Fig. 6) and statistically (Tables 2 and 3) into essentially the same geographic regions as wind stress. For example, the relatively poor correlation of SST series off northern California with those in the south (Table 2) imply a different pattern of interannual ocean variability in the central CCS. However SST is more correlated in space than wind stress on interannual (1-5 year) scales (Fig. 6). SST decreased consistently with latitude from about 22°N to 40°N (fine lines), coincident with a region of equatorward wind stress. SST north of 40°N (bold lines) was nearly uniform with latitude, an area where stress was either generally poleward or becoming less equatorward over time. While ENSO wind events are relatively ephemeral, and thus are relegated to the model AR term, warmer conditions associated with ENSOs are obvious in the SST trend series, and appear to gradually dissipate long after the ENSO atmospheric signal (compare also Fig. 2 and 3). However some ENSO signals appear in the SST AR component as well (Fig. 3c). Interannual variations in the series (e.g. the 1957 ENSO event) are greatest off central and southern California (Fig. 6). In contrast to the 1957 event, the 1982 ENSO is reflected in SST as a smaller local maximum relative to adjacent years.

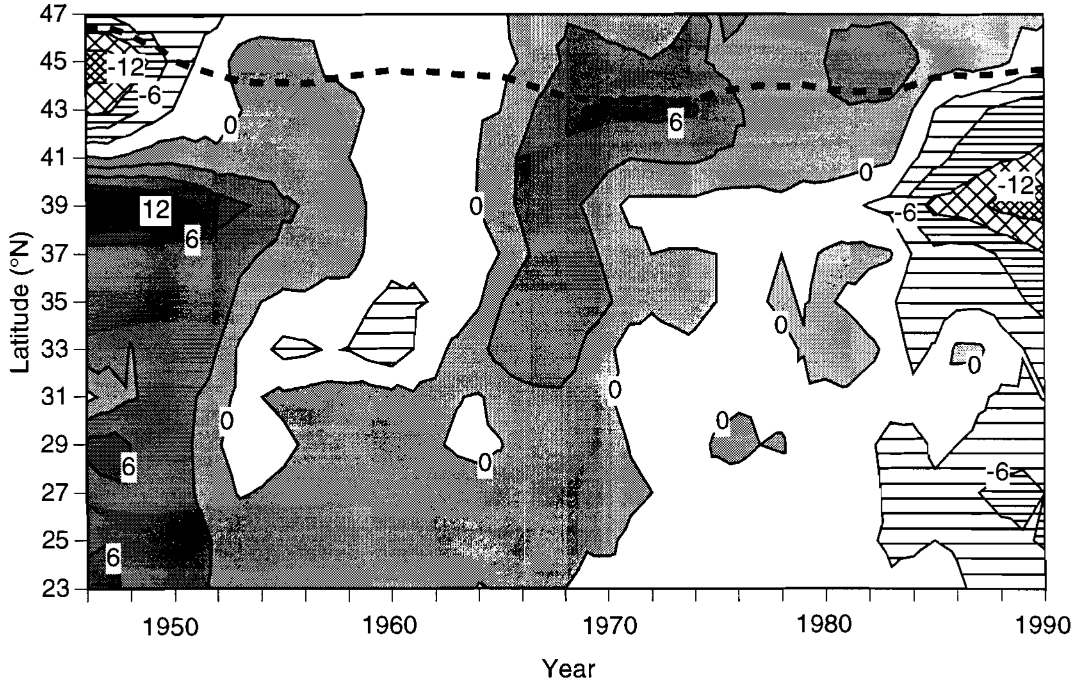

Fig. 5: Contours of poleward wind stress trend anomaly series for COADS boxes. Anomalies are with respect to series means for each 2° box. Shading denotes positive anomalies; hatching denotes negative anomalies. Contour interval is 3 m^2/s^2. Broken line denotes location of zero wind stress.

The obvious warming beginning in 1976, a climate shift not reflected in stress, suggests that decadal-scale SST variability in the CCS is controlled by the large-scale pressure and wind fields, rather than local wind forcing. The shift in 1976 rivals the degree of warming associated with the 1957 ENSO. Since the mid-1980s, SST south of 32°N increased slightly, but cooled substantially north of 34°N. The series-length linear tendencies (linear regressions of time series, Table 3) are significantly positive (increasing SST) south of 34°N and in the 43°N box, but significantly negative north of 36°N (save 43°N). The alongshore SST gradient off southern California strengthened over time (Fig. 6). Simultaneously the SST gradient along northern California decreased. SST at 39°N (fine broken line) decreased gradually over time, cooling to values seen at higher latitudes. At the same time, 43°N SST (bold broken line) warmed relative to nearby boxes. The convergence of SST in the 38-42°N region coincides geographically with the strong temporal intensification in stress at these latitudes (Fig. 4 and 5).

Contours of SST trend anomaly series for the COADS 2° boxes (Fig. 7) reinforce the idea that decadal-scale variability in SST is generally coherent throughout the CCS. Anomalously cool periods prior to 1956 and during 1968-1977 contrast with warm events during 1956-1968 (following the 1957 ENSO) and since 1977 (following the 1976 regime shift). These warm and cool periods are not coherent with any periods of anomalous wind stress (Fig. 5). Years featuring ENSO events were characterized by rapid warming. Warm conditions remained several years after the 1957 event. However the warming and cooling associated with the 1983 ENSO was more symmetric. Since about 1985, conditions have remained warm south of 34°N, but have been cooler in the north. The strong series-long cooling trend at 39°N (Table 3) can be seen in the anomalies (particularly when contrasted with regions to the south), which corresponds to strengthening equatorward stress

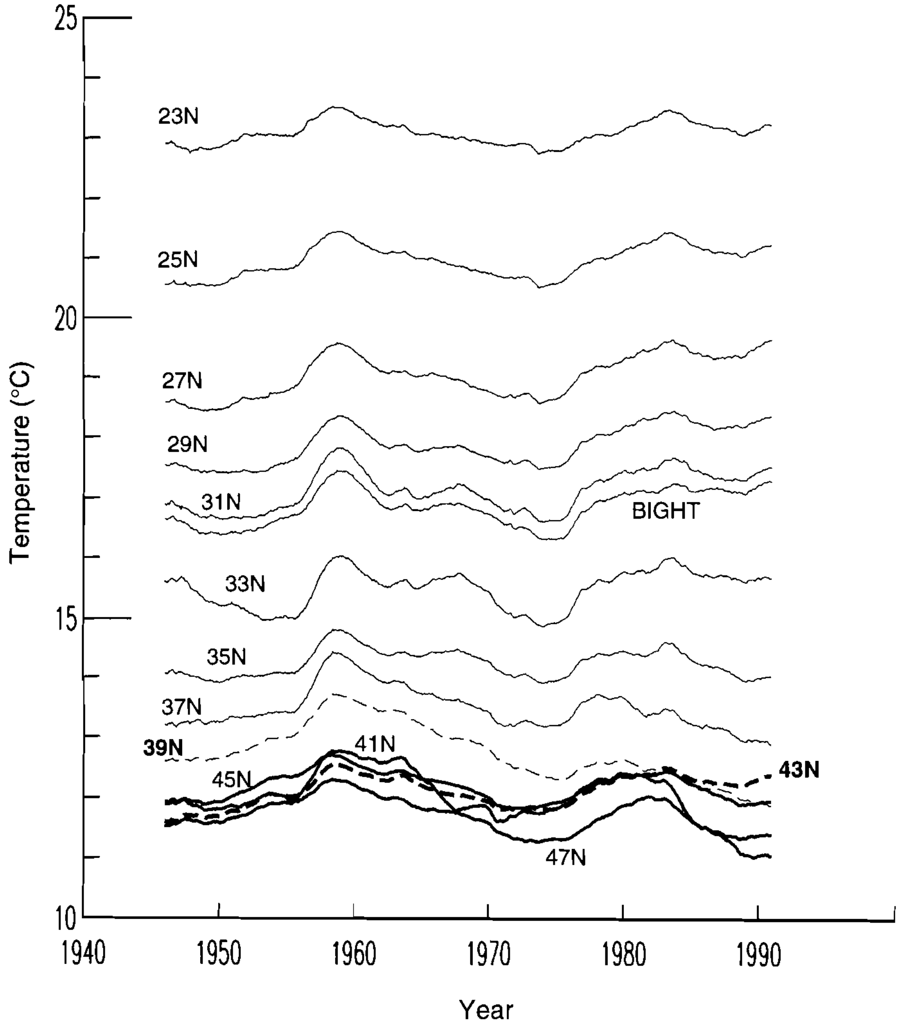

Fig. 6: Time series of SST trends for COADS boxes. Fine lines denote time series south of 40°N. Bold lines denote time series north of 40°N. Fine and bold broken lines denote time series for 39°N and 43°N COADS boxes, respectively.

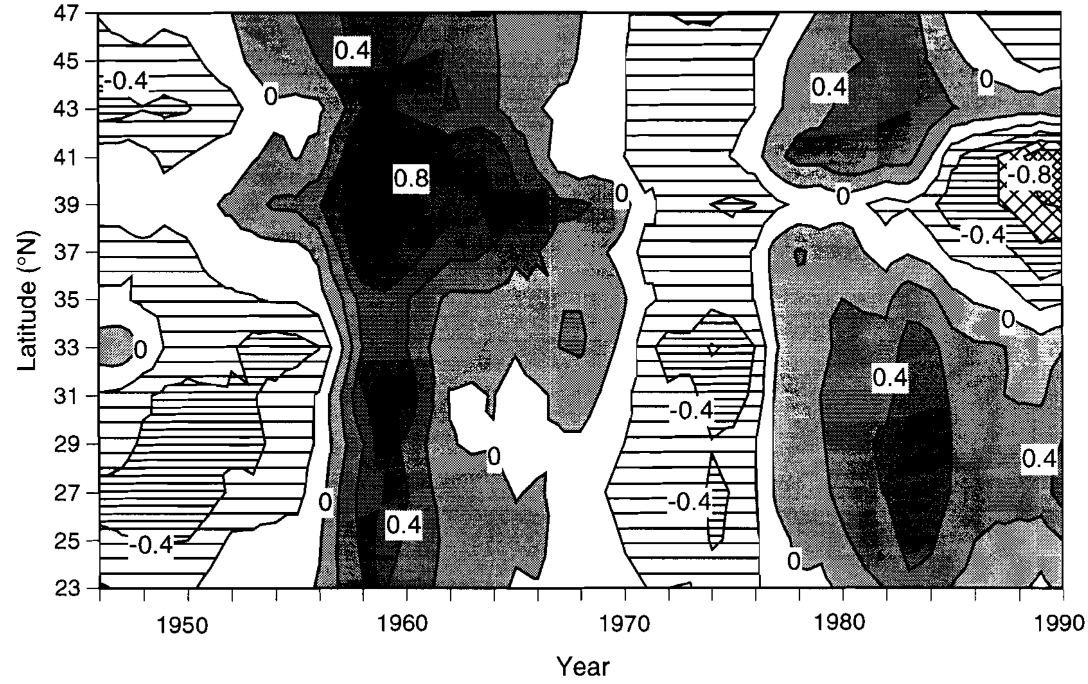

Fig. 7: Contours of SST trend anomaly series for COADS boxes (°C). Anomalies are with respect to series means for each 2° box. Shading denotes positive anomalies; hatching denotes negative anomalies. Contour interval is 0.2°C.

(Fig. 4 and 5). As mentioned earlier, however, the SST (Fig. 7) and wind stress (Fig. 5) anomalies do not agree otherwise, suggesting that local winds are not the primary factor controlling decadal-scale temperature variations in the CCS.

Shore-based SST trend time series along the western North American coast (Fig. 8), derived with the state-space model, provide an independent assessment of SST variability, extended in space and time. These series also allow a finer (along- and across-shore) spatial scale look at temporal variability. As with the COADS SSTs (Fig. 6 and 7), the shore series demonstrate well-defined latitudinal regimes in ocean temperature on decadal scales. ENSO events (Quinn *et al.*, 1987) are shown by the shaded vertical lines in Fig. 8; their large-scale warming influence is seen. Coastal warming associated with ENSOs was greatest along central California. The SST signal of some ENSO events (e.g., 1972-1973) appears to be weak and constrained to southern stations.

The shore series (Fig. 8) show that many of the temporal features of CCS SST extend north into the Gulf of Alaska and well offshore (Ocean Stations P and N). However there also are obvious regional differences between the CCS and coastal locations off British Columbia and Alaska, particularly during ENSO events and on decadal scales. Numerous other regional differences in the trends are evident. Most coastal sites feature series-long warming trends that are highly non-linear and display considerable variability on annual-to-decadal scales. Most series have 10-20 year periods of relatively level temperature, followed by similar periods of rapid temperature increase. Some series have multi-year periods of decreasing temperature. Higher latitude sites have a well-defined cycle of about 20 years, which Royer (1993) attributes to the 18.6-year tide.

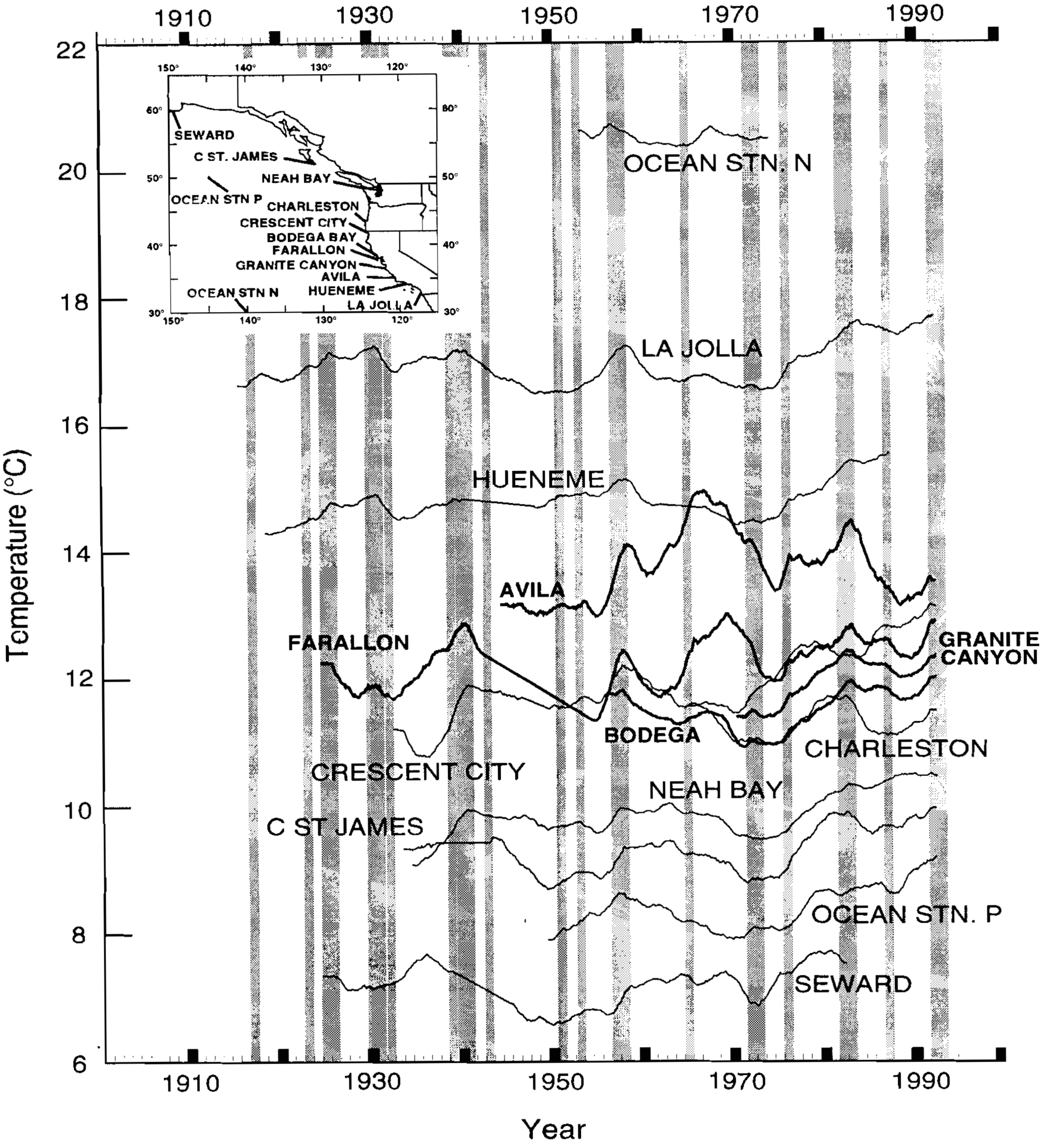

Fig. 8: Trend time series of SST (°C) from several coastal sites along North American west coast (locations shown on map in inset). Time series for Ocean Stations P and N also shown. Bold lines denote time series from central California locations. Shaded vertical bars denote ENSO periods, based on Quinn *et al.* (1987).

The shifts to a cool regime in 1941 and to a warm regime in 1976 (MacCall and Prager, 1988) are evident in the shore series as well. The 1976 shift occurred rapidly along southern California. However it was less dramatic and occurred over several years at more northern sites, thus appearing more as a gradual warming. The 1941 transition is more difficult to document, but appears less dramatic relative to the 1976 shift. The regime shift concept may be valid for some regions (e.g., southern California), but displays a considerable degree of inter-regional difference.

In addition to alongshore differences in CCS SST, a comparison of selected COADS SST and nearby coastal SST trend time series (Fig. 9) suggests there also are significant differences between nearshore and offshore temperature trends. SST in the Southern California Bight agrees well with shore-based SST at La Jolla. Further north, however, offshore and shore SST series at corresponding latitudes are poorly correlated. Although the COADS SST trends cooled over time north of about 36°N, the coastal SST trend series warmed over time along the entire U.S. west coast. Shore series accentuate interannual-to-decadal changes as well. Like the COADS SSTs, shore SST trend series are poorly correlated with COADS poleward wind stress.

A particularly interesting feature is the close positive correlation between Crescent City and adjacent COADS SST from about 1970-1983, followed by an apparent inverse relationship since. The adjacent wind stress also appears to be negatively correlated with shore SST, and positively correlated with COADS SST, since 1983. Another intriguing relationship is the close correspondence between an approximately five-year period of weakening equatorward stress and warming shore SST in the late 1960s, centered along central California (e.g., Farallon, Avila). This was followed by a similar length period when wind stress and SST returned to values seen in the early 1960s. This warming/cooling event is not reflected in the adjacent COADS boxes. Both of these events attest to the considerable decadal-scale variability inherent in the CCS, which is not always associated with ENSO events, and merit a closer analysis. The results also suggest the CCS may experience a substantial degree of cross-shelf variability as well.

Although the COADS observations do not have sufficient wide-spread density of coverage to produce monthly time series at 2° resolution for the greater northeast Pacific, or to resolve the spatial variability of the CCS on finer scales, we can examine spatial differences in the area's SST and wind fields at a 1° resolution by averaging the observations for two separate decades (1966-1975 and 1977-1986) to contrast conditions prior to and after the 1976 climate shift. Differences in SST between these periods (Fig. 10) corroborates the monthly time series' patterns. SST in recent years south of Oregon has been warmer (gray shades) in, and well offshore of, the CCS. The region north of California also appears to have been warmer at the coast and to about 150 km offshore after 1976. However SST in 1977-1986 in an offshore area off Oregon and Washington was cooler (hatched areas) relative to the earlier period. A closer analysis of these differences by season (not shown) suggests the cool anomaly in the northern CCS is connected to a much larger cool anomaly that covers much of the central North Pacific. Furthermore the eastern edge of this large cool anomaly moves eastward from February to September. Negative SST anomalies nearly reach the coast of Oregon and Washington by summer.

Like the relationship between the wind and SST time series, however, the distribution of SST anomalies over the northeast Pacific since 1976 is not coherent with changes in local wind stress or mixing. For example, most of the CCS south of 40°N, which was warmer in 1977-1986 relative to 1966-1975, featured greater equatorward stress and turbulent wind mixing during the latter period, which should lead to cooler SST. Thus it does not appear that interannual to decadal changes in SST, and more generally upper ocean conditions, are dominated by climate shifts in local wind forcing. We conclude that a complex interaction of local and remote Ekman advection, wind mixing and direct heating is responsible for the long-term fluctuations in SST in the CCS and northeast Pacific. Regional-scale differences in the relative importance of the mechanisms responsible for decadal-scale climate change in the northeastern Pacific is subject of ongoing research.

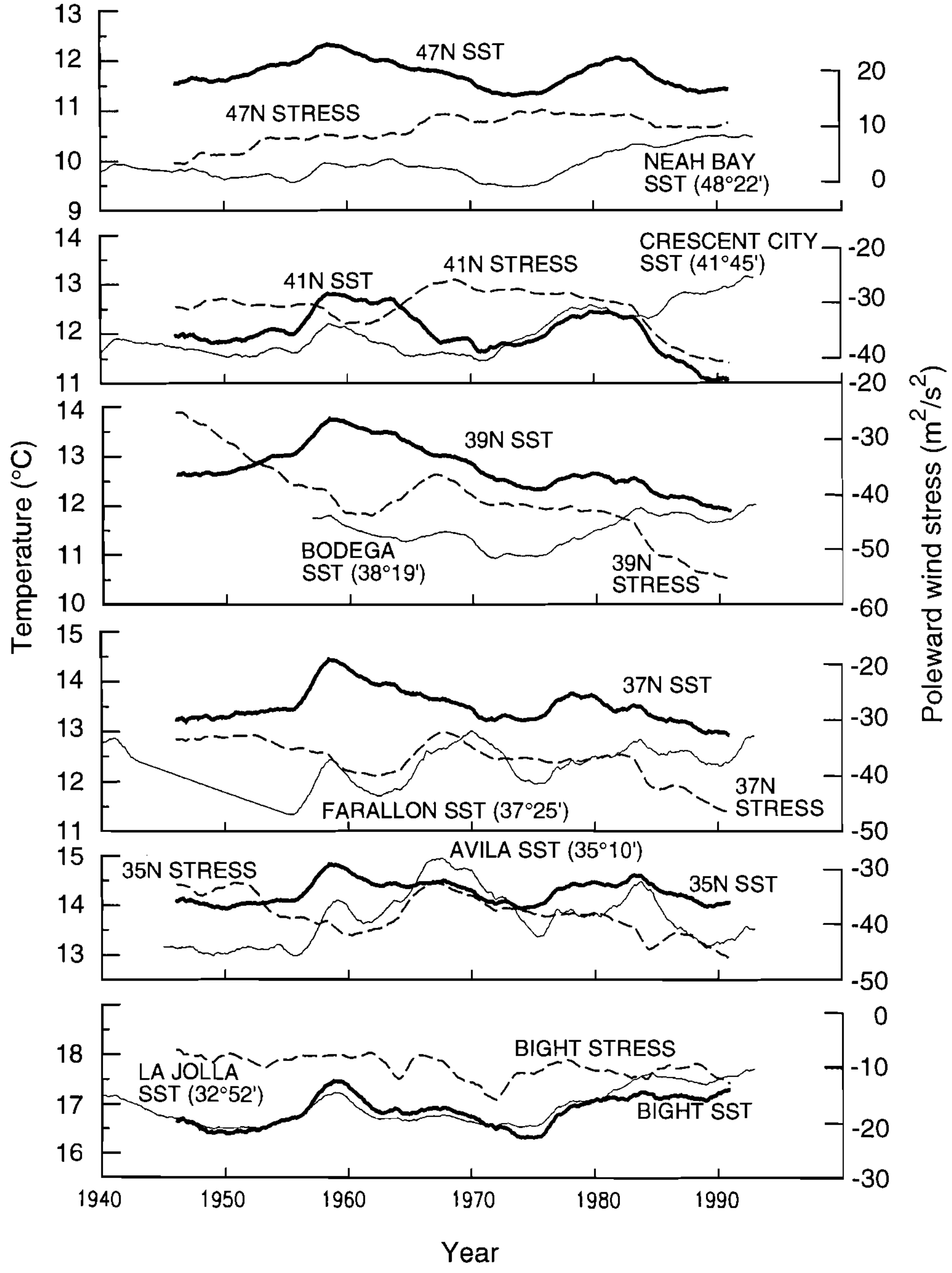

Fig. 9: Trend time series of COADS SST and poleward wind stress, compared with selected nearby coastal SST series. Bold solid lines represent COADS SST series. Fine solid lines represent coastal SST series. Broken lines represent wind stress series. Location of the time series are shown in each plot.

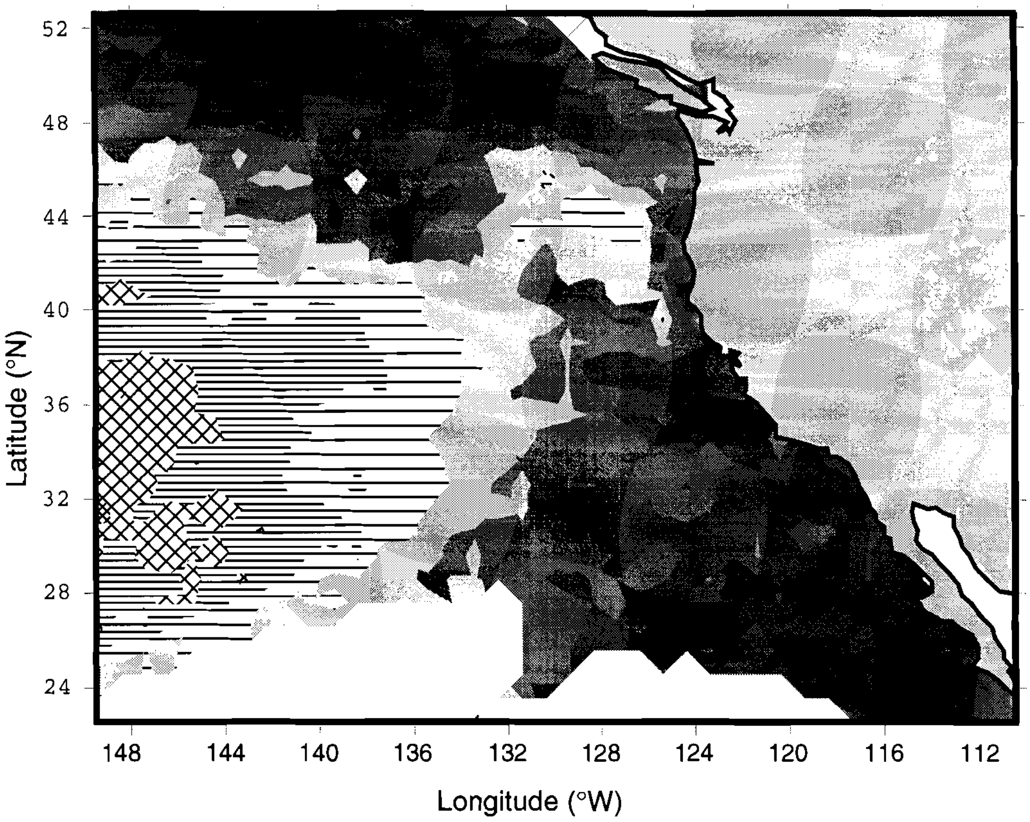

Fig. 10: Difference map of SST for northeast Pacific comparing annual means in 1° by 1° boxes from two ten-year periods (1977-1986 less 1966-1975). Positive values (shaded areas) denote relatively warmer SST in 1977-1986; negative values (hatched areas) denote relatively cooler SST in 1977-1986. Contour interval is 0.25°C. Range of contours is -0.75 to +1.25°C.

3. DISCUSSION

The different regions of the CCS and the likely relationships between wind forcing and SST on long time scales are illustrated in Figure 11. The Figure shows the slope (+/- 99% confidence intervals) of a linear fit to poleward stress and SST trend time series in each COADS box; i.e., the linear tendency of each series (Table 3). A statistically significant tendency of increasing equatorward stress coincides with a cooling trend in much of the central region (34-42°N). A reasonable explanation for this pattern is that increasing stress leads to greater offshore Ekman transport and more coastal upwelling, which cools the surface waters of this portion of the California Current. This region coincides with the geographic range of the upwelling maxima along the west coast (Parrish *et al.*, 1981). However shore-based SSTs feature a long-term warming tendency, countering the argument for greater coastal upwelling. A more likely explanation is that SST in the CCS is responding to large-scale atmospheric forcing that is changing in a way that leads to cooler surface conditions in the CCS at these latitudes. It is also possible that an increase in the positive wind curl occurring off northern California (Bakun and Nelson, 1991) could have accompanied the greater equatorward stress, and led to cooler SST through intensified Ekman pumping. Increased equatorward stress also would contribute to cooler SST through greater turbulent mixing of the upper ocean, and may be associated with increased southward transport of cool water by the California Current.

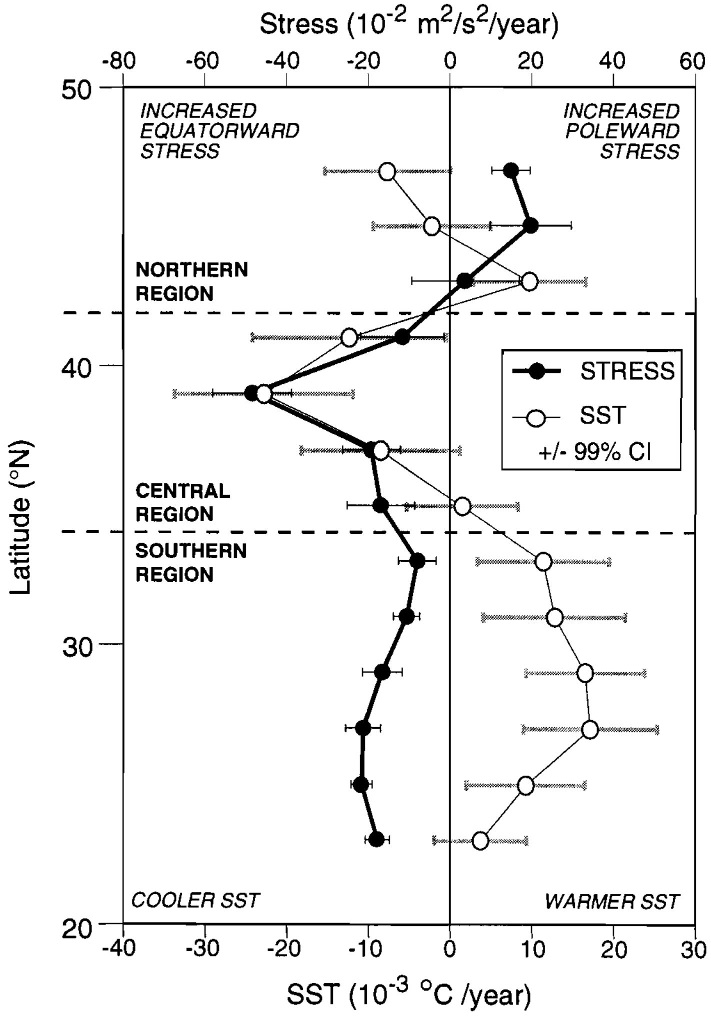

Fig. 11: Slopes of a linear fit to COADS poleward stress (solid circles) and SST (open circles) time series. 99% confidence intervals shown by horizontal bars (gray for stress, black for SST). Dashed lines denote boundaries of three geographic regions within CCS.

Outside of the central region the trends in stress and SST are negatively correlated. Increasing equatorward stress coincides with warming SST south of 34°N, while greater poleward stress accompanies a cooling trend north of 44°N. The cooler SSTs off Oregon and Washington may be due to greater wind mixing. Greater poleward stress could be linked to a larger (gyre) scale pattern in atmospheric circulation, such as the documented intensification of the Aleutian Low, which could lead to fundamental changes in the region's ocean circulation. However, a more rapid cyclonic transport of the Subarctic Current, typically associated with a deeper low, should increase SST. An examination of long-term changes in Ekman divergence due to variability in the wind field is beyond the scope of this study, but this could impact SST as well. We suspect that the transitional region between the Subarctic and California Currents could be extending southward, based on the expanding region of spatially uniform SST (Fig. 6). This would be consistent with cooler SSTs. We also believe, based on preliminary analysis of data from the entire north Pacific, that major shifts in the magnitude, position, and composition of the West Wind Drift feeding into these boundary currents may have changed over time. This is currently an active area of investigation.

The relationship between wind stress and SST in the southern region (22-34°N) is more difficult to explain. It is difficult to arrive at a scenario that is consistent with a long-term tendency for greater equatorward stress and warmer SST. Roemmich and McGowan (1995) present results for southern California consistent with those here, and speculate that increasing stratification over the last 45 years (due to an increasing heat flux from the atmosphere into the upper ocean) has more than compensated for greater wind stress, leading to shallower upwelling and a less effective 'cooling' from upwelling-favorable stress. Extending this idea to the regions farther north implies a different dynamical balance, such that the SST signal associated with greater stratification, a consequence of atmospheric warming, is overwhelmed by the role of changing wind patterns in driving more cool water into the surface layer of the CCS, through a combination of lateral advection from the central north Pacific, and upward movement by greater upwelling and vertical mixing.

In any case, it is apparent that over the last several decades surface waters in the CCS south of 34°N have experienced a different set of forcing conditions from those farther north. Not only are the tendencies of wind and SST different in these regions of the CCS (Fig. 11), but the spatially changing relationship between stress and SST implies that the primary mechanisms driving variability in SST, and probably the general circulation, on decadal time scales are fundamentally different in these various regions. It is not possible to develop a more firm conclusion about the mechanisms leading to these tendencies without a more thorough analysis of the temporal variability of wind vector fields over the north Pacific Ocean. However it is important to recognize that, over the last 50 years, wind and SST over the extent of the CCS has not fluctuated in a uniform manner (Tables 2 and 3). Thus using a single time series to represent climate variability in this ecosystem will give an incomplete, if not inaccurate, view of decadal changes in the CCS.

3.1. Ecological impacts of environmental variability

The temporal and spatial variability of the physical environment of the CCS described here must be considered when analyzing changes in the biological structure of this and other EBC ecosystems. Parrish *et al.* (1981) concluded that the larval assemblages and reproductive strategies of coastal fish species can be divided into regions that approximate the three areas defined from the long-term wind and SST patterns described here. Roemmich and McGowan (1995) have found that zooplankton biomass off southern California has decreased by 80% since 1951, while the surface layer has warmed by more than 1.5°C over the same time. They suggest this is due to an increase in stratification of the surface layer, which has led to a shallower, hence lower nutrient, source of upwelling. However their observations are restricted to south of 34°N. The results reported here show that regional differences in environmental variability have existed in the CCS over the last five decades, therefore it is conceivable that analogous differences in biological productivity have occurred as well. Specifically Roemmich and McGowan (1995) note a correlation between declining zooplankton biomass and increasing near-surface temperature and stratification. If this model is correct, then could biomass be increasing in the northern portions of the CCS in association with the cooling tendencies of the COADS SST series? This cannot be immediately concluded, since SST variability may be linked with other variations (e.g., mixed layer depth) that influence production more directly.

It has been shown here that decadal-scale climate variability has considerable regional differences as well. Considerable evidence suggests that environmental conditions in the northeast Pacific in recent years can be described in terms of two climate phases, separated by a transition occurring in about 1976. From the early 1940s to about 1976, the eastern north Pacific was under the influence of increased equatorward stress (associated with a weaker than normal Aleutian Low in winter and a southward flowing jet stream), resulting in a cool pool of water along the entire North American west coast, and a warm pool in the central north Pacific. Beginning in 1976, the Aleutian Low deepened and shifted eastward each winter, which altered large-scale wind patterns, storm tracks and ocean currents. The resulting ocean thermal structure featured a warm water mass off central and southern California, but cooler water in the northern portion of the CCS and over much of the north subtropical Pacific (Fig. 10).

Anchovies were the dominant small pelagic in the CCS prior to 1976 (MacCall, 1986); however sardines have shown evidence of increasing biomass since (Barnes *et al.*, 1992). The decadal-scale fluctuations of the two dominant pelagic fishes appear to be associated with the larger scale variations in the CCS. From the mid-1920s to the early 1940s sardines dominated the entire CCS. This population collapsed during the 1950s and did not show any evidence of recovery until after the environmental shift in 1976; since then the population has shown a very large increase in its rate of growth (MacCall, 1979; Barnes *et al.*, 1992). Anchovies were not abundant in the southern region during the 1950s, but the population increased during the 1960s and reached a short term peak in the early 1970s. The California anchovy fishery peaked in 1975 and then declined sharply; whereas the Mexican anchovy fishery expanded after the mid-1970s peak in population, reached a maximum in 1981 and then totally collapsed in 1990 (Ainley *et al.*, 1993). These regional differences may be linked to spatial differences in the rate and magnitude of environmental changes. Based on the fishery information available since the 1920s, it appears that the CCS sardine stock rises during warm water periods and the southern region's anchovy stock rises during cold water periods. Conditions prior to the early 1940s, when sardines dominated the CCS, were similar to those since 1976. Baumgartner *et al.* (1992) analyzed anaerobic sediments off southern California and concluded that alternating dominance between sardines and anchovies has occurred back to at least 300 AD.

Although they are similar in many other respects, it appears that the anchovy and sardine utilize the CCS in quite different ways. Sardines, which are larger and more mobile than anchovies, migrate from the southern region into the central and northern regions for feeding and then return to the southern region to spawn. Anchovies, although they occur over the entire CCS, appear to be much more localized in their movements. They have separate genetic stocks in the northern and southern regions and, within the historical record, have not been very abundant in the central region. Thus it appears that anchovy populations may rise and fall based on differences in the environmental conditions in the three CCS regions; whereas the single sardine population may be affected by environmental conditions in any or all of the three CCS regions.

On shorter time scales, studies in the CCS demonstrate that biological production decreases dramatically during ENSO events (McGowan, 1985). ENSOs also are responsible for poor salmon survival off the northwest U.S. (Pearcy *et al.*, 1985), reduced recruitment, growth and condition of groundfish (Lenarz *et al.*, 1995), and dramatic range extensions for fish

(Radovich, 1961). While ENSOs have a large-scale influence, it is shown here that their relative environmental signal is highly variable over the length of the CCS ecosystem. In addition, individual ENSOs appear to have unique characteristics of timing, intensity and extent, superimposed on their canonical signal (1957, 1983). The corresponding biological effects presumably vary as well.

It is important to note that we observed substantial anomalies in the CCS that are unrelated to these well-defined climate events (e.g., 1965-1975, Fig. 9). Nevertheless, these periods of unusual environmental conditions are likely to have significant consequences for the ecosystem. 'Warm' years, when conditions off California are similar to those during ENSO events despite the absence of an equatorial ENSO signal, are linked to poor recruitment of central California rockfish, while 'cool' years feature enhanced recruitment (S.V. Ralston, Tiburon, NMFS, pers. comm.). Extreme year classes of several species of fish over large geographical areas tend to occur in association with unusual environmental conditions (Hollowed and Wooster, 1992).

The results presented here clearly demonstrate the highly variable nature of the CCS environment in time and space, and argue against oversimplifying EBC climate change as a constant linear trend, or in terms of the climate record from a single location. The distinct latitudinal regionalization and cross-shelf variability of the CCS wind and SST fields has key implications for fisheries. For example, which time series or regions are more important in terms of defining a stock's environment? Regional differences also mean that widespread stocks, or stocks that are highly migratory over their life history, face a spatially heterogeneous changing climate. Widespread stocks also may display a very different long-term variability from species whose domain is limited to the homogeneous regions of the CCS described here. Fisheries scientists must evaluate the relative environmental differences in each region, as they pertain to the climate signal and its variability, and compare them to a species' distribution and behavior as a function of life stage, to fully understand the consequences of climate change on populations.

CONCLUSION

State-space statistical models are applied to long environmental time series of monthly COADS northward wind stress and sea surface temperature (SST) from the California Current System (CCS) off the west coast of North America (22-48°N) for the period 1946-1990. The models estimate a non-parametric and non-linear trend, a non-stationary and non-deterministic seasonal signal, and an autoregressive (AR) term. The models are applied to long time series of SST from selected coastal sites as well, for comparison to the COADS series.

Based on a visual and statistical comparison of the model trend series, the CCS can be divided into three distinct geographical regions, which roughly correspond to the biological regions defined by Parrish *et al.* (1981) from mean meteorological and oceanic relationships and coastal fish reproduction patterns. The northern region (42-48°N) features a strong transition from strongly equatorward to poleward with distance north (compare 41°N, 43°N and 45°N stress time series in Fig. 4). The mean stress north of 44°N is poleward and has become increasingly poleward over time (Table 3). The transition zone in wind stress has expanded southward over time, strengthening the zonal gradient in poleward stress. The CCS north of 40°N features spatially uniform mean SST (Fig. 6), and SST trends show a series-length cooling tendency (Table 3). This region of uniform SST has expanded southward over time as well.

Winds trend series south of 40°N are equatorward and can be described in terms of a central and southern region (Fig. 4, Table 2). The central region (34-42°N) exhibits the strongest wind stress in the CCS. Equatorward stress has intensified over time more than in the northern and southern regions. This region features the greatest interannual to decadal variation as well. Like wind stress, interannual to decadal variability in SST is greatest in the central region (Fig. 6). Stress in the southern region (22-34°N) has become increasingly equatorward over time in a relatively monotonic pattern. Mean SST decreases consistently with increasing latitude in the central and southern regions. SST over about 30-38°N appears to warm rapidly in response to the 1957 and 1983 ENSO events as well as the 1976 regime shift. SSTs off Washington, Oregon and most of Baja California, on the other hand, take several months to years to warm by similar amounts.

While SST trends at all coastal sites display a significant warming tendency for the past several decades (Fig. 8), COADS (i.e., offshore) SST has warmed south of 36°N, but cooled north of 36°N (Fig. 6, Table 3). On shorter time scales, SST has decreased significantly since the 1983 ENSO north of about 34°N, but SST south of about 32°N has returned to near-1983 levels, after initially declining following this event. Prior to 1983, SST in the CCS warmed and cooled system-wide on decadal time scales, but has displayed a more incoherent pattern since 1983 (Fig. 7). A lack of correspondence between the COADS and coastal SST time series (Fig. 9) suggests there is considerable cross-shelf as well as latitudinal variability in the CCS. This is confirmed by the comparison of the 1° COADS SST data from two decades (Fig. 10).

SST trends are visually and statistically more correlated on interannual scales than are wind stress trends. Major ENSOs (i e., 1957, 1983) and a well-documented regime shift in about 1976 dominate the SST trend series, particularly south of 38°N, but are not apparent in the wind trends. Instead ENSO wind variance is seen more clearly in the model AR and error series (Fig. 2), presumably because of the rapid atmospheric response to ENSO events. SST also shows decadal-scale periods of warm and cool anomalies that extend through the entire CCS. Wind stress anomalies are less extensive latitudinally and generally uncorrelated with SST (Table 3), suggesting that decadal-scale SST variability in the CCS is controlled by fluctuations in the basin- to global-scale pressure and wind fields, rather than local wind forcing.

In closing, we cannot consider the long-term trends described here without considering changes in the seasonal patterns at a location. Durand and Mendelssohn (this vol.) provide a discussion of how climate change can be interpreted in a number of ways. Schwing and Mendelssohn (this vol.) highlight an example of how seasonal changes over long time scales can have a clear signal that is independent of patterns in the long-term trends. The state-space model is a powerful tool for separating interannual-to-interdecadal fluctuations in environmental time series from seasonal patterns of variability. The results presented here demonstrate the importance of evaluating temporal and spatial variations over the entire spectrum, rather than simply at global climate scales, when examining long-term environmental fluctuations. This will improve our understanding of the linkages between shifts in atmospheric forcing and the coastal ocean's response on regional scales, and ultimately an improved assessment of the impact of climate change on living marine resources.

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REFERENCES CITED

Ainley D., B. DeLong, S. Herrick, L. Jacobson, E. Konno, J. Lanfersieck, M. Lowry, R. Parrish, C. Thomson, and P. Wolf. 1993. *Draft fishery description for the Pacific Coastal Pelagic Species Fishery Management Plan.* NMFS, SWFSC, Admin. Rep., LJ-93,15.

Bakun A. and C.S. Nelson. 1991. The seasonal cycle of wind-stress curl in subtropical eastern boundary current regions. *J. Phys. Oceanogr.*, 21: 1815-1834.

Barnes J.T., L.D. Jacobson, A.D. MacCall and P. Wolf. 1992. Recent population trends and abundance estimates for sardine (*Sardinops sagax*). California. *Calif. Coop. Oceanic Fish. Invest. Rep.*, 33: 60-75.

Baumgartner T.R., A. Soutar and V. Ferreira-Bartrina. 1992. Reconstruction of the history of Pacific sardine and northern anchovy populations over the past two millennia from sediments of the Santa Barbara Basin. California. *Calif. Coop. Oceanic Fish. Invest. Rep.*, 33: 24-40.

Cardone V.J., J.G. Greenwood and M. Cane. 1990. On trends in the historical marine wind data. *J. Climate*, 3: 113-127.

Ebbesmeyer C.C., D.R. Cayan, D.R. McLain, F.H. Nichols, D.H. Peterson and K.T. Redmond. 1991. 1976 step in the Pacific climate: Forty environmental changes between 1968-1975 and 1977-1984. *In*: J. Betancourt and V.L. Sharp (eds.). *Proc. 7th Ann. Pacific Climate Workshop, Calif. Dept. of Water Resources, Interagency Ecol. Stud. Prog. Tech. Rep.*, 26: 129-141.

Hollowed A.B. and W.S. Wooster. 1992. Variability of winter ocean conditions and strong year classes of northeast Pacific fish stocks. *ICES Mar. Sci. Symp.*, 195: 433-444.

Isemer H.-J. 1992. Comparison of estimated and measured marine surface wind speed. *In*: H.F. Diaz, K. Wolter and S.D. Woodruff (eds.). *Proceedings of the International COADS Workshop*, Boulder, Colorado, 13-15 January 1992. U.S. Dep. Comm. 142-158.

Kitagawa G. and W. Gersch. 1984. A smoothness priors - state space modeling of time series with trend and seasonality. *J. Am. Statist. Assoc.*, 79: 378-389.

Kitagawa G. and W. Gersch. 1988. Smoothness priors in time series. *In*: J. Spall (ed.). *Bayesian analysis of time series and dynamic models.* Marcel Dekker, N.Y.

Lenarz W.H., D. VenTresca, W.M. Graham, F.B. Schwing and F. Chavez. 1995. Explorations of El Niños and associated biological population dynamics off central California. *Calif. Coop. Oceanic Fish. Invest. Rep.*, 36: 106-119.

MacCall A.D. 1979. Population estimates for the waning years of the Pacific sardine fishery. *Calif. Coop. Oceanic Fish. Invest. Rep.*, 20: 72-82.

MacCall A.D. 1986. Changes in the biomass of the California Current ecosystems. *In*: K. Sherman and L.M. Alexander (eds.) *Variability and management of large marine ecosystems.* AAAS Selected Symposia 99, Westview Press, Boulder, CO: 33-54.

MacCall A.D. and M.H. Prager. 1988. Historical changes in abundance of six fish species off southern California, based on CalCOFI egg and larva samples. *Calif. Coop. Oceanic Fish. Invest.* Rep., 29: 91-101.

McGowan J.A. 1985. El Niño 1983 in the southern California Bight. *In*: W.S. Wooster and D.L. Fluharty (eds.). *El Niño north: El Niño effects in the eastern subarctic Pacific Ocean.* University of Washington Press, Seattle, WA: 166-184.

Mendelssohn R. and C. Roy. 1996. Comprehensive Ocean Data Extraction Users Guide. *U.S. Dep. Comm., NOAA Tech. Memo.* NOAA-TM-NMFS-SWFSC-228, La Jolla, CA, 67p.

Miller A.J., D.R. Cayan, T.P. Barnett, N.E. Graham and J.M. Oberhuber. 1994. The 1976-77 climate shift of the Pacific Ocean. *Oceanography*, 7: 21-26.

Parrish R.H., C.S. Nelson and A. Bakun. 1981. Transport mechanisms and reproductive success of fishes in the California Current. *Biol. Oceanogr.*, 1: 175-203.

Pearcy W., J. Fisher, R. Brodeur and S. Johnson. 1985. Effects of the 1983 El Niño on coastal nekton off Oregon and Washington. *In*: W.S. Wooster and D.L. Fluharty (eds.). *El Niño north: El Niño effects in the eastern subarctic Pacific Ocean.* University of Washington Press, Seattle, WA: 188-204.

Quinn W.H., V.T. Neal and S.E. Antunez de Mayolo. 1987. El Niño occurrences over the past four and a half centuries. *J. Geophys. Res.*, 92: 14449-14461.

Radovich J. 1961. Relationships of some marine organisms of the northeast Pacific to water temperatures: particularly during 1957 through 1959. Calif. Dep. *Fish Game Fish. Bull.*, 112, 62 p.

Roemmich D. and J. McGowan. 1995. Climatic warming and the decline of zooplankton in the California Current. *Science*, 267: 1324-1326.

Royer T.C. 1993. High-latitude oceanic variability associated with the 18.6-year nodal tide. *J. Geophys. Res.*, 98: 4639-4644.

Skillman J.B. 1993. *ENSO forced variations of the sea surface temperature and adjusted sea level along the west coast of the United States*. M.S. thesis, Naval Postgraduate School, Monterey, CA, 92 p.

Slutz R.J., S.J. Lubker, J.D. Hiscox, S.D. Woodruff, R.L. Jenne, D.H. Joseph, P.M. Steurer and J.D. Elms. 1985. *Comprehensive Ocean-Atmosphere Data Set*; Release 1. NOAA Environmental Research Laboratories, Climate Research Program, Boulder, CO, 268 p.

Trenberth K.E. 1990. Recent observed interdecadal climate changes in the northern hemisphere. *Bull. Amer. Meteor. Soc.*, 71: 938-993.

Trenberth K.E. and J.W. Hurrell. 1994. Decadal atmospheric-ocean variations in the Pacific. *Clim. Dyn.*, 9: 303-319.

Walker P.M., D.M. Newton and A.W. Mantyla. 1993. *Surface water temperatures, salinities and densities at shore stations, United States West Coast, 1992*. University of California, San Diego, Scripps Institution of Oceanography, La Jolla, CA, SIO Ref., 93 (18), 46 p.

Woodruff S.D., R.J. Slutz, R.L. Jenne and P.M. Steurer. 1987. A Comprehensive Ocean-Atmosphere Data Set. *Bull. Amer. Meteor. Soc.*, 68: 1239-1250.

Wu Z. and R.E. Newell. 1992. The wind problem in COADS and its influence on the water balance. *In*: H.F. Diaz, K. Wolter and S.D. Woodruff (eds.). *Proceedings of the International COADS Workshop*, Boulder, Colorado, 13-15 January 1992. U.S. Dep. Comm.: 189-200.

Freshwater Yields to the Atlantic Ocean: Local and Regional Variations from Senegal to Angola

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ABSTRACT

The total annual yield of freshwater flowing into the Atlantic Ocean from West and Central Africa is computed over the 1951-1989 period. Interannual variations are presented for 34 rivers. Water yields are computed by decades using a data base composed of 57 rivers, and also considers water originating from coastal areas. These coastal areas represent 20% of the 7.7 million km^2 of total surface area studied and contribute approximately 25% of the water yield to the sea, due to high runoff coefficients. The total annual water yield to the Atlantic Ocean is about 2700 billion m^3. The study of the interannual variations of water yield shows two periods, namely wetter before 1970 and drier afterwards. During the period 1981-1989, total yield fell by 28% as compared to the mean during the period 1951-1980.

RÉSUMÉ

Le débit total d'eau douce arrivant dans l'océan Atlantique de l'Afrique de l'Ouest et Central est calculé pendant une période allant de 1951 à 1989. Les variations d'une année sur l'autre sont présentées pour 34 rivières. Les débits sont calculés par décennie en utilisant une base de données composée de 57 rivières, mais aussi en utilisant les débits des stations côtières.

Ces zones côtières représentent 20 % des 7,7 millions de km^2 de la surface totale étudiée, et en raison de leurs forts coefficients de débit, contribuent à 25 % des débits partant en mer. Le débit total arrivant dans l'océan Atlantique est de 2 700 milliards de m^3. L'étude des variations interannuelles des débits montre l'existence de deux périodes, humide avant 1970 et plus sèche après. Pendant la période 1981-1989, les débits ont chuté de 28 % par rapport à ceux de 1951-1980.

INTRODUCTION

On the coasts of the Atlantic Ocean from Senegal to Angola, and in particular along the coast of the Guinea Gulf, fishing is an important social and economic activity for the region's populations. For many years researchers have sought to understand the reasons for stock variations of coastal fishes. Studies have focused on environmental factors such as salinity, wind, and coastal freshwater yields.

From the mouth of the Senegal River, at the Senegalese-Mauritanian border, to the mouth of the Cunene River, at the Angolan-Namibian border, tributary rivers which flow into the Atlantic Ocean drain a basin of about 7.7 million km^2 (Fig. 1). Data regarding this runoff have been recorded for 57 rivers. For 33 of these rivers, it is possible to use or extrapolate from annual series for the period 1951 to 1989, which will be studied. The surface area drained by these 33 rivers occupies 81% of the total surface area considered here, with the Congo river basin alone contributing 46% (Table 1).

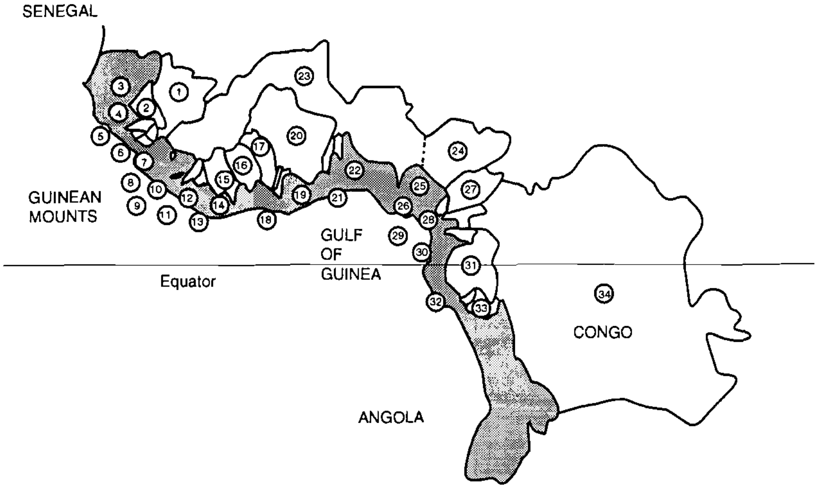

Fig. 1: Contours of the 34 basins studied in West and Central Africa, with numbers presented in Table 1. The non-controlled zones are shaded in grey.

N°	RIVER	STATION	BASIN SURFACE KM^2	% OF TOTAL SURFACE
1	SENEGAL	Bakel	218 000	2.83
2	GAMBIE	Gouloumbo	42 200	0.55
3	CASAMANCE	Kolda	3 700	0.05
4	CORUBAL	Saltinho Amont	23 800	0.31
5	FATALA	Bindan	5 100	0.07
6	KONKOURE	Amaria	16 200	0.21
7	KOLENTE	Tassin	6 600	0.09
8	ROKEL	Bumbuna	4 000	0.05
9	PAMPANA	Matatota	2 400	0.03
10	SEWA	Jaïama	6 900	0.09
11	MANO	Mano Mines	5 500	0.07
12	ST PAUL	Mount Coffe	21 400	0.28
13	ST JOHN	St John Falls	11 400	0.15
14	CESTOS	Sawolo	4 600	0.06
15	SASSANDRA	Gaoulou	70 600	0.92
16	BANDAMA	Daboitié	60 000	0.78
17	COMOE	Mbasso	70 500	0.92
18	BIA	Ayamé	10 000	0.13
19	TANO	Alenda	16 000	0.21
20	VOLTA	Senchi Halcrow	394 000	5.11
21	MONO	Tététou	20 500	0.27
22	OUEME	Pont de Savé	23 600	0.31
23	NIGER	Onitsha	1 100 000	14.28
24	BENOUE (NIGER)	Makurdi	300 000	(3.89)
25	WOURI	Yabassi	8 200	0.11
26	MUNGO	Mundame	2 400	0.03
27	SANAGA	Edéa	132 000	1.71
28	NYONG	Dehane	26 400	0.34
29	KIENKE	Kribi	1 100	0.01
30	NTEM	Nyabessan	26 300	0.34
31	OGOOUE	Lambaréné	203 000	2.64
32	NYANGA	Tchibanga	12 400	0.16
33	KOUILOU	Sounda	56 600	0.73
34	CONGO	Brazzaville	3 550 000	46.08

Table 1: The 34 rivers studied during the period 1951-1989: stations, surface areas, and percent of basin surface compared to total surface area of 7.7 million km^2 (see Fig. 1 for location of river basins, by number).

Thus, it appears that for the 19% of the total surface, the 'non-controlled zones' of about 1.5 million km^2, it is impossible to generate time series of annual runoff values for the period 1951-1989. The non-controlled zones are found particularly along the coastal bands (Fig. 1), where gauging stations are rarely located due to the anomalies of water height measurements caused by tides and sedimentation near river mouths. However, in coastal regions, rainfall is often more abundant than on the continent. With only few exceptions, such rain exceeds 1500 mm per year, and even reaches 10 meters on average at the foot of Mount Cameroon at Debundsha Station. Using the example of the rivers of Cameroon, Olivry (1986) showed that in the zones of average annual rainfall greater than 1500 mm the runoff coefficients rapidly increase up to 70% for rains of 3.5 meters per year. Due to these higher runoff coefficients, as compared to continental regions, these non-controlled zones represent a considerable yield of freshwater, which must be included in estimates to total yields.

For Angola, we have not been able to gather information more detailed than the average runoffs presented in a reference book (Angola, 1974) published for the international decade of hydrology. Hence, for Angola, we only present water yields variations by decades.

The freshwater yields to coastal marine waters directly influence salinity and retention of nutrients. Hence, variations of freshwater yields impact marine life. Numerous authors (e.g., Binet, 1983; Caverivière, 1991) have reported correlations between variations in coastal fish stock sizes and the variations of freshwater yields.

Since the creation of ORSTOM, 50 years ago, its Hydrologic Service, integrated today with ORSTOM's Department of Continental Waters (DEC), has been at the forefront of developing networks of runoff measures for numerous African rivers. Not surprisingly, results regarding freshwater yields were collected and compiled at ORSTOM, by the former Research Unit A7, now UR22. Thus, we can benefit from ORSTOM's extensive experience in Africa, most notably from runoff results that represent years of uninterrupted work by generations of hydrologists working in Africa. However, in the interest of thoroughness, in addition to the data from ORSTOM, we have gathered runoff data from non-francophone countries, namely Nigeria, Angola, Equatorial Guinea, Guinea Bissau, Ghana, Sierra Leone and Liberia.

1. BACKGROUND AND DATA

The runoff values used in this study come from different sources. For most of the rivers the yearly runoff values are taken from daily or monthly runoffs measured at gauging stations. Some gaps in certain series have forced us to reconstruct or extrapolate certain daily, monthly, or yearly values, or even to establish correlations between data from several stations or several rivers near the stations, for periods greater than ten years. In certain cases, we have been unable to establish correlations between different runoff data, and, thus, have had to establish rainfall/runoff correlations both on a monthly basis (at Saint John, Saint Paul, and Ogooue) or, more generally, on an annual basis. Details regarding such calculations are found in Mahé (1993). Time series are analyzed in two ways. First an annual representation is given for the period 1951-1989 (Fig.2 and 3). This concerns 33 rivers (Fig. 1, Table 1) as well as the Benoue, the principal tributary of the Niger River. This tributary represents the runoff of a vast hydroclimatic region which is very different from the rest of the Niger River basin. Secondly a decadal representation is given for the four decades studied, 1951-1960, 1961-1970, 1971-1980, 1981-1989 (only nine years). By chance, these decades correspond to four different climatic periods. Space is used in the same way as time. First, regarding the interannual study, the hydrologic units used are individual basins. Second, regarding the study by decades, we have grouped the rivers, as well as the non-controlled zones, into eight regional entities (Fig. 2, Table 2). Among these eight zones, two are individual basins of the largest rivers in Africa, as measured by runoff, namely the Congo (second largest river in the world after the Amazon) and the Niger.

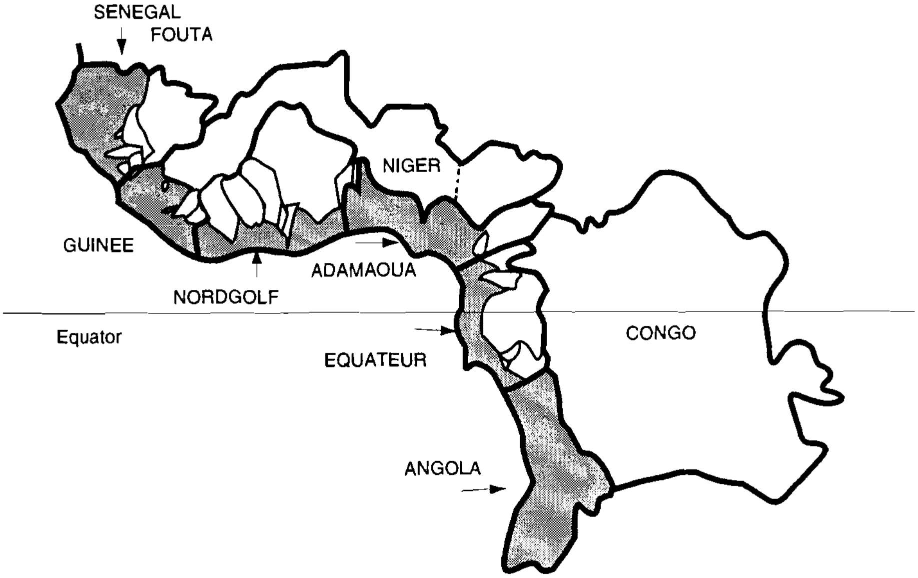

Fig. 2: French names and locations of the eight major hydroclimatic regions of Western/Central Africa. The non-controlled zones are shaded in grey.

REGION	BASIN SURFACE (10^3 KM^2)	% OF TOTAL SURFACE	NON CONTROLLED SURFACE (10^3 KM^2)	% OF TOTAL SURFACE
SENEGAL-FOUTA	590	7.7	230	3.0
GUINEE	182	2.4	120	1.6
NORDGOLF	900	11.7	210	2.7
NIGER	1 100	14.3	0	0
ADAMAOUA	355	4.6	215	2.8
EQUATEUR	475	6.2	150	2.0
CONGO	3 550	46.1	0	0
ANGOLA	551	7.0	551	7.0

Table 2: The eight hydroclimatic regions of Western/Central Africa: surface area of each region, non-controlled surface area of each region, and each region's area compared to total surface area.

2. VARIATIONS IN FRESHWATER YIELDS TO THE ATLANTIC OCEAN

2.1. Interannual variations

2.1.1- Normalized runoffs

Figure 3 illustrates variations of normalized runoffs (= yearly/total runoff) of 34 rivers for the period 1951-1989, following from left-to-right the geographic location of the river's mouths as one moves northward from the Equator. The black rectangles correspond to a normalized runoff greater than 1.05. The white rectangles correspond to a normalized runoff less than 0.95. The rectangles with a dash indicate a normalized runoff between 0.95 and 1.05. The choice of rivers depended on the length of the original data series, as well as on the size of the basins, and on their location on the coast. Runoff of small coastal rivers were not reconstructed; it can be assumed that their runoff variations are similar to the overvall pattern presented here.

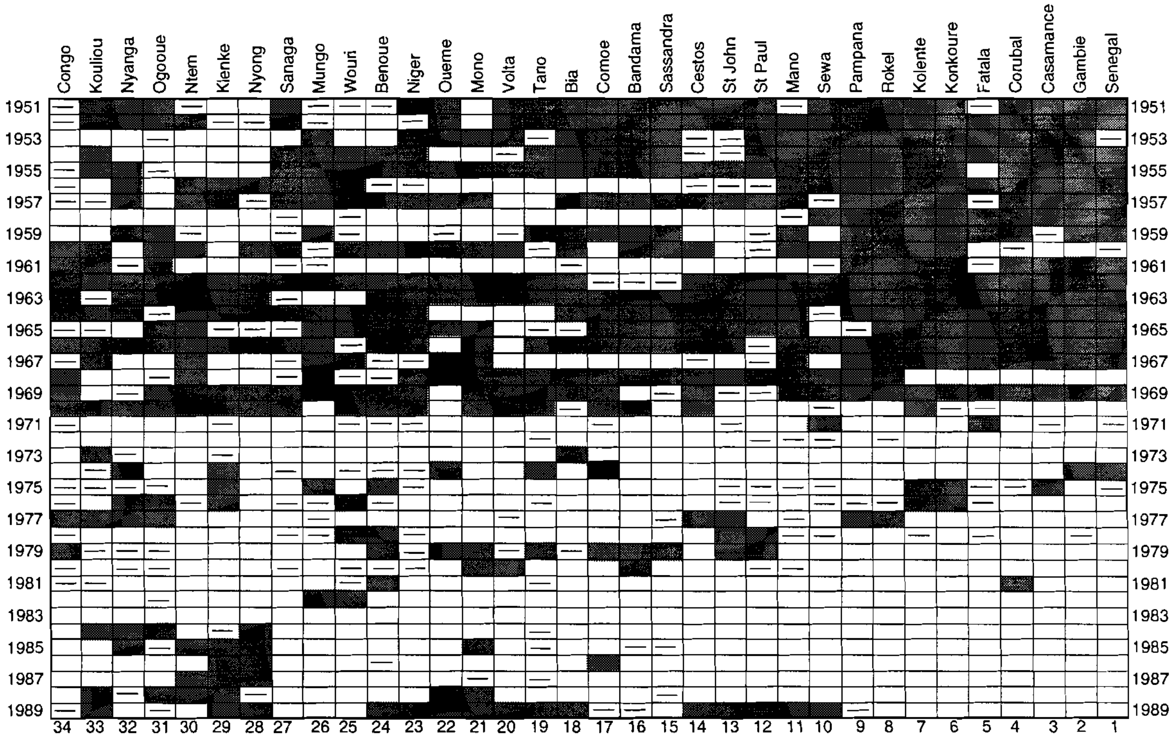

Fig. 3: Normalized runoffs of the 34 rivers studied from 1951-1989, and corresponding hydroclimatic regions. The black rectangles correspond to H > 1.05; the white rectangles correspond to H < 0.95; and the dashes mean that H is between 0.95 and 1.05.

Two periods are distinguishable in Figure 3: before 1970, with high values and after 1970, with low values. This pattern is very visible to the west of the mouth of the Niger River, but becomes less clear to the south of the Sanaga River. In this regard, it is appropriate to mention that runoff variations are rarely the same for all rivers at the same time. In fact, 1983 is the only year where every values of normalized runoff are negative, while 1962 is the only year where all normalised runoffs are positive. Likewise, all rivers experienced a runoff minimum between 1972 and 1973. Also, during the last decade, the rivers in the Adamaoua (Sanaga, Mungo, and Wouri) region here displayed different normalized runoffs than other rivers in the same area. Runoff variations are more similar to those of rivers in more tropical climates which flow from the Pampana River of the Guinean Mountains, to Senegal.

Figure 3 also presents contrasts between rivers in the north and coastal rivers of the littoral of the Gulf of Guinea. For example, in 1958, runoff deficits were only observed to the northward of the Sewa River in northern Sierra Leone, at 10°N latitude. An almost completely opposite case occurred in 1968. In 1989 numerous regions displayed greater-than-average runoffs, except for the Mungo, Wouri and Sanaga River basins in Cameroon, the Senegal-Fouta region, and the northern Guinea region. Since 1970, the only rivers which have experienced at least four years of greater-than-average runoffs were the Kouilou, the Nyanga, the Ogooue, the Kienke, and the Nyong in the Equator region; and more northwards, the Benoue, the Oueme, the Mono, the Comoe, and the St. John Rivers. Finally, during the last decade, the only rivers which have not been in continual deficit have been the equatorial rivers the Nyong and the Kouilou, as illustrated in Figure 4.

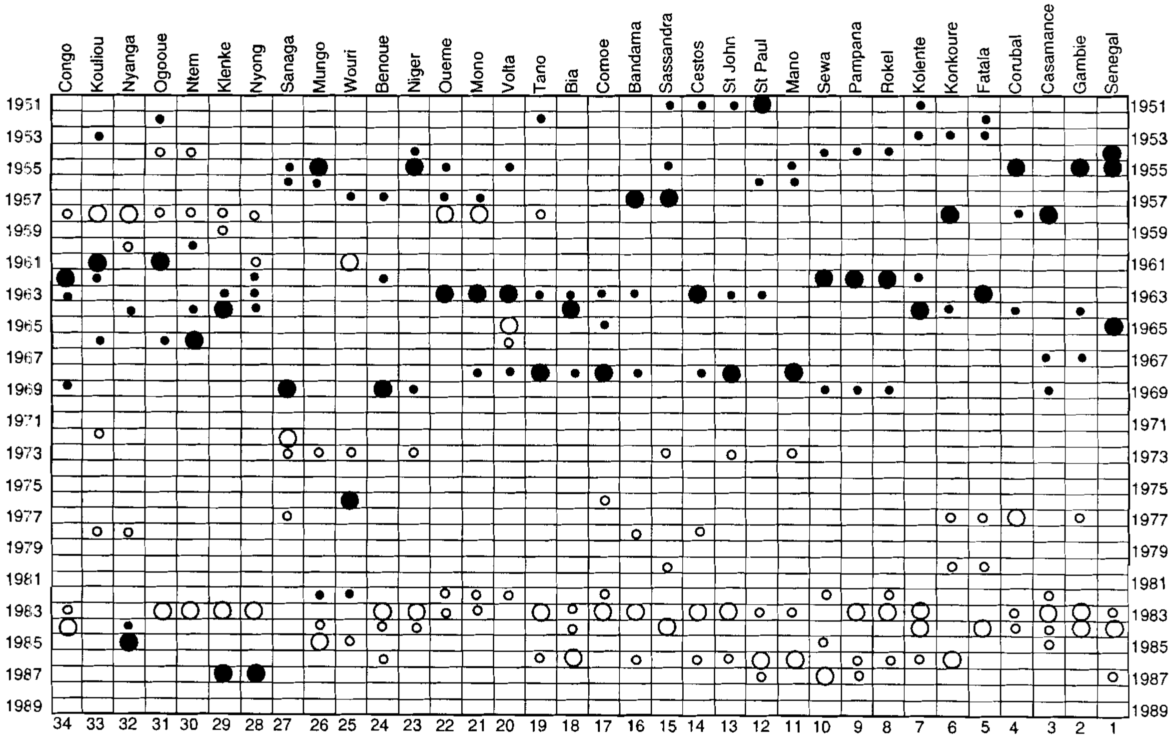

Fig. 4: Years of occurrence of maximum and minimum annual runoffs for each of the 34 rivers studied from 1951-1989. Primary maximum and secondary maximum are represented by big and small black circles, respectively; primary minimum and secondary minimum are represented by large and small white circles, respectively.

2.1.2- *Extreme runoffs*

As illustrated in Figure 4, years of maximum and minimum runoffs for the period 1951-1989 are indicated respectively by black dots and white circles.

In the Equator region, primary maxima are observed during 1980-1989 only for the Nyanga, the Kienke, and the Nyong. The Mungo and the Wouri present secondary maxima in 1982. Almost all rivers experienced a minimum between 1982 and 1987, except the Sanaga (data extrapolated from rainfall), the Nyanga, and the Kouilou. The runoffs were so weak during the last decade in this study (1981-1989) that the minima of the 1970 decade are only secondary minima. In fact, during this last decade only the Sanaga and the Corubal experienced primary minima. From the Equator region to the Nordgolf region, 1958 is a year of marked deficits, and of occurrences of primary minima (Kouilou, Nyanga, Mono, Oueme). Finally, minima for the Volta in 1965 and 1966 coincide with the filling of the Lake Akosombo, a reservoir. The maxima are divided between two decades, 1950-1959 and 1960-1969. For the Senegal Fouta region and for the Niger, the main period for maxima is the decade 1950-1959. In contrast, for the Equator and the Nordgolf regions from the Oueme to the Comoe, the maxima are concentrated in the decade 1960-1969. The years with the greater number of maxima are 1955, 1963, and 1968.

For purely informative purposes, and without drawing any definitive conclusions, we remark finally a progressive time lag in the timing of maxima from west to east. In the middle of the period of deficits of the last twenty years, we observe that the Senegal and the Gambia have higher-than-average runoffs in 1974/75. This period of higher-than-average runoffs moves in 1975/76 to the Kolente and the Konkoure, in 1977/79 to the St. Paul and the St. John, in 1979/80 to the north coast of the Gulf of Guinea, and in 1981/82 to the Mungo and the Wouri.

2.2. Decadal freshwater yields variations

This section of the study fulfills two objectives :
- to synthesize the results from every river basins by grouping them into larger hydroclimatic regions ;
- to integrate the contribution of non-controlled zones into our calculations of freshwater yields to the Atlantic Ocean.

We do not have complete runoff data for the period 1951-1989 for the non-controlled coastal zones. Nevertheless, we can obtain information on the order of magnitude of specific runoffs for these zones from the results of studies undertaken periodically on small coastal rivers (24 in all, representing 5% of the total surface area). To estimate these runoffs from non-controlled zones, the simplest solution is to first calculate an average runoff value from known values for nearby rivers in the same zones, then apply annual coefficients of variation also derived from the same time-series of runoffs of nearby rivers. The problem with this method is that it does not consider specific coastal runoffs and rainfall variations. The solution that we have chosen for reconstructing runoff time series, taking into consideration coastal specificity, was inspired by Olivry (1986) who, after studying rainfall and runoff of the rivers of Cameroon, proposed a relationship between total annual rainfall and specific runoff values. This relation demonstrated a correlation between rainfall and specific runoffs, applicable to cases of annual rainfall of at least 1500-2000 mm/year.

The transposition of Olivry's relation to regions other than those of the Cameroon coast is problematic, due to differences in climatic conditions. On the Cameroon coast, the climate can be classified as equatorial transition, with a small dry season and significant cloudiness. We use this relationship for the coastal zones from the Guinean Mountains to the Gabonese and Congolese coasts. In these littoral zones, rains reach and often exceed 1500-2000 mm/year, with the length of the dry season as the only factor that makes such zones different from the Cameroon coast. The conditions for optimal utilization of the relation between rain and runoff are thus largely met, and specific runoffs can be deduced from the relationship described by Olivry. Then the runoff is calculated from the surface of the areas. Hence, Olivry's relationship requires calculation of average rainfall on the surface area of the non-controlled zones. The annual rainfall values for each zone during the period 1951-1989 are calculated automatically through spline interpolation, based on data on annual rainfall at about 900 rainfall stations covering the total surface of the basins under study. Details of the method are described in Mahé and L'Hôte (1992) and Mahé *et al.* (in press). Thus, we have precipitation time-series, which, with Olivry's equation, can be transposed into time-series of annual runoff, with the specific variability of coastal precipitation being preserved in the constructed data series, as well as the nuances of specific runoffs along the coast. However, the accuracy of the calculation of annual runoff from these zones obtained through graphical methods and the accuracy of the runoff coefficients (ratio of runoff to rainfall, in percentages), are not identical for the past four decades of study (Mahé, 1993). Specifically, annual runoff values from non-controlled zones are only qualitative, and runoff averages by decades are much more reliable.

For each hydroclimatic region we can present freshwater yields and estimated freshwater yields from non-controlled zones. Figure 5 displays interannual variations of annual runoff, by hydroclimatic regions, with average runoffs by decades represented with thin horizontal lines. For Angola, due to the lack of information concerning runoffs, it is not possible to reconstruct annual values. During the last decade, the runoffs of the Senegal-Fouta and the Nordgolf regions were more than half as weak than during the decade 1950-1959. For the Niger and the Guinea regions, the decrease is only one-third. It is also noticeable in the Adamaoua region, but much less perceptible in the Congo Basin and the Equator region, where, however, very strong runoffs are observed during the 1960s.

To illustrate the variations of freshwater yields, Table 4 presents the volumes of freshwater yields by decades and by region. As illustrated, each year approximately 2.7 10^{12} m^3 of freshwater enters the Atlantic Ocean between Senegal and Angola. About half of this amount comes from the Congo River. The decrease in freshwater yields during the last decade is considerable, with a 28% annual average decline during 1981-1989 as compared to 1951-1980. This decline is also not equal throughout Central and West Africa. Specifically, in Central Africa the decrease in freshwater yields is small in the Adamaoua region, and very small in the Equator region and in Angola, where periods of drought affected only slightly the runoffs. In West Africa, the decline in freshwater yields becomes greater as one advances from Cameroon to the northwest (Guinea, Mali, Senegal, Mauritania). During the decade 1981-1989, the yields from the Senegal-Fouta region fell by more than half in comparison to their average value during the 1951-1960 decade. As a result, runoff changed, with a fall in ground water reserves, and in river recharge during dry seasons. This phenomenon is the intensification of depletion, as described by Olivry *et al.* (1993).

One example should suffice to illustrate the observed magnitude of the runoff deficits. In 1983, the year of maximum rainfall decline both during the 1951-1989 period and since the beginning of the century (Sircoulon, 1989); for all regions, freshwater yields to the Atlantic Ocean have been 34% less than the average from 1951-1989, which represents a decline of about 900 billion m^3. This value corresponds to total annual runoff of all of West Africa from Senegal to the Cameroon Mountains in a normal year.

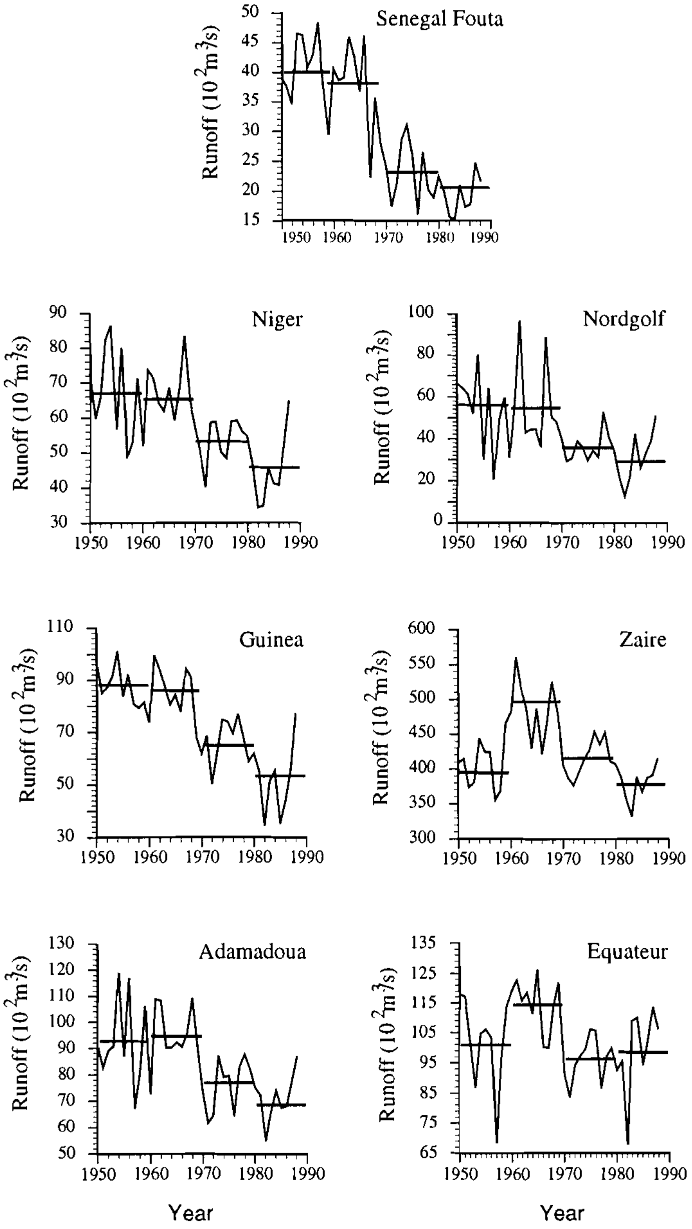

Fig. 5: Annual runoff by hydroclimatic region, in m^{3}s^{-1}, 1951-1989, (Angola not included). Decadal means are indicated by horizontal lines. For each region, the runoff values represent the sum of yields in controlled and non-controlled zones.

REGION	1951 - 1960	1961 - 1970	1971 - 1980	1981 - 1989	MEAN
	MEAN ANNUAL YIELD (m^3 10^9), BY PERIOD				
SENEGAL - FOUTA	127	119	73	62	96
GUINEE	278	269	211	165	233
NORDGOLF	173	171	115	98	140
NIGER	214	211	170	146	186
ADAMAOUA	294	300	241	225	266
EQUATEUR	321	362	303	312	325
CONGO	1280	1530	1310	1200	1335
ANGOLA	87	94	80	83	86
TOTAL	2780	2870	2500	2290	2670

Table 3: Volume of freshwater yield to the Atlantic Ocean, by hydroclimatic region and decade, in billions of m^3 per year. The means for 1951-1989 are presented in the right column.

CONCLUSION

Of the 2.7 10^{12} m^3 of freshwater reaching the Atlantic Ocean each year from West and Central Africa, approximately half, i.e., 1.34 10^{12} m^3, come from the Congo River. The freshwater yields from the non-controlled zones (19 % of the total surface) where rainfall is stronger and hydrologic studies rare, represent about 25% of total runoff to the ocean. Estimation of this part of the runoff, which has not been previously calculated, constitutes an addition to previous estimates. In relation to the average runoff for the period 1951-1989, maximum runoffs occurred between 1951 and 1970. Since 1970, freshwater yields have decreased. This study constitutes a first synthesis of freshwater yields on the Atlantic side of the African continent. Results presented, however, can be further refined. For example, complementary information on runoffs from non-francophone countries such as Angola and southern Nigeria would improve on the results of this study.

ACKNOWLEDGMENTS

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REFERENCES CITED

Angola. 1974. Collectanea de estudos hidrologicos. Direcçao-General de Obras publicas e Communicaçoes. Grupo de trabalho para o decenio hidrologico internacional. Lisboa, 400 p.

Binet D. 1983. Phytoplancton et production primaire des régions côtières à upwellings saisonniers dans le golfe de Guinée. *Océanographie tropicale*, 18 (2): 331-355.

Caverivière A. 1991. L'explosion démographique du baliste (*Balistes carolinensis*) en Afrique de l'ouest et son évolution en relation avec les tendances climatiques. *In*: P.Cury et C.Roy (eds.). Pêcheries ouest-africaines: variabilité, instabilité et changement. ORSTOM: 354-367.

Mahé G. 1993. *Les écoulements fluviaux sur la façade atlantique de l'Afrique. Etude des éléments du bilan hydrique et variabilité interannuelle, analyse de situations hydroclimatiques moyennes et extrêmes*. Thèse, Université Paris-Sud-Orsay/ORSTOM. Coll. Etudes et Thèses, ORSTOM, 438 p.

Mahé G. and Y. L'Hôte. 1992. *Utilisation de la méthode du vecteur régional pour la description des variations pluviométriques interannuelles en Afrique de l'ouest et centrale de 1951 à 1989*. Huitièmes Journées hydrologiques de l'ORSTOM, Montpellier, Septembre 1992, 14 p.

Mahé G., F. Delclaux and A. Crespy. In press. Elaboration d'une chaîne de traitement pluviométrique et application au calcul automatique de lames précipitées (bassin versant de l'Ogooué au Gabon). *Hydrologie continentale*, 9 (2).

Olivry J.C. 1986. *Fleuves et rivières du Cameroun*. Thèse d'Etat. MESRES-ORSTOM. Coll. Monographies hydrologiques ORSTOM, Paris, 9, 733 p., 360 tab., 2 cartes.

Olivry J.C., J.P. Bricquet and G. Mahé. 1993. Vers un appauvrissement durable des ressources en eau de l'Afrique humide ? *In* : J.S. Gladwell (ed.). Hydrology of warm humid regions. 4ème Assemblée AISH, Yokohama, *AISH Publ.*, 216: 67-78.

Sircoulon J. 1989. Bilan hydropluviométrique de la sécheresse 1968-84 au Sahel et comparaison avec des sécheresses des années 1910 à 1916 et 1940 à 1949. *In*: *Les hommes face aux sécheresses. Nordeste brésilien. Sabel africain*: 107-114.

Spatial Dynamics of the Coastal Upwelling off Côte-d'Ivoire

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ABSTRACT

Coastal SST measurements and images derived from Meteosat Satellit TIR channel are used to study the spatio-temporal evolution of the minor upwelling off Côte-d'Ivoire. The TIR images derived from Meteosat provide a comprehensive view of the spatial dynamics of the upwelling off Côte-d'Ivoire. The cooling water was detected by Meteosat sensors because there is generally a clear sky situation and a sufficient spatial extension of the upwelling each time it takes place. The use of the Meteosat data seems to be sufficient to localize the surface cooling off Côte-d'Ivoire. The minor upwelling appears to be more persistent in the western side than in the eastern side off Côte-d'Ivoire. In spite of its local aspect, the use of the coastal SST measurements can be considered as a good tool to detect the presence of the coastal upwelling.

RÉSUMÉ

Les mesures de SST côtières et les images dérivées du canal IR du satellite Météosat sont utilisées pour étudier l'évolution spatio-temporelle du petit upwelling devant la Côte-d'Ivoire. Les images TIR dérivées de Météosat donnent une image interprétable des dynamiques spatiales des upwellings devant la Côte-d'Ivoire. Les refroidissements sont détectés par les capteurs de Météosat parce qu'en général un ciel clair et une extension suffisante au large se produit. L'utilisation de Météosat apparaît satisfaisante pour localiser les zones de refroidissement devant la Côte-d'Ivoire. Le petit upwelling apparaît plus persistant dans la partie ouest que dans la partie est de la Côte-d'Ivoire. En dépit de son aspect local, l'utilisation des mesures de SST côtières peuvent être considérées comme un bon moyen pour détecter la présence de l'upwelling côtier.

INTRODUCTION

The temperature of the uppermost layer of the ocean determines the heat content and affects biological activity. Observed large-scale and persistent anomalies in sea surface temperature are of great interest in the context of global climate change monitoring (McClain *et al.*, 1985; Bakun, 1990). Sea surface temperature (SST) is also known to affect the spatial distribution of marine species (Brown and Winn, 1989). Thus, knowledge of the spatio-temporal evolution of SST can be related to annual indices of the abundance of fishes and to the impact of climate changes on the spatial distribution of pelagic fishes (Mendelssohn and Cury, 1989; Pezennec and Koranteng, this vol.).

Coastal SST measurements have shown that, twice a year, there is a moderate, then a great decrease of the SST between January and March (minor upwelling) and between July and September (major upwelling) along the coasts of Côte-d'Ivoire and Ghana. Upwellings-induced plankton production maintain large stocks of pelagic fishes. Indeed, there has been an increase of catches of *Sardinella aurita* in Côte-d'ivoire and Ghana during the last decade and a new spatial and seasonal distribution of the stock (Binet and Servain, 1993; Pezennec and Bard, 1992).

Generally, the large-scale behaviour of coastal upwelling can be better observed from geostationary satellites imagery than by coastal SST measurements. Satellite data provide uniform and continuous coverage of the SST when there is a clear sky situation. The Meteosat data derived from the Thermal Infra Red (TIR) channel have been shown to be appropriate for these studies because they provide the kind of spatial and temporal coverage required for fisheries related investigations.

Since 1991, the Meteosat high resolution transmission can be received by a Primary Data User Station (PDUS) installed at the University of Abidjan (Côte-d'Ivoire). This ensures that we receive regular half hourly Visible, Water Vapor and Thermal Infrared images data with a spatial resolution of 5km for the TIR channel, only a few minutes after they have been scanned.

In its initial form, the PDUS system has been installed to satellite estimation of rainfall over Côte-d'Ivoire. However, images data derived from TIR channel have been archived for the purpose of sea surface temperature monitoring.

In the present paper, coastal SST measurements and TIR images from Meteosat are used to study the spatio-temporal evolution of the SST off Côte-d'Ivoire. This preliminary study is focused on the minor upwelling of the year 1993.

1. DESCRIPTION OF THE STUDY AREA

1.1. General climatology along the coastline of Côte-d'Ivoire

A knowledge of the Ivoirian and Ghanaian coastal upwelling mechanism requires to study the climatology of the Gulf of Guinea and to pay attention to the local climate of Cape Palmas and Cape Three Points, because it is recognized that surface cooling is strongest on the eastern sides of these two capes (Ingham, 1970).

The climate of South Côte-d'Ivoire and Ghana is characterized by four seasons:
a) The long dry season, which begins in December and ends in March;
b) The long rainy season, which starts in May and lasts three months, with rain storm events from April to May;
c) August and September, which correspond to the short dry season;
d) October and November, which correspond to the short rainy season.

According to Cautenet (1979), the precipitations are more important at Axim (1969 mm) than at Takoradi (1068 mm) and at Accra (659 mm), whatever the season. Axim and Takoradi are 56 km faraway and are symmetrical in relation to Cape Three Points (Fig. 1). The same trend is also observed at Tabou near Cape Palmas. The effective level of rainfall records at Tabou is about 2100 mm/year. The levels of rainfall recorded at San Pedro and Fresco are less important than the levels of rainfall at Tabou.

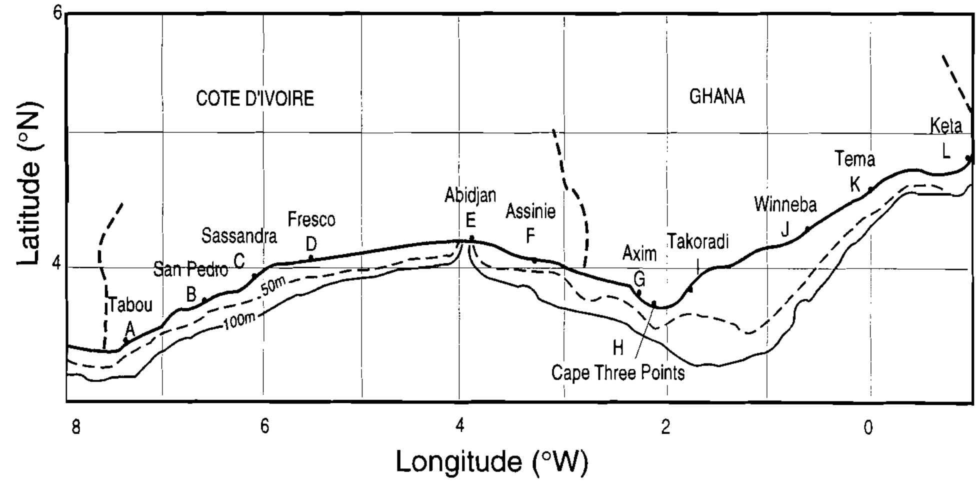

Fig. 1: The study area, along the coasts of Côte-d'Ivoire and Ghana.

In these two cases, there is a decrease of the level of rainfalls in the eastern sides of the capes (Cautenet, 1979). The monsoon is the main provider of precipitations during the long rainy season along the Gulf of Guinea, while the sea breeze circulation is the only factor which determines the precipitations during the dry season (Cautenet, 1979). The sea breeze circulation is due to the difference (ΔT) between the air temperature on the ground and the sea surface temperature. During the minor upwelling, ΔT is positive and favours the development of the sea breeze circulation. Thus, SST can be considered as an important factor for determining rainfall during the minor upwelling period.

2. THE DATA SET AND THEIR PROCESSING

We have two data sources for this preliminary study:

a) The five coastal stations sampled by the Centre de Recherches Océanologiques (CRO) of Abidjan. These stations are located along the open Ivoirian gulf (Fig. 1), from Tabou (near Cape Palmas) to Assinie (near the border of Ghana). The available ground SST measurements are carried out from January to March 1993;

b) The Meteosat data, which cover the coast of Ghana and Côte-d'Ivoire for the year 1993. These data consist of TIR images over the area from 10°W to 0° and 0° to 10°N (from Cape Palmas to Takoradi). The TIR images acquired cover the two upwelling periods.

Scanning of the earth nominally takes place every half-an-hour, providing images in all three spectral channels. The infrared and water vapour images are composed of 2500 lines, each of 2500 pixels, whilst the visible image consists of 5000 lines of 5000 pixels. The corresponding spatial resolution at the sub-satellite point are 5 km and 2.5 km, respectively. The TIR images used for this study are from the formats AI and AIVH. The latter is a combination of visible and infrared images. In the AIVH format, visible channel data is reduced to the spatial resolution of the infrared channel. The Thermal InfraRed image, the administrative message and the calibration coefficients are extracted from the raw data. The raw TIR is converted to radiance image by using:

$$\text{Radiance} = (NC - SPC) \times Ircal. \qquad (1)$$

where NC is the numerical count, and SPC and Ircal are calibration coefficients disseminated with the raw image.

The radiance data, in the form of digital counts for each pixel, are produced by transcription to temperature through transcription table (inversion of Planck's Law). The spatial resolution of the images is 5 km and the temperature resolution is 0.5°C.

47 digital TIR half- hourly images are received, processed and archived every day by the Department of Physics of the University of Abidjan. A daily synthesis image is obtained from the 47 half-hourly images of temperature brightness maxima. The presence of cloud cover leads to a severe reduction of our ability to observe daily oceanic structures. So, for every period of five days, a period synthesis of temperature brightness maxima is routinely carried out. No correction for atmospheric attenuation is carried out, but the method of processing the synthesis image minimizes this attenuation effect. In our study, the image of January 12th was used to hide the land. Meteosat images data from January 1st, 1993 to September 31th, 1993 have been analyzed at the time of writing.

3. RESULTS AND DISCUSSION

3.1. Minor upwelling

Table 1 presents the percentage of cloudless daily images (56% of total) archived from January to March. The observational studies based on Meteosat TIR images have shown that the diurnal cycle of convective activity can be described by a beginning of cloud growth around 12h and a maximum of cloudiness 5 or 6 hours later; this process occurs in similar fashion along the West African coastline, from Côte-d'Ivoire to Nigeria.

Location	Tabou	San Pedro	Fresco	Abidjan	Assinie
Cloudless images (%)	57	53	60	56	53

Table 1: Percentage of cloudless images from January 1993 to March 1993 for the five coastal stations.

Figure 2 shows the temporal evolution of ground SST measurements in January 1993. This figure documents a decrease of the SST from January 4 to January 9, 1993 for the all sites studied, except Assinie, where there was a weak increase of SST during this same period.

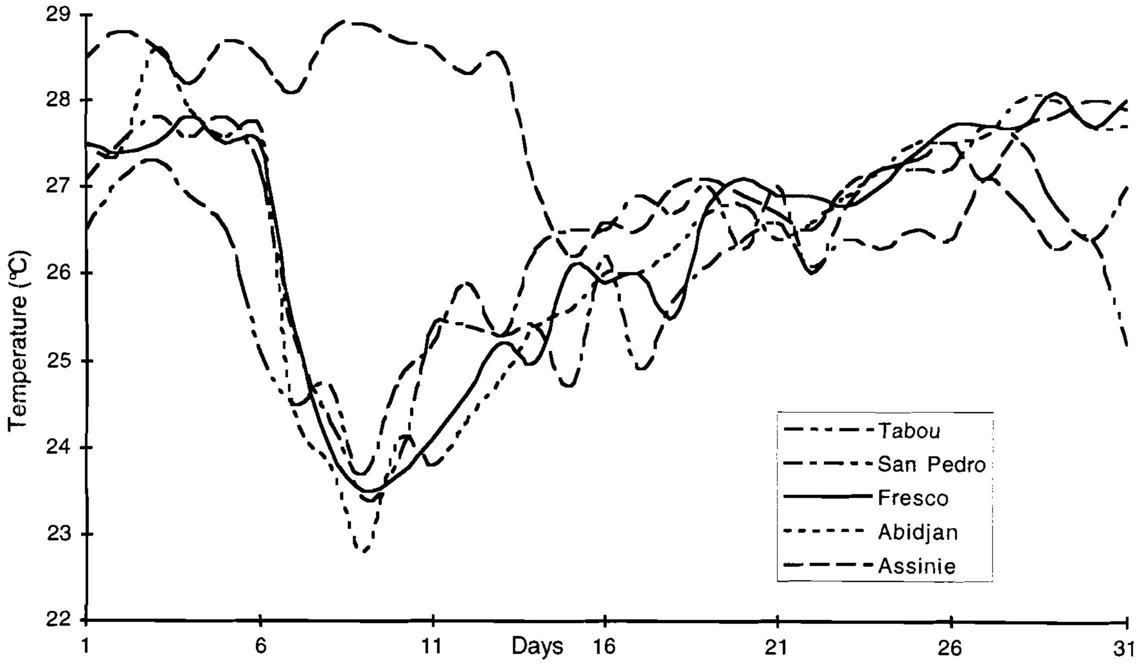

Fig. 2: Temporal evolution of ground SST measurements in January 1993 at different coastal stations off Côte-d'Ivoire.

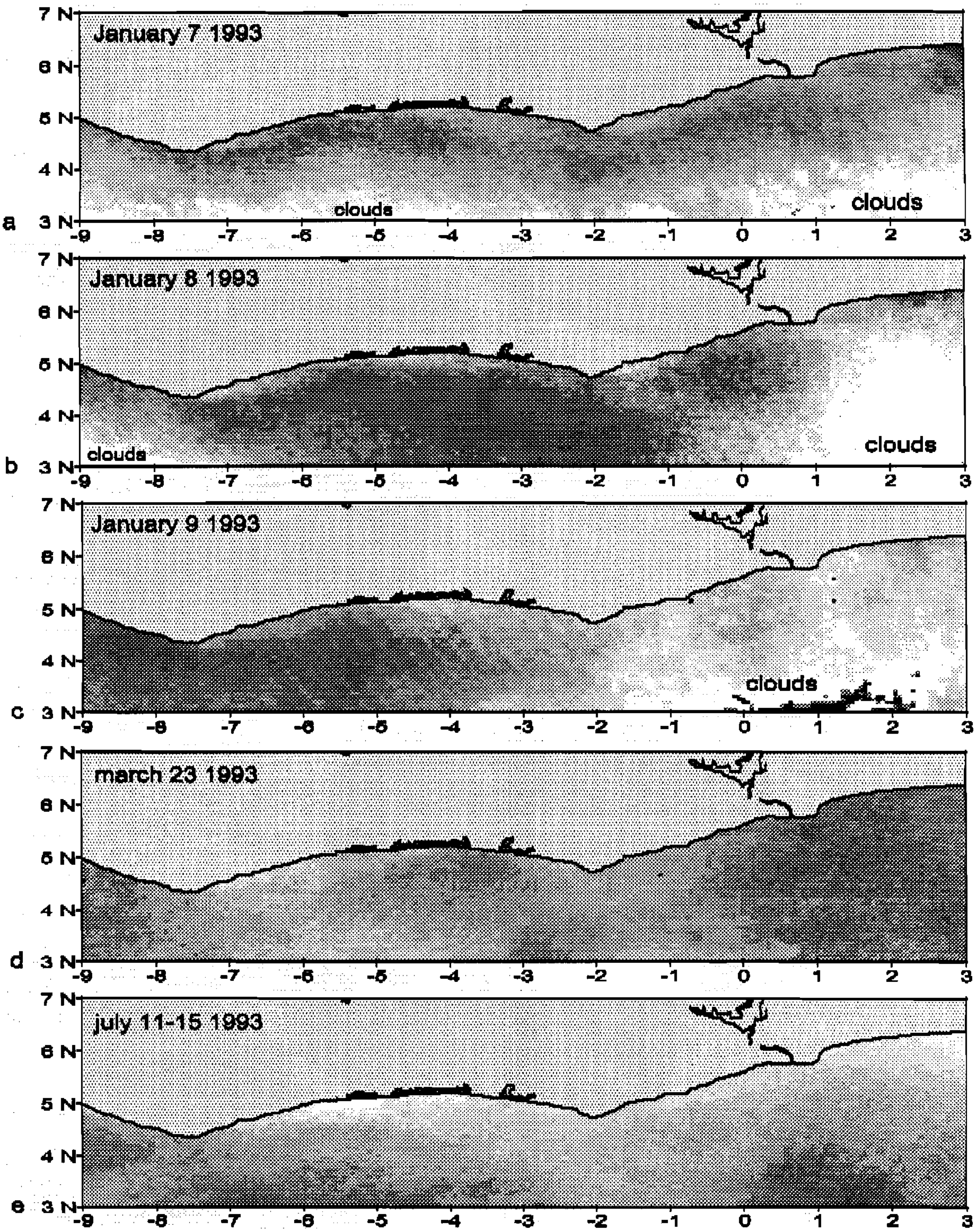

Fig. 3: Daily synthesis images derived from Meteosat TIR Channel off Côte-d'Ivoire and Ghana, January-July 1993.

In order to better detect and analyze the spatial extension of this phenomenon, three daily SST images derived from Meteosat TIR channel were carried out from January 7 to 9 (Fig. 3a,b,c). They confirm the cooling observed with the coastal SST measurements and show that the eastern sides of the two capes were more affected by the decrease of the sea surface temperature than the western sides. The coastal SST during March 1993 at Assinie and Tabou (Fig. 4) show a global decrease from March 6 to March 11. The minimum SST is observed on March 11. The relative decrease of the SST was not observed on the corresponding TIR images because of the strong nebulosity dynamic during this period. The same figures show another decrease of the sea surface temperature during the fourth five-day period of March. The cooling trend seems more persistent at Tabou than at Assinie. The analysis of the SST images corresponding to March shows that the second minor upwelling took place during the fourth five-day period of March. The daily synthesis image of March 23 (Fig. 3d) was selected to illustrate this phenomenon, located in the western coast of Côte-d'Ivoire, from Tabou to Grand Lahou along 200 km approximately. The observed sea surface temperature was about 23°C.

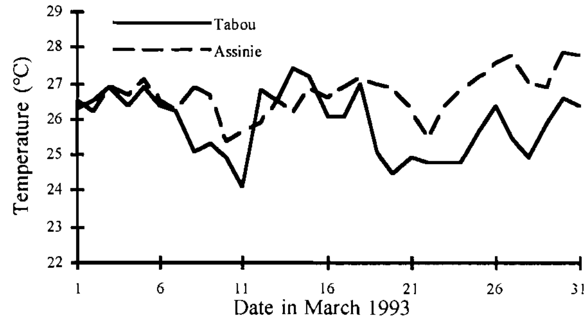

Fig. 4: SST in March 1993, at Tabou and Assinie, Côte-d'Ivoire.

3.2. Major upwelling

In contrast to the minor upwelling, the major upwelling is not difficult to observe, as it lasts approximately 3 months. Thus, it is straightforward to observe this phenomenon with Meteosat. However the occurrence of cloud is important during this period; it is quite common to have four or five consecutive cloudy days.

The available Meteosat SST images reveal that in 1993, the major upwelling effectively began on July, or even at the end of June. It was located all along the coast of Côte-d'Ivoire and Ghana and its offshore extension reached to 2°S. Figure 3e shows the clearest five-day period synthesis image for July.

3.3. Cumulative negative thermal anomalies on the coastal stations: case of the minor upwelling

A computation of the cumulative thermal negative anomalies (T_a) was carried out from January to March in relation to the monthly mean SST value.

For a given site, T_a is obtained by:

$$T_a = \sum_{i=1}^{n} (T_i - T_m) \qquad (2)$$

where T_m represents the monthly mean SST value and T_i the daily SST value, with $T_i < T_m$

Four sites have been chosen: Assinie and Abidjan (eastern coastal stations) and San Pedro and Tabou (western coastal stations). T_a gives an indication on the intensity of the upwelling (Fig.5).

Two patterns were observed:

a) The cumulative index of negative anomalies observed during the study period is relatively high for the eastern coastal stations (Fig. 5). There is a weak decrease of T_a in February and March;

b) In the western stations, the cumulative total index of negative anomalies is relatively important in January and March and very weak in February. Fig. 5 shows that Tabou is the only station affected by the cooling water in March.

These patterns show that there is a spatial variability of the SST between Assinie and Tabou. In the west of Côte-d'Ivoire, there is a global trend of increase of the SST between the two periods of upwelling.

In conclusion, the net cold ocean negative anomalies observed in January and March are in agreement with the temporal evolution of coastal SST measurements (Fig. 2 and 4)

CONCLUSION

In this paper, coastal SST measurements and images derived from Meteosat TIR channel are used to study the spatio-temporal evolution of the minor upwelling off Côte-d'Ivoire. This study shows that:

a) in spite of its local aspect, the use of the coastal SST measurements can be considered as a good parameter to detect the presence of the coastal upwelling. The TIR images derived from Meteosat provide a comprehensive view of the spatial dynamics of the upwelling off Côte-d'Ivoire. However, the cooling water has been detected by Meteosat sensors because there is generally a clear sky situation and a sufficient spatial extension of the upwelling each time it takes place. The use of the Meteosat data seems to be sufficient to localize the surface coolings off Côte-d'Ivoire;

b) the minor upwelling is more persistent in the western sides than in the eastern sides off Côte-d'Ivoire;

c) there is a need for collecting data along the two capes from January to March for a better knowledge of the decrease of sea surface temperature as these play an important role in determining the minor upwelling.

For future investigations, it should be required to analyze the impact of SST on rainfall during the dry season, when there is an important development of convective clouds in the study region; this may be very useful for local and global climate monitoring.

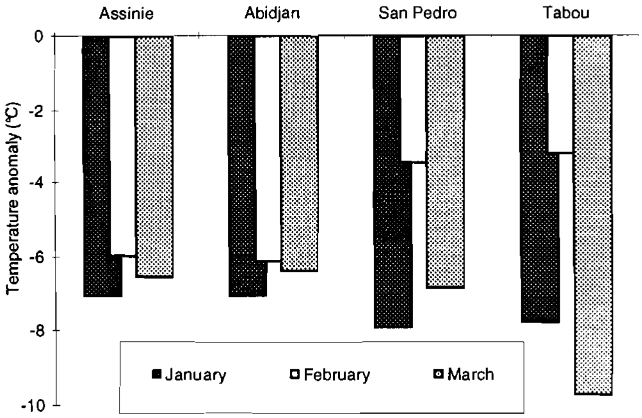

Fig. 5: Cumulative index of negative SST anomalies off Côte-d'Ivoire.

ACKNOWLEDGMENTS

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REFERENCES CITED

Bakun A. 1990. Global climatic change and intensification of coastal ocean upwelling. *Science*, 247: 198-201.

Binet J. and Servain J. 1993. Have the recent hydrological changes in the northern Gulf of Guinea induced the *Sardinella aurita* outburst? *Oceanologica Acta*, 16 (3): 247-258.

Brown C.W. and H.E. Winn. 1989. Relationship between the distribution pattern of right whales, *Eubalaena glacialis*, and satellite-derived sea surface thermal structure in the Great South Channel. *Cont.-Shelf-Res.*, 9(3): 247-260.

Cautenet S. 1979. *Interaction d'une circulation méso-échelle de brise de mer avec un cisaillement de vent synoptique. Application au golfe de Guinée.* Thèse de Doctorat, Université Blaise Pascal (Clermont-Ferrand II).

Ingham M.C. 1970. Coastal upwelling in the northwestern Gulf of Guinea. *Bull. Mar. Sci.*, 20(1): 1-34.

McClain E., W.G. Pichel and C.C. Walton. 1985. Comparative performance of AVHRR-based multichannel sea surface temperatures. *J. Geoph. Res.*, 90 (C6): 11,587- 11,601.

Mendelssohn R. and P. Cury. 1989. Fluctuations of a fortnightly abundance index of the Ivoirian coastal pelagic species and associated environmental conditions. *Can. J. Fish. Aquat. Sci.*, 44: 408-428.

Pezennec O. and F.X. Bard. 1992. Importance écologique de la petite saison d'upwelling ivoiro-ghanéenne et changements dans la pêcherie de *Sardinella aurita*. *Aquat. Liv. Res.*, 5(4): 249-259.

Spatial and Temporal Dynamics of the Upwelling off Senegal and Mauritania: Local Change and Trend

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ABSTRACT

A specific processing chain applied to the infrared data of the Météosat series satellites has been elaborated. The high repetitiveness of the observations allows to obtain 5 days synthesis SST maps over West Africa at a 6 km resolution. The resulting data set precisely describes the spatio-temporal dynamic of the coastal upwelling, from Mauritania to Guinea (21°N-9°N), since 1984. The study area is dominated by the seasonal coastal upwelling which displays important interannual variations. The study of the superficial thermal field structure enables to link the mean position of the upwelled water to the topography of the continental shelf. Continuous monitoring of SST along the shelf allows the spatial estimation of an upwelling index and to characterize the seasonal dynamic of the upwelling via parameters such as the intensity and the duration of the seasonal transition phase and its seasonal lags. The example of an anomalous migration of *Sardina pilchardus* in Senegal leads to the hypothesis that neither the mean seasonal intensity nor the precocity of the upwelling is sufficient to initiate an abnormal southward migration and that the seasonal transition leads may be a key parameter in this process.

RÉSUMÉ

L'élaboration d'une chaîne de traitement spécifique aux données infrarouge thermique des satellites de la série METEOSAT a été réalisée. L'abondance des données satellitales liées à la répétitivité des observations permet d'accéder à une résolution de 5 jours et 6 km, soit très en deçà des méthodes d'investigation utilisables en routine en océanographie côtière. La description spatio-temporelle précise et régulière de l'upwelling côtier de la Mauritanie à la Guinée est ainsi accessible depuis 1984. La zone étudiée est soumise à la très forte saisonnalité de l'upwelling côtier, lequel présente aussi de fortes anomalies interannuelles. La connaissance de la structure des champs thermiques superficiels permet de relier la position moyenne des zones de remontée à la topographie du plateau continental. La détermination de la TSM sur une bande continue centrée sur le maximum de résurgence permet le calcul d'indices d'upwelling spatialisés et de caractériser la dynamique saisonnière de l'upwelling à travers des paramètres tels que : intensité et durée mais aussi décalages saisonniers et progressivité des transitions saisonnières. A partir de l'exemple de *Sardina pilchardus* au Sénégal, on émet l'hypothèse que ni l'intensité saisonnière moyenne, ni la précocité de l'upwelling ne permettent d'expliquer à eux seuls certaines migrations exceptionnelles de cette espèce, mais que la dynamique des transitions saisonnières semble également déterminante.

INTRODUCTION

Remote sensing of sea surface provides synoptic and repetitive overviews, especially for large scale monitoring of climatic parameters. At a lower space and time scale, satellite infrared imagery allows satisfactory observation of coastal areas. Due to their low cloud coverage, coastal upwelling areas may be particularly well monitored via sea surface temperature (SST) mapping, at a time and a space scale adapted to their particularly high dynamic. A specific data processing chain has been developed from METEOSAT infrared data and ships of opportunity data (Citeau and Demarcq, 1990; Demarcq and Citeau, 1995) and tested in West African upwellings.

The upwelling zone studied extends from North Mauritania to Guinea and corresponds to the seasonal zonal displacement of the trade winds along the western African coast. Directly depending on this dynamic, the seasonal variability of the SST reaches 14°C (Rébert, 1983), and is one of the largest in the world. The high pressure regime of the northern anticyclone which governs NE trades leads to weaker cloudiness (and permits better remote sensed observations of SST) during the cold season (October to June, depending on the latitude).

The enrichment of these coastal areas depends on both intensity and variability of the corresponding upwellings. Important fluctuations of pelagic fishes population abundance and particularly of *Sardinella* species, a major resource for Senegal, have been recorded, in spite of the ability of these species to tolerate some environmental fluctuations (Fréon, 1988; Cury and Fontana, 1988). The irregular presence of species depending of geographically neighboring stocks (as for *Sardina pilchardus*) is noticeable and may also be related to environmental fluctuations.

1. THE SPECIFIC DATA PROCESSING FOR SST RETRIEVAL FROM METEOSAT INFRARED IMAGERY

In terms of radiometric and spatial resolution, the accuracy permitted by geostationary satellites (0.5°C and 5 x 5 km subsatellite in the case of METEOSAT infra-red channel) is lower than the accuracy currently obtained from polar orbital satellites (0.12°C and 1 km for NOAA/AVHRR). Nevertheless, this lowest resolution is not really a constraint, even in coastal areas, if compared with the size of the oceanic structures observed at sea level, on the one hand, and with the strong thermal gradients encountered, on the other hand. On the contrary, the regularity of the earth scan provided by METEOSAT allows a simpler processing for geometric corrections, while its repetitiveness (every 30 minutes) allows improvements in discriminating the sea from clouds.

1.1. Pre-processing

Data pre-processing takes advantage of the half-hourly availability of earth scans by METEOSAT. Each satellite view of the earth is classically calibrated (transformation of the energy emitted by the earth to temperature by inversion of Planck's Law). An extraction of the working area is then performed and the image is geometrically corrected to a linear latitude and longitude projection.

In tropical areas, the infra-red radiance measured by the satellite sensor is systematically lower than the infra-red rariance emitted by the sea surface (except in the presence of suspended dusts), due to cold atmospheric water vapor. Consequently, by assuming that the SST is constant over 24 hours, the 48 images of the day are combined into a new image synthesis, retaining for each pixel the 'warmest' one of the time series.

Cloud cover in west Africa may strongly vary during one day, especially when the trade winds are weak. The efficiency of the 'maximum temperature method' is shown for 27 days, from 5 to 31 May 1991 (Fig. 1) by comparing the instantaneous cloud cover at 12h00 GMT (generally low cloud cover) and the daily synthesis index. The advantage of the repetitiveness of observations by a geostationary orbit appears clearly.

This important benefit in term of usable pixels for SST retrieval will also determine the performance of the sea-cloud discrimination, the major step of the processing in SST restitution.

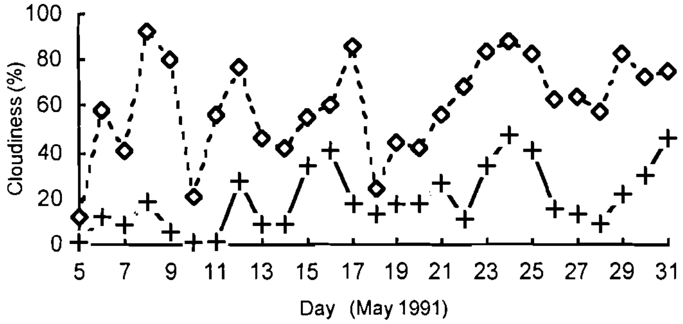


Fig. 1: Reduction of the cloud cover (%) on the daily thermal synthesis (solid line; crosses) compared to the instantaneous cloud cover (dotted line; open dots) at 12h00 GMT.

1.2. Sea-cloud discrimination

In remote sensing processing, sea-cloud discriminations are very often based on visible/infra-red comparisons. Nevertheless, this technique has some constraints. The major one for acquisition and processing is the large amount of data required, five times more in the case of METEOSAT. Furthermore, some low level clouds are strongly absorbent in the IR channel and remains transparent in the VIS one. The visible/infrared algorithm is then unusable.

The method we developed for sea-cloud discrimination is based on a comparison of a daily synthesis with the 'most probable' real SST field. This field is provided either from a climatology of SST or, more often, from a previously processed SST field. For adequate masking, this reference situation is chosen as close as possible to the daily synthesis, in terms of upwelling spatial extent.

A comparison of the radiative temperature synthesis (Fig. 2a) with this reference is then performed and the values with temperature deviation greater than a definite threshold (around 3°C according to the similarities of both fields) are considered to refer to clouds, and are masked (in black on Fig. 2b).

1.3. Atmospheric correction and SST restitution

The above resulting temperature field remains affected by atmospheric absorption, mainly due to the atmospherical water vapor. In tropical area, the apparent thermal absorption generally lies between 2°C (trade wind region) and 5°C or more (equatorial region).

According to the previous pre-processing steps (maximum temperature synthesis), and considering the difficulty to obtain direct information on atmosphere structure compatible with space and time resolution of the SST fields (6 km and 5 days in our case) the most adequate way to correct this temperature field from the atmospheric absorption is to use an exogenous source of SST data. The ships of opportunity data disseminated by the Global Transmission System (GTS) in the 'SHIP' meteorological messages (including SST, wind, air temperature, etc.) and synthesized in

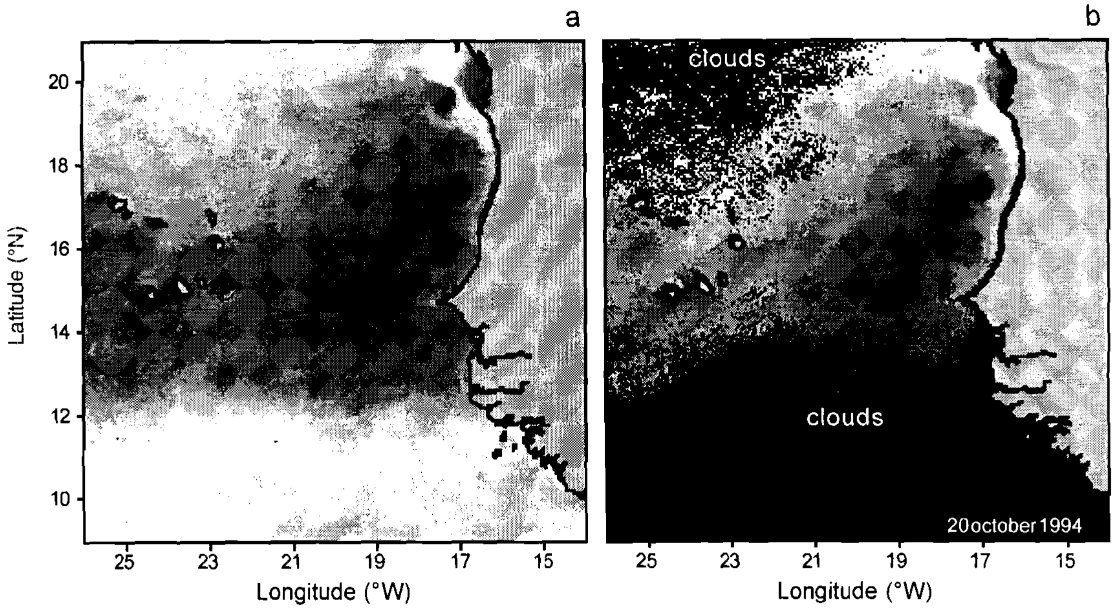


Fig. 2: Raw daily infrared synthesis on October 20, 1994 (a) and after cloud masking (b) in the beginning of the cold season. The SST decrease from dark grey to white while the cloudy area is displayed in black.

the COADS database (Roy and Mendelssohn,1994, this vol.) are rather convenient for this, by providing an adequate density of SST measurements, especially in Mauritanian and Senegalese areas (Fig. 3). Note that Figure 3a corresponds to the satellite situation displayed in Figure 2 and that SHIP data would not allow to detect the presence of the coastal upwelling in South Mauritania and North Senegal.

Because of their generally irregular spatial distribution, their poor sampling of the coastal area, (especially damaging during the beginning and the end of the upwelling season) and their relatively high instrumental noise, the usefulness of the SHIP *in-situ* data for precisely describing the SST field in coastal upwelling areas is generally very low.

The suspect SHIP data are first eliminated from the original data set, initially by comparison with a global SST climatology i.e., the Reynolds monthly SST climatology (Reynolds, 1982) or with our own climatology, preliminary computed from 1984 to 1989 (Demarcq and Citeau, 1995). Only values whose departure from the climatology is greater than 5°C are removed given the strong SST anomalies that are encountered in this upwelling area.

Despite the above limitations, the SHIP data provide a very satisfying estimation of the residual atmospheric absorption field. The latter is obtained by coupling ship data with the uncorrected satellite data (Fig. 2b) in order to give corrected SST field: the field of 'atmospheric correction' is then computed as the statistical departures of the satellite synthesis from the *in-situ* SHIP SSTs. An example of atmospheric field and the resulting corrected satellite SST field is displayed on Figure 4.

Standard SST processing was applied on a temporal basis of 5 days from 1984 to 1995. During the upwelling season off Senegal and Mauritania (from October to June), approximately 90% of the daily METEOSAT infrared synthesis can be used. This percentage is in fact seasonally variable, and depends on the mean coastal nebulosity, which is inversely proportional to trade wind intensity.

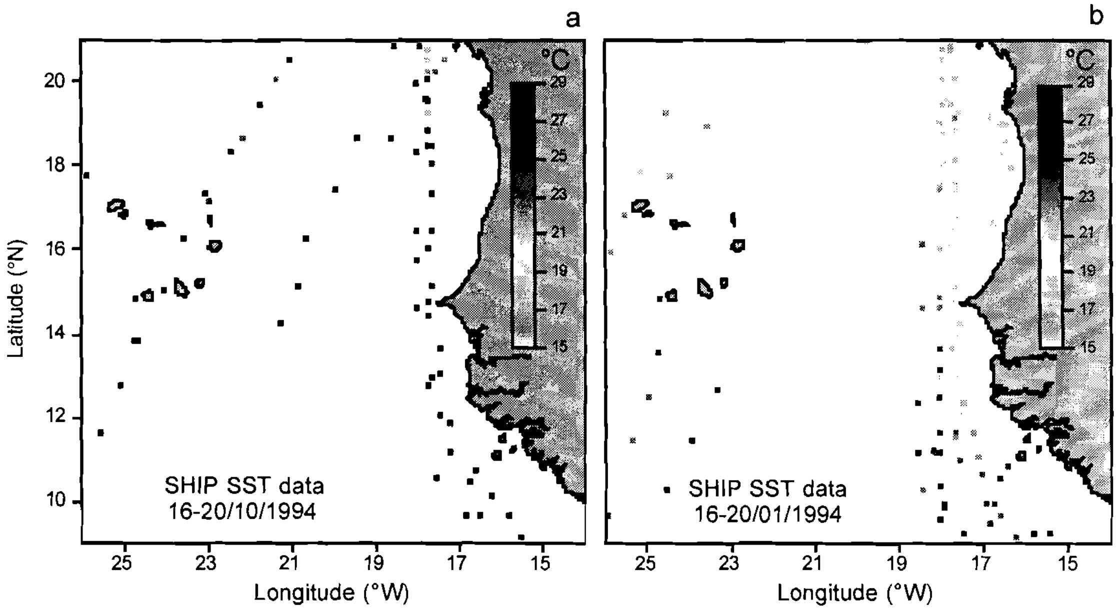


Fig. 3: Typical examples of "SHIP" data distribution offshore Mauritania and Senegal during 5-days periods at the beginning (a) and in the middle (b) of the upwelling season.

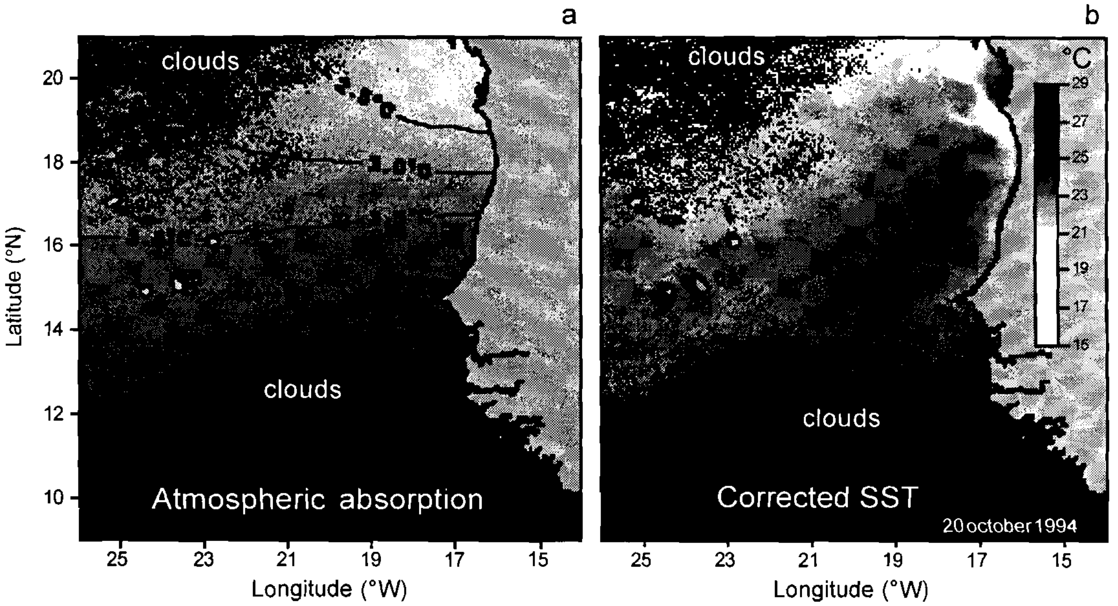


Fig. 4: Example of atmospheric absorption field (a) on 20 October 1994 (beginning of the upwelling season) and the resulting corrected satellite SST field (b).

For each daily synthesis, the cloudy area is masked and a radiative temperature field is calculated by a 5 day period. This field is then atmospherically corrected by adjusting the raw temperature values with the corrected SHIP SST measurements as described above.

2. COMPUTATION OF COASTAL UPWELLING INDEXES FROM SST FIELDS OFF MAURITANIA AND SENEGAL

The upwelling structures observed off Mauritania and Senegal from October to June are representative of a complex spatial dynamic, characterized by several local SST minima, mainly depending on wind direction and local bathymetry. The SST contrast with offshore waters depends mainly on the history of the upwelling in the preceding few weeks and tends to decrease during weak upwelling episodes. Superficial upwelling filaments moving offshore are frequently observed and reveal the concentrating effect of the shelf topography.

Figure 5 displays some commonly observed features. The main differences in SST field are linked to the large scale wind field variation, in both intensity and direction. According to Ekman's theory (Ekman, 1905), upwelling is maximum along coast lines parallel to the wind. The localization of this maximum varies according to wind direction and is particularly visible during the beginning of an upwelling event (see for example Figure 5a, b). During more intense phase of the trade winds, the cooling extent is continuous along the coast line, from 21°N to 10°N approximately (Fig. 5c). The southern most extent occurs around March, according to the most southern latitudinal position of the ITCZ/trades system which occurs in February and March (Citeau *et al.*, 1989).

The localization of the maximum flow of upwelled waters at the sea surface can be defined by a continuous area of minimum SST. This area is relatively fixed and closely linked to the local bathymetry (Fig. 6). SST at these locations is related to the instantaneous response of the upwelling system to wind forcing. This local spatio-temporal signal does not reflect the dilution effects due to past upwelling events that would be reflected in the mean SST calculated on a larger space scale.

An SST based upwelling index is calculated by differencing the local SST ('SSTsat') located at the minimum SST line (see Fig. 6) and a reference offshore temperature at the same latitude, to avoid taking into account large scale SST anomalies due to planetary climatic anomalies, not reflected in coastal areas. This reference temperature is chosen as the climatic SST temperature (and not the current offshore SST), calculated from 1984 to 1994 in the tropical Atlantic from a routinely elaborated product calculated from METEOSAT and SHIP data (Demarcq and Citeau, 1995; Demarcq and Suisse de Sainte-Claire, 1995).

According to Jacques and Tréguer (1986), the upwelled water off Mauritania and Senegal is essentially composed of SACW (South Atlantic Central Water). Regular coastal measurements in several oceanographic stations in Senegal (Roy *et al.*, 1985) show that the extreme coldest events correspond to very stable values of SST between 14.0°C and 14.5 °C. In this case, the salinity of the upwelled water (between 35.4‰ and 35.5‰) confirms its SACW origin.

According to the Ekman's theory and oceanographic coastal measurements off Senegal, the departure of the SST (measured as close as possible to its arrival location at the sea surface) from its minimum value (pure SACW) is

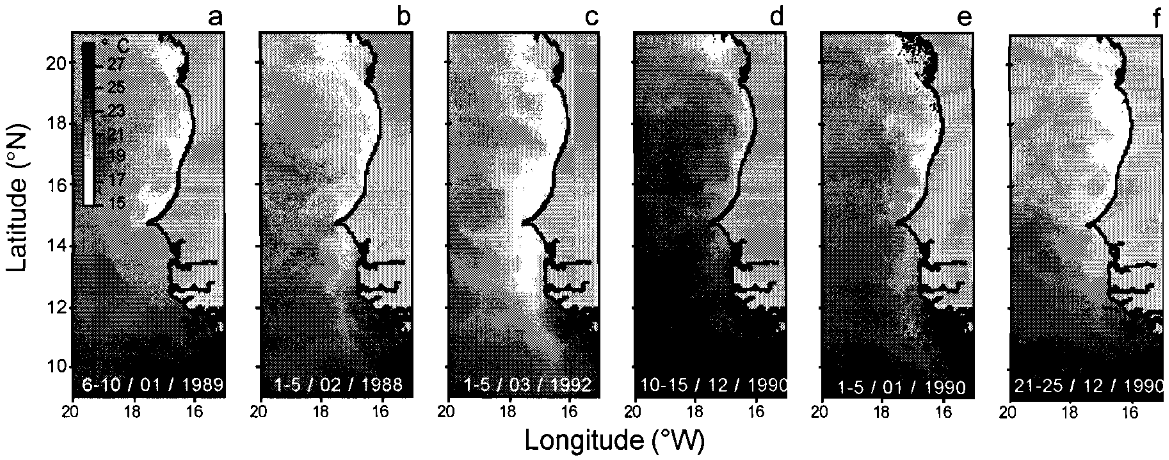


Fig. 5: Commonly observed superficial SST fields during the upwelling season off Mauritania and Senegal. The SST decrease from black (27°C) to white (17°C) for all images. Numerous filaments of upwelled waters moving offshore are clearly visible.

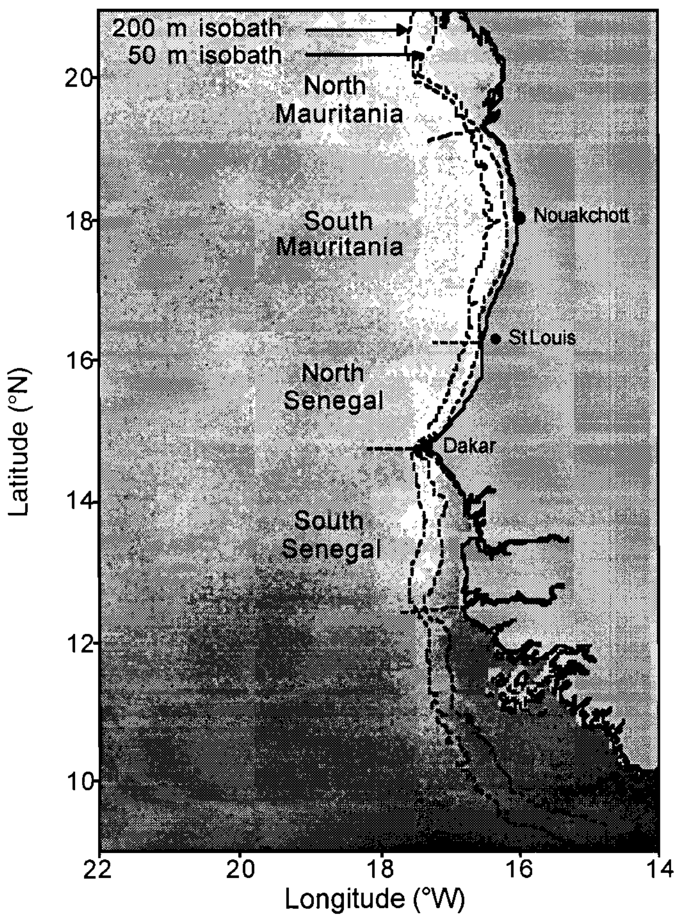
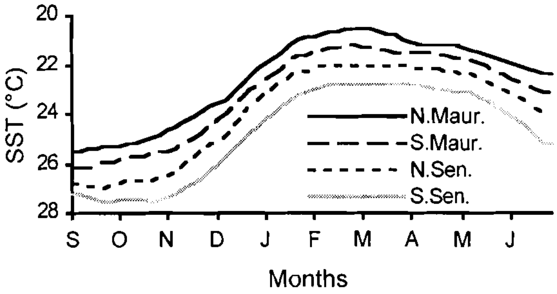


Fig. 6: Localization of the maximum flow of upwelled waters at the surface in relation to the local bathymetry and localization of coastal areas for upwelling index computation.

Fig. 7: Offshore SST (SSTmax [lat,month]) at 23°W off Mauritania and Senegal, calculated for the upwelling season of the years 1984-94 from satellite climatology.



directly linked to the upwelling flow. On the other hand, the maximum SST recorded from oceanographic coastal measurements in upwelling season during very weak upwelling phases varies seasonally, and converges towards the offshore SST at the same latitude, where the upwelling influence is negligible (because of the dilution of the upwelled water due to wind-generated turbulence).

The minimum value of SST expected at the upwelling centers, noted SSTmin, is the temperature of SACW as it reaches the surface. The maximum temperature, noted SSTmax, is chosen as the offshore climatic SST recorded at 23°W. Figure 7 displays this mean seasonal signal, calculated from the satellite climatology elaborated for the 1984-1994 period, from North Mauritania to South Senegal. This offshore signal is representative of the mean offshore upwelling influence. For a given year, it reflects the mean 'seasonal past' of the upwelling in the coastal area, but not its current intensity.

As reported in the time series of coastal oceanographic measurements of wind and SST, the seasonal variation of the observed value of SSTsat reflects the fact that, for a definite level of wind forcing, SST cooling is greater at the beginning or at the end of the upwelling season in a relatively warm environment than during the middle of the season in colder surrounding waters (Teisson, 1982). This makes it possible to compare the upwelling intensity during the whole season. The main difference with the Ekman index is the spatio-temporal integrating effect intrinsically linked to an SST based index and clearly displayed in Figure 8.

Important discrepancies remain between these two parameters (Fig. 8) partly due to the spotty sampling of the ship data close to the coast (especially in the south Mauritania region), because of the ship route locations (see Fig. 3). This fact is clearly shown across the differences in mean SST separately calculated from SHIP data (by objective analysis) and from satellite data over the same coastal area (Fig. 9). This difference leads to a severe under-estimation of upwelling extent and intensity calculated from the SHIP data. This under-estimation is high at the beginning of the upwelling season (when the offshore extent of the upwelling is generally weak, see for example Fig. 4 and 5d). In addition this under-estimation is different from one year to another, depending on the variability in the distribution of SHIP data.

From these observations, a relative SST-based upwelling index, ('SSTI') was calculated from the deviations of the locally observed SST from their extreme theoretical values, respectively fixed and seasonally varying.

To take into account the effect of the spatial dilution of the upwelled waters at the surface mixed layer, the SSTI may

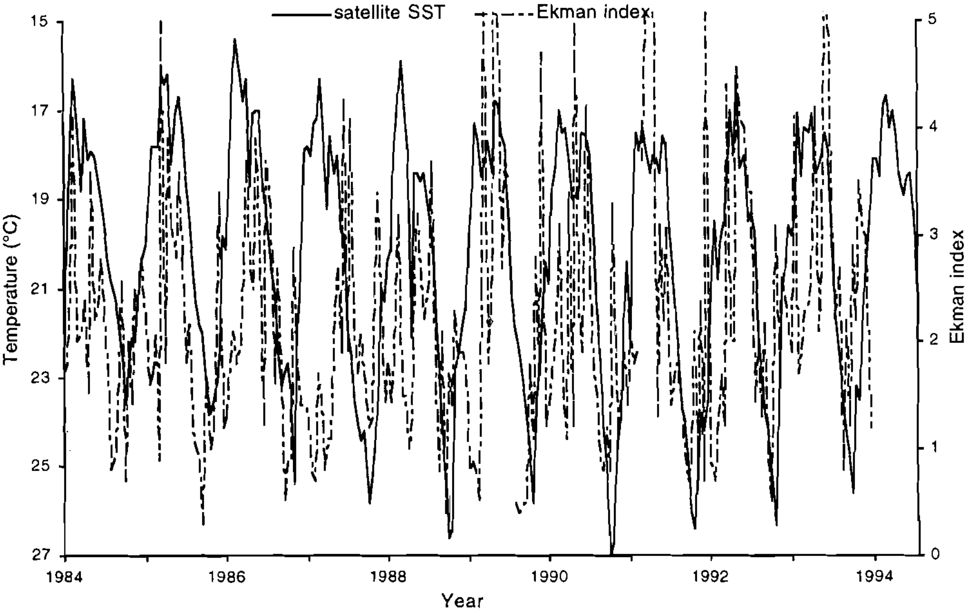


Fig. 8: Direct comparison of Ekman index and satellite SST (°C).

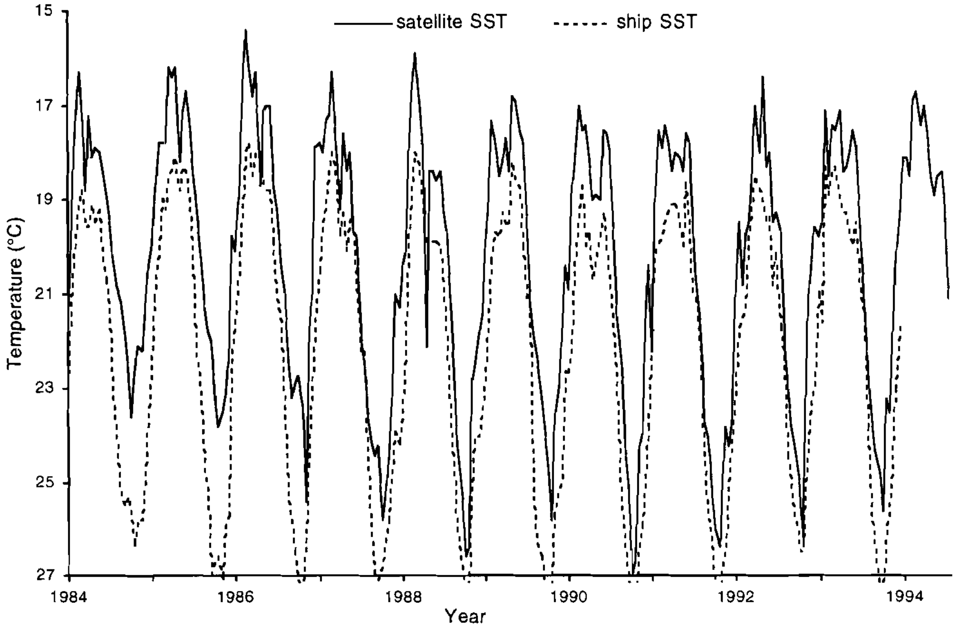


Fig. 9: Simple SST-based index calculated from SHIP data only (dotted line) and from the satellite product (solid line) in the south Mauritania region.

be expressed by the relation:

$$SSTI = (SST_{sat}\text{-}SST_{max}[lat,month]) /(SST_{min}\text{-}SST_{max}[lat,month])$$

Figure 10 shows the upwelling dynamic calculated using this index for 4 areas (see also Fig. 6) from North Mauritania to South Senegal for the 1984-1993 period. The 5-days time scale reproduces the short term dynamic of the upwelling intensity. Major bias (other than a systematic one) seem improbable, considering the large amount of input data and the processing homogeneity of the time series.

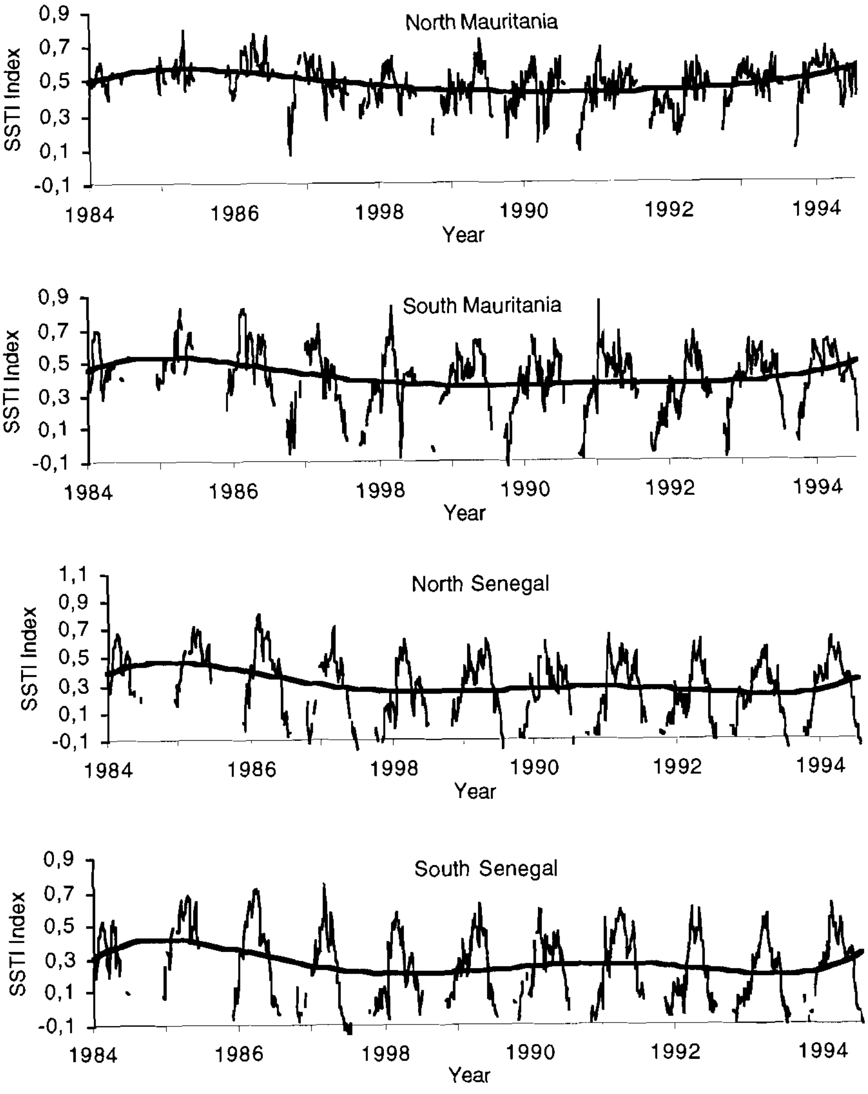


Fig. 10: SSTI index calculated from North Mauritania to South Senegal from 1984 to 1993.

3. TRENDS AND RELEVANT PARAMETERS IN UPWELLING DYNAMIC

The very high seasonal upwelling dynamic off West Africa is clearly shown through the SST-based upwelling index from 1984 to 1993 (Fig. 10) and is indirectly confirmed by the short scale spatial dynamics seen across the series of daily satellite images which suggest a daily response to the wind forcing, according to previous coastal measurements of SST.

Relative bias seems avoided in such SST satellite product, and no linear trend is obvious in term of upwelling intensity change considering a period of 11 years. Nevertheless, groups of 'cold' and 'warm' years are exhibited when a polynomial adjustment of 5th degree is used (Fig. 10, heavy lines). The years 1984 and 1985 are the coldest of the time series and 1988, 1989 and 1992 the warmest. It is interesting to note that 1985 was a warm year in the tropical Atlantic, due to the impact of the 1982-83 El Niño, and that the intensification of the coastal upwelling off Mauritania may be a local effect of this warming.

The general similarity of the short term trends of SSTI is obvious for the four areas (Fig. 11). An interesting observation is the case of the 89/90 and 90/91 cold seasons, for which an inversion of the trends is observed, from warm years in North Mauritania to cold years in South Senegal. The very regular North-South gradient of this phenomenon allows to reject the hypothesis of a processing artifact and to think that a temporary change in the zonal trade wind fields for this years did occur. This observation expresses a decline of the normal decreasing zonal gradient of the upwelling-favorable component of the trade winds, from Mauritania to Senegal. The temporal evolution of the SSTI (Fig. 11) shows that a strengthening in the trade winds in this region is sometimes in phase (in the case of the 85-90 period) and sometimes in opposing phase (in the case of the 90-94 period). It has been shown in this region that the intensity of the zonal gradient between the north of Mauritania and the Senegal enhances the migratory response of several migratory species (Cury and Roy, 1988; Binet, 1988; Binet this vol.).

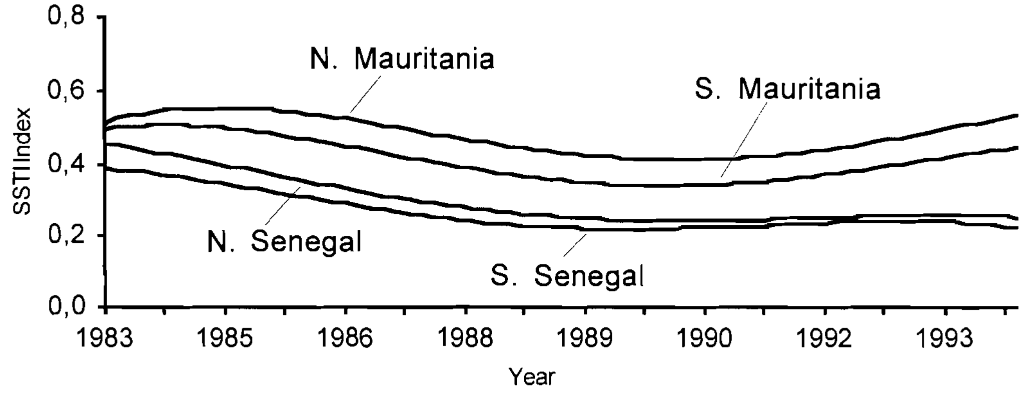


Fig. 11: Zonal structure of SSTI trends from North Mauritania to South Senegal (1984-93).

Long term changes in upwelling intensity have been examined from 1964 to 1993 from SHIP data. Both Ekman CUI (Fig. 12) and SST (Fig. 13) show a weak increase of upwelling intensity. This increase seems coherent with the other long-term observations in trade wind intensity (Bakun, 1990, 1992). Nevertheless, reducing potential impact on coastal fish populations to the unique long term trend due to the global warming would be restrictive, as it can be shown that the amplitude of the medium-term interannual variations are several times greater (or inverse) than the global warming amplitude. Also, the upwelling intensity off Senegal measured from remote sensed data presents a weak decrease in the trade winds for the 84-93 period (see Fig. 10).

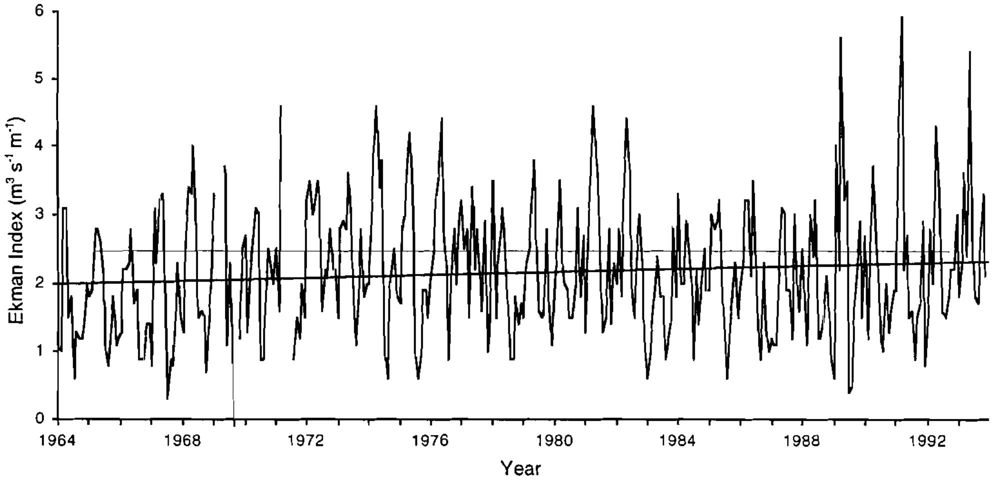


Fig. 12: Ekman CUI calculated from SHIP data in the Mauritania region, from 1964 to 1992.

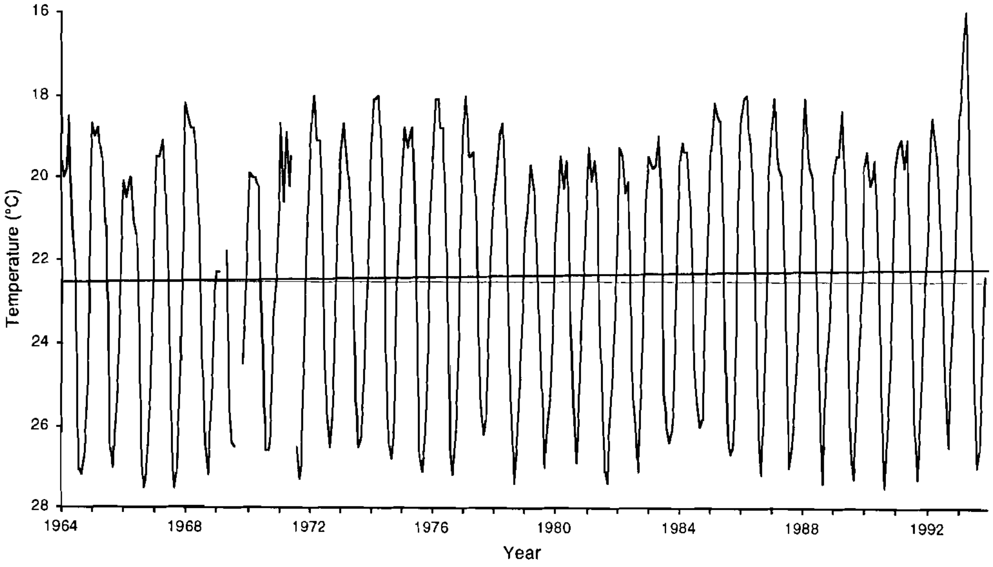


Fig. 13: SST from SHIP data in Mauritania region from 1964 to 1993.

Also, reducing upwelling dynamic to its mean intensity term would be restrictive, as it is obvious that many parameters are required to describe the upwelling dynamic at the different space and time scales involved. Among these, the duration of the upwelling season seems to be a very complementary parameter since no relation can be shown among upwelling intensity, season duration and seasonal timing, whether one uses satellite data or coastal oceanographic measurements (Portolano, 1986).

Similarly, the importance of timing of the hydrological transition on the local fisheries has been shown in Mauritania (Chavance *et al.*, 1991). In other upwelling regions, e.g., in Côte-d'Ivoire, the trend in upwelling season duration appears to have played a major role in the recovery of the *Sardinella aurita* fishery during the last years (Pezennec and Bard, 1992).

4. AN APPLICATION TO THE UNDERSTANDING OF THE SARDINE MIGRATION OFF SENEGAL

A very exceptional seasonal migration of *Sardina pilchardus* (Walb.) occured in Senegal at the end of 1993 (Binet, this vol.; I. Sow, pers. comm.), and represents the main event of the 93-94 fishing cold season for the local small-scale fishery. It seems interesting to examine some possible environmental causes for this anomaly, based on the dynamic of the upwelling seasonality observed from satellite data.

Sardina pilchardus is a pelagic species whose southern occurence (and the associated fishery) in West Africa was extended gradually from north Morocco in the 1920s, to South Morocco and North Mauritania around the 1950s (Belvèze, 1984). The southern extent of the fishery was estimated at 18°N in 1973 (Domanovsky and Barkova, 1981), while specimens where occasionally fished in Senegal in 1974 (Conand, 1975) and 1976 (Fréon, 1988). This species supports important fisheries in Morocco since the 1950s, the main period of southern extension of the species. The microphageous/phytoplanctonic regime of this species enables its development in strong upwelling ecosystems, as off Morocco and Mauritania, where the food web is short and dominated by phytoplanctonic production (Binet, 1991).

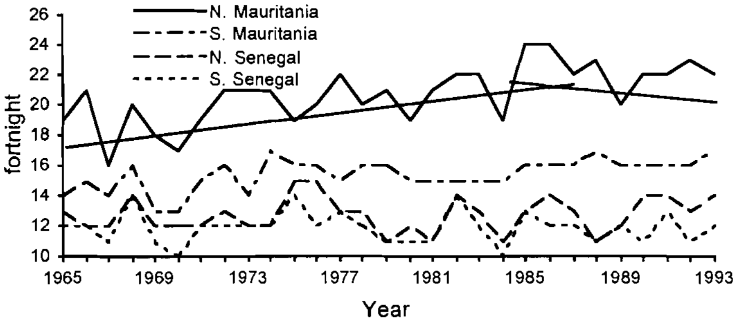
The long-term trade winds' increase from 1964 was related to the sardine fishery changes from 26°N to 14°N by Binet (this vol.). The dynamic of the upwelling as depicted from satellite observation from 1984 to 1994 is synthesized in a latitude/time diagram (Fig. 15), Binet's hypothesis.

Satellite observations show that the 1985-86 upwelling season was one of the coldest in term of both mean upwelling intensity and duration. These mean characteristics are confirmed by the SHIP observations, especially for the duration parameter (Fig. 14), while the satellite data shows that the cooling was particularly sudden and uniform from 20°N to 15°N (Cape Vert).

On the contrary, the 1992-93 cold season was characterized by a weak upwelling, associated with a remarkable regularity in the seasonal southward cooling.

We hypothesize that this progressive dynamic – induced by the same regularly zonal propagation of the trade winds – may have an 'attractive' effect on the seasonal migration amplitude of *Sardina pilchardus*, by reducing the natural barrier caused by the spatio-temporal discontinuities of SST it usually encounters. The 19-20°N upwelling discontinuity due to the local upwelling unfavorable coast line orientation (Fig. 5 and Fig. 6) may constitute a thermal barrier to the southward

Fig. 14: Cold season duration from North Mauritania to South Senegal calculated from SHIP data for the 1965-1993 period.



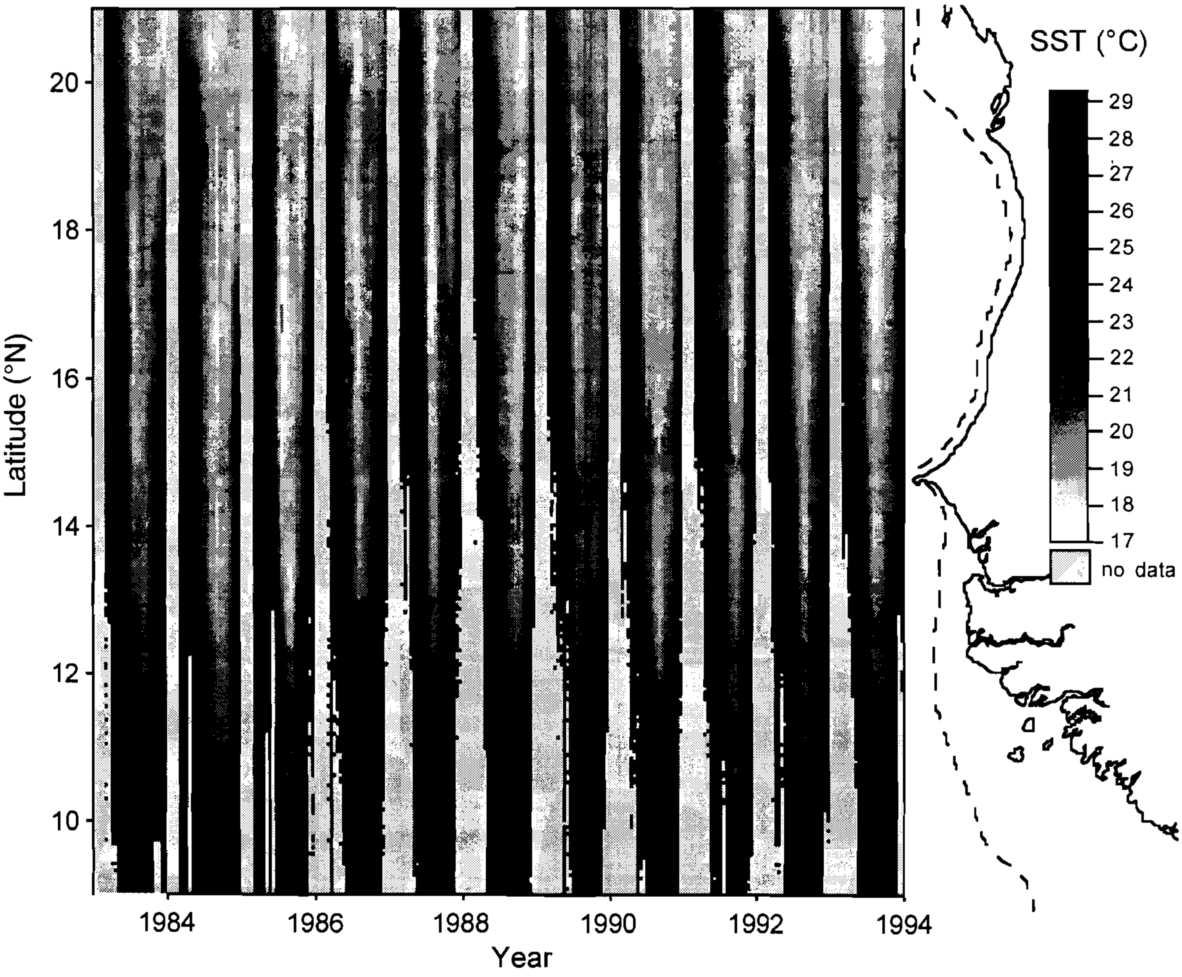


Fig. 15: Spatio-temporal dynamic of SST off West Africa, computed from satellite data for the 1984-1994 period.

migration of *S. pilchardus*. This discontinuity, very well evidenced by satellite observations (Demarcq and Citeau, 1995), reinforces the annual mean thermal gradient around 20°N and may be related to the estimated southern limit of *S. pilchardus*, which fluctuates around 18°N to 21°N since the 1970s.

Thus, the dynamic of the seasonal southward cooling seems to be one of the key parameters that affects the large amplitude seasonal migration of *S. pilchardus*. Thus, Binet's hypothesis appear validated.

CONCLUSION

Calculation of an SST based coastal upwelling index from satellite data made it possible to describe the short-term dynamic of the coastal upwellings off West Africa. Parameters such as mean upwelling intensity, long-term, trends, short-term, variability, SST zonal gradient, duration of the upwelling season, trends in seasonal variations and spatio-temporal modalities of seasonal transitions must be taken into account to understand the key processes that govern the biological cycles of fish species of economical importance in coastal upwelling areas. This is particularly true regarding the seasonal migrations of small pelagic species in upwelling areas,which are affected by long-term environmental variations and exceptional seasonal conditions. These changes may be considered responsible for the major species substitutions and alternation generally observed in upwelling regions, independently of the effects of fishing effort.

The processed data set shows that the informative potential of precise spatial and temporal remote sensed information would be of great interest for wider areas (such as the whole West African coast). Comparative studies should be conducted to analyze the impact of local environmental anomalies on biological processes in similar coastal upwelling ecosystems.

REFERENCES CITED

Bakun A. 1990. Global climate change and intensification of coastal ocean upwelling. *Science*, 247: 198-201.

Bakun A. 1992. Global greenhouse effects, multi-decadal wind trends and potential impacts on coastal pelagic fish populations. *ICES Mar. Sci. Symp.*, 195: 316-325.

Belvèze H. 1984. *Biologie et dynamique des populations de sardine (Sardina pilchardus Walbaum) peuplant les côtes atlantiques marocaines et propositions pour un aménagement des pêcheries.* Thèse Univ. Bret. occident., 532 p.

Binet D. 1988. Rôle possible d'une intensification des alizés sur le changement de répartition des sardines et sardinelles le long de la côte ouest-africaine. *Aquat. Living Resour.*, 1: 115-132.

Binet D. 1991. Dynamique du plancton dans les eaux côtières ouest-africaines: écosystèmes équilibrés et déséquilibrés. *In*: P. Cury et C. Roy (eds.). *Pêcheries ouest-africaines: variabilité, instabilité et changement*, ORSTOM, Paris. 117-136.

Chavance P., Y. Loktionov and M. Mahfoud. 1991. Importance des saisons de transition hydrologique et impact des anomalies climatiques sur l'activité d'une flottille industrielle pélagique en ZEE mauritanienne. *In*: P. Cury et C. Roy (eds.). *Pêcheries ouest-africaines: variabilité, instabilité et changement*, ORSTOM, Paris: 246-258.

Conand F. 1975. *Distribution et abondance des larves de clupéidés au large des côtes du Sénégal et de la Mauritanie en septembre, octobre et novembre 1972.* ICES, C.M. 1975/J:4, 9 p.

Citeau J., L. Finaud, J.P. Cammas and H. Demarcq. 1989. Questions relative to ITCZ migrations over the tropical Atlantic ocean, sea surface temperature and Senegal river runoff. *Meteorol. Atmos. Phys.*, 41 (4): 181-190.

Citeau J. and H. Demarcq. 1990. Restitution de la température de surface océanique en zone intertropicale à partir des données du satellite METEOSAT, *Bulletin de l'Institut Océanographique de Monaco*, numéro spécial 6: 142-172.

Cury P. and C. Roy. 1988. Migration saisonnière du thiof *(Epinephelus Aeneus)* au Sénégal: influence des upwellings sénégalais et mauritaniens. *Oceanol. Acta*, 11 (1): 25-36.

Cury P. and A. Fontana. 1988. Compétition et stratégies démographiques comparées de deux espèces de sardinelles (*Sardinella aurita* et *Sardinella maderensis*) des côtes ouest-africaines. *Aquat. Living Resour.*, 1: 165-180.

Demarcq H. and J. Citeau. 1995. Sea surface temperature retrieval in tropical area with METEOSAT: the case of the Senegalese coastal upwelling. *Int. J. Remote Sensing*, 16, 1371-1395.

Demarcq H. and E. Suisse de Sainte-Claire. 1995. Atlas satellitaire de la temperature de surface de l'Atlantique tropical est 1984-1993.

Domanevsky L.N. and N.A. Barkova. 1981. State of Sardine Sardina pilchardus Walb. stock, clupeiformes Clupeidae, in the region of Northwest Africa. FAO COPACE/TECH/81/31, 19-30.

Ekman V.W. 1905. On the influence of the earth's rotation on ocean currents. *Ark. f. Mat. Astr. och Fysik. K*; Sv. Vet. Ak., Stockholm, 1905-06 (2), 11p.

Fréon P. 1988. *Réponses et adaptations des stocks de clupéidés d'Afrique de l'ouest à la variabilité du milieu et de l'exploitation. Analyse et réflexion à partir de l'exemple du Sénégal*. ORSTOM, Coll. Etudes et Thèses, Paris, 287p.

Jacques G. and P. Treguer. 1986. *Ecosystèmes pélagiques marins*. Masson, 243 p.

Pezennec O. and F.X. Bard. 1992. Importance écologique de la petite saison d'upwelling ivoiro-ghanéenne et changements dans la pêcherie de *Sardinella aurita*. *Aquat. Living Resour.*, 5, 249-259.

Portolano P. 1986. Analyse des séries vents-températures de la mer en surface le long des côtes sénégalaises. Océanogr. trop., 21 (2): 205-227.

Reynolds R.W. 1982. Monthly averaged climatology of sea surface temperature. *NOAA Technical Report, NWS 31*, NOAA/National Meteorological Center, Silver Spring, MD., 40 p.

Rébert J.P. 1983. Hydrologie et dynamique des eaux du plateau continental sénégalais. *Doc. scient., Cent. Rech. Océanogr. Dakar-Thiaroye*, 106, 186 p.

Roy C., P. Jamin and A.O. Ba. 1985. Recueil des données de températures relevées aux stations côtières du Sénégal de 1947 à 1983. Arch., Cent. Rech. Océanogr. Dakar-Thiaroye, 138, 153 p.

Roy C. and R. Mendelssohn. 1994. *The COADS database on CD-rom*. First international CEOS meeting. Monterey 6-8 septembre 1994.

Teisson C. 1982. Application de la théorie d'Ekman à l'étude des courants et des remontées d'eaux profondes le long des côtes sénégalaises, Arch. Cent. Rech. Océanogr. Dakar-Thiaroye, 106, 79 p.

Variability and Trends in some Environmental Time Series along the Ivoirian and the Ghanaian Coasts

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ABSTRACT

Changes observed since 1966 in the Côte-d'Ivoire-Ghana coastal ecosystem are described. The specific characteristics of this ecosystem appear to be unique in the Guinea Current large marine ecosystem of which it is part. An analysis of several temperature data set is performed; this shows that the two upwelling seasons which occur in this ecosystem, have both changed in intensity, resulting in a weaker contrast between them. Also observed is a decrease in rainfall and an increase in wind speed. Some of these local environmental changes are in consonance with global changes.

RÉSUMÉ

Depuis 1966, les changements observés dans l'écosystème de Côte-d'Ivoire-Ghana sont décrits. Cet écosystème, aux caractéristiques spécifiques, apparaît comme unique dans l'ensemble plus vaste que représente l'écosystème du courant de Guinée auquel il appartient. L'analyse de différents jeux de données de température montrent que les deux upwellings sai-

sonniers qui se produisent dans cet écosystème ont vu leur intensité changer, d'où résulte un moindre contraste entre leurs intensités respectives. L'intensité des pluies a décru tandis que celle des vents s'est accrue. Certains de ces changements environnementaux sont à mettre en parrallèle avec des changements plus globaux.

1. SPECIFICITY OF THE CÔTE-D'IVOIRE-GHANA ECOSYSTEM

The Western Gulf of Guinea is part of the Guinea Current large marine ecosystem (Sherman *et al.*, 1991). The upwellings which occur in this area, especially off Côte-d'Ivoire and Ghana, (Fig. 1) have been actively studied since the early 1960s. Two upwelling seasons occur: a major one (in French the 'grande saison froide') and a minor one ('petite saison froide') have been identified (Morlière, 1970; Arfi *et al.*, 1991). Each of these two upwelling events has a main center and creates an important spatial and temporal heterogeneity in the Ivoiro-Ghanaian coastal marine ecosystem. Furthermore, the upwellings observed off Côte-d'Ivoire and Ghana are rather peculiar in that they cannot be said to be of the Ekman-type (Houghton, 1976; Bakun, 1978). The mechanisms causing the upwelling are not well understood, thus complex interactions among several processes are thought to contribute to the observed coolings and the related upwelling (Ingham, 1970; Marchal and Picaut, 1977; Picaut, 1983; Colin, 1988; Bard and Koranteng, 1995). As the observed cooling cannot be only related to wind intensity, analysis of sea temperatures has been the main approach to quantitatively assess the upwelling. In this paper, therefore, results are presented which are based on the analysis of available series of sea temperatures.

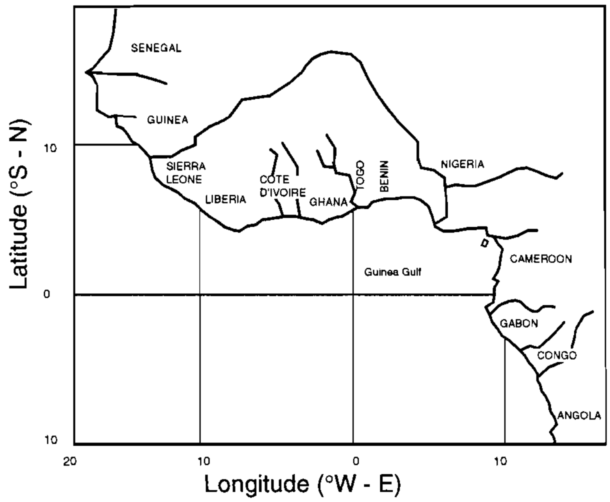


Fig. 1a: West Africa from Senegal to Angola, also showing the course of major rivers.

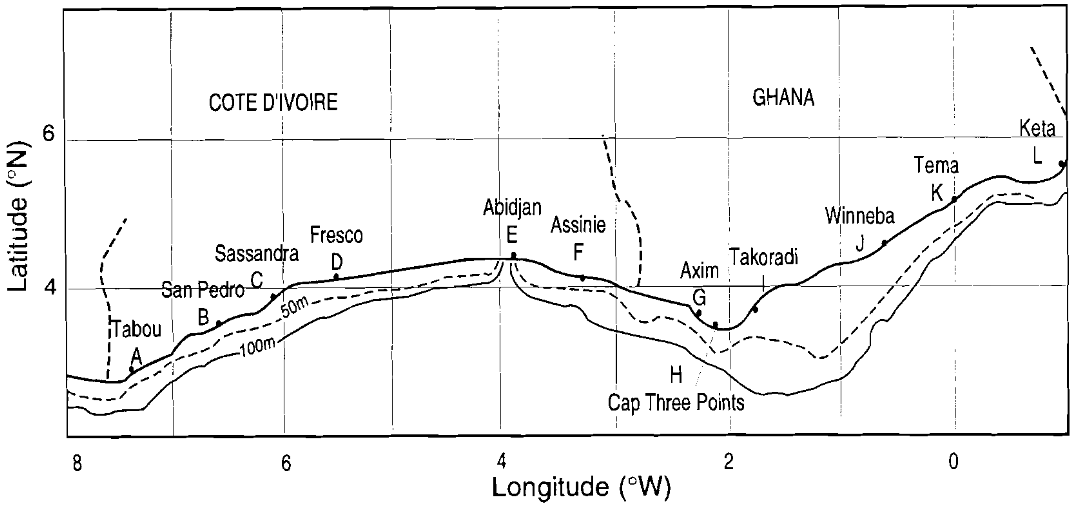


Fig. 1b: Continental shelves off Côte-d'Ivoire and Ghana and coastal stations mentioned in the text.

2. IMPORTANCE OF THE ENVIRONMENT TO THE IVOIRIAN AND GHANAIAN SMALL PELAGIC FISHERIES

Numerous scientific contributions on the fisheries for small pelagics of this area have acknowledged the importance of the marine environment to the abundance and availability of these fishes. The key factors in this ecosystem that have been considered to affect the pelagic fishery were the occurrence of two upwellings (ORSTOM/FRU, 1976; Cury and Roy, 1987; Mendelssohn and Cury, 1987; Le Loeuff *et al.*, 1993; Bard and Koranteng, 1995) freshwater discharge from major rivers (Binet, 1982; Mahé, this vol.) and water currents (Binet *et al.*, 1991). Consequently, observed patterns and trends of rainfall and river discharge in the area are included in this paper. No consistent time series exist on currents. Key results of the analysis of time series of wind data are also presented, because of the known influence of wind on physical processes such as upwelling intensity, turbulence, and surface mixing in the upper layer of the ocean.

3. AVAILABLE DATA: RAINFALL AND RIVER DISCHARGE, SEA TEMPERATURES AND WIND

The pattern and trends of rainfall observed at some coastal Ivoirian (Tabou, Grand-Lahou and Abidjan) stations (Pezennec, 1994) and Ghanaian (Axim, Saltpond, Takoradi, Tema) stations (Mensah, 1991) are presented. The data are available as monthly means of rainfall. Monthly volume of the river discharge for the four major Ivoirian rivers recorded in the last four decades were used; similar data could not be obtained in Ghana (see Mahé, this vol.).

Several sea temperature data set are used in order to explore changes that may have occurred in the ecosystem. Beach sea surface temperatures have been recorded daily at twelve coastal stations in Côte-d'Ivoire and Ghana since the 1970s and 1960s respectively (Arfi *et al.*, 1991). Offshore sea surface temperature for the area were obtained from the Comprehensive Oceanic and Atmospheric Data Sets (COADS) database (Roy and Mendelssohn, this vol.). Monthly means for two by two degree squares (longitude and latitude) for the area between 4 - 6°N and 2 - 8°W (off Côte-d'Ivoire), and 2°W - 2°E (off Ghana) are used in the analysis. SST and the cooling events which affect these coastal waters were also followed using METEOSAT infrared satellite imagery received and processed at the 'Unité de Traitement des Images Satellitales' (UTIS; ISRA/ORSTOM) in Dakar, Senegal. Available data from vertical profiles of sea temperatures recorded off Abidjan (Côte-d'Ivoire) and Tema (Ghana) were also examined, as well as the depth of the 21°C isotherm, which corresponds to the depth of the top of the thermocline in the Gulf of Guinea (Merle, 1978).

Values of the two components (zonal and meridian) of the wind were obtained from the COADS database; the resultant intensity and direction of the wind were computed using these values.

All analyses start from 1966, the year from which reliable fisheries data in the two countries begin.

4. OBSERVED GENERAL PATTERNS

4.1. Rainfall and river discharge

The seasons observed in the Ivoirian and Ghanaian coastal area could be classified as follows:

i) main dry season (December -May);
ii) main raining season (May-July);
iii) a second dry season (July-September);
iv) a second raining season (September-November).

The rainfall patterns observed at the selected Ivoirian and Ghanaian stations are in agreement with this classification (Fig. 2). It rains less in coastal Ghana than in coastal Côte-d'Ivoire. The volume of river discharge recorded in the western part of Côte-d'Ivoire is much more important than in the central or eastern parts. A first, minor period of flood is observed in June, the major flood occurs from August to November.

4.2. Wind intensity and direction

The major winds in this area are southerly to south-westerly. This direction is the same in both countries from January to April but for the rest of the year the south-westerly direction is more pronounced in Ghana. During the period 1966-1990,

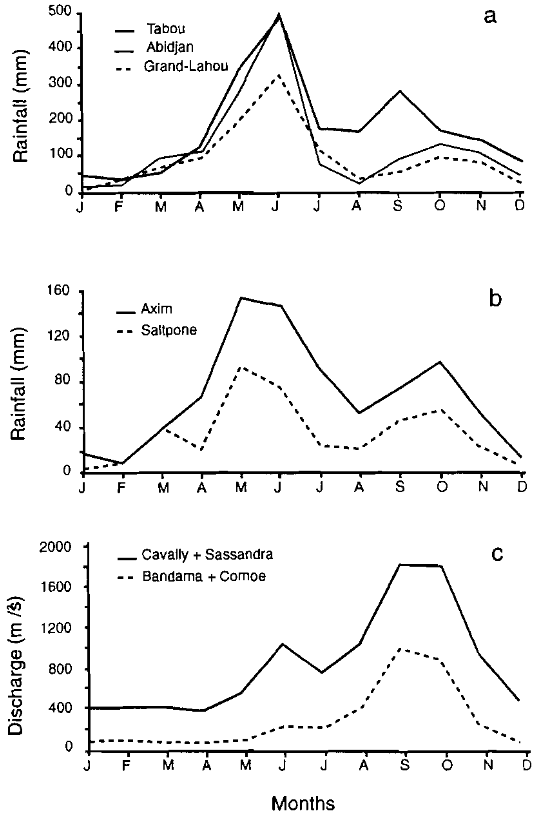


Fig. 2: Monthly means of rainfall in Côte-d'Ivoire (a), in Ghana (b) and river discharge in Côte-d'Ivoire (c).

the following were observed (Fig. 3):

- the meridian component of the wind increases between April and June, peaks in June-July and declines steadily untill January;
- the zonal component has two maxima, one in February-March and the other in August-October.

The resultant wind follows a pattern similar to that of the meridian component, with a maximum in June-July.

4.3. Intensity and extent of the two upwellings

Figure 4 shows fortnightly average temperatures recorded at coastal stations in Ghana and Côte-d'Ivoire in the period 1978-1991. The means for each station clearly show the two upwelling seasons occuring in this ecosystem. The minor upwelling season is observed between January and March, is more intense in Côte-d'Ivoire, especially in the western part, obviously than in Ghana (Fig. 5). The major upwelling is observed between July and September along the entire coastline. However, the configuration of the continental shelf in western Ghana favours a stronger development of this upwelling in that area. From the remote sensing pictures (Fig. 6), the surface isotherms recorded during the minor upwelling season are typical of an upwelling event which affects western Côte-d' Ivoire (East of Cape Palmas) and extends to the eastern part of Côte-d'Ivoire but which is not very visible off Ghana. During the major upwelling season, the upwelling is well

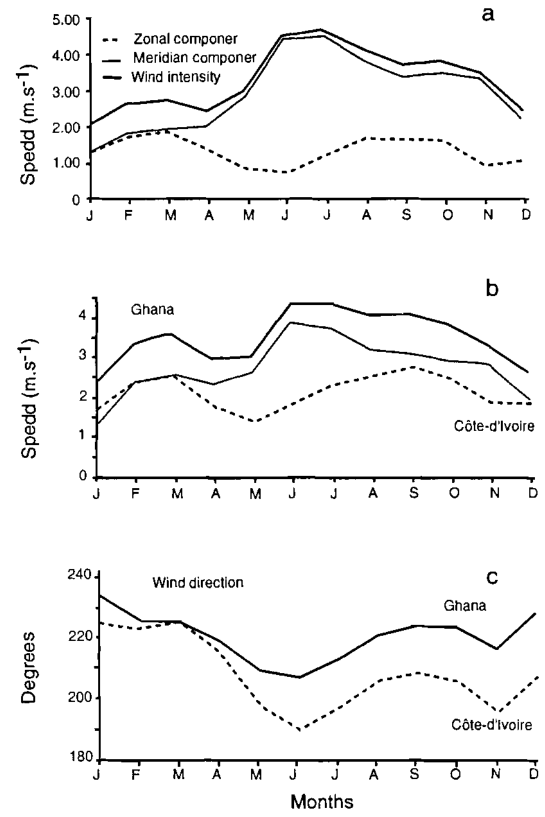


Fig. 3: Monthly means of the zonal and meridian components of the wind (a), of wind intensity (resultant) (b) and of wind direction (in degrees from the South-North direction) (c) along the Côte-d'Ivoire and Ghana coasts.

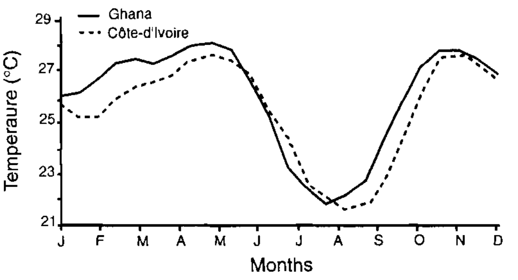


Fig. 4: Fortnightly means of the sea surface temperature from the coastal stations of the Côte-d'Ivoire and of Ghana (1978-1991 average).

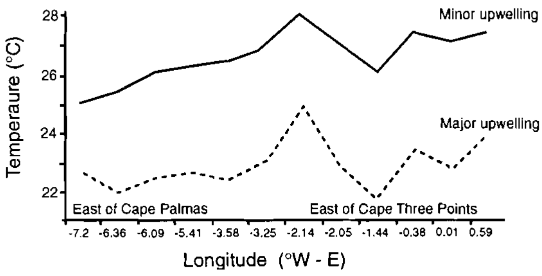
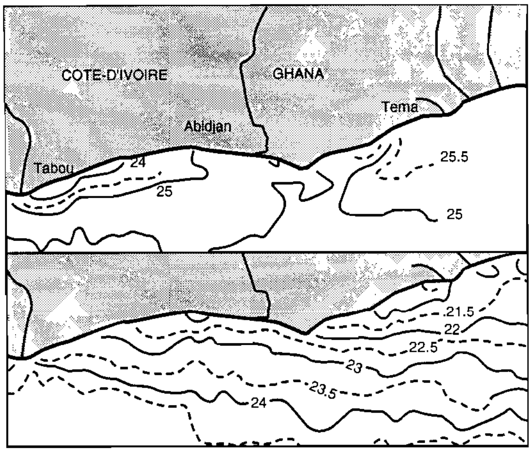


Fig. 5: Means of the sea surface temperature during the two upwelling seasons from western Côte-d'Ivoire to eastern Ghana. (1978-1991 average for each station).

Fig. 6: Surface isotherms (in °C) in the Ivoirian and Ghanaian coastal regions (from Meteosat remote sensing picture, UTIS):
-upper panel, minor upwelling season (January 26-31, 1990);
-lower panel, major upwelling season (September 01-05, 1986). From Pezennec and Bard (1992).



developed over the Ghanaian continental shelf and extends to Côte-d'Ivoire. Even though the difference between the two upwelling seasons seems quite important, it has been observed that the minor upwelling off Côte-d'Ivoire may occasionally be as strong as the major upwelling. For example, the 1986, 1987 and 1990 minor upwelling seasons were very intense off Côte-d'Ivoire and as, indicated in Figure 7, the rise of the thermocline during these seasons was quite similar to the situation observed during the major upwelling season.

4.4. Trends in environmental time series

The mean annual rainfall recorded at stations in Côte-d'Ivoire and Ghana showed a significantly decreasing trend from 1968 to 1990 (Fig. 8). According to Lamb *et al.* (1986), this decrease of rainfall was a general observation in sub-saharan Africa during the 1970s and 1980s (see also Mahé, this vol.). A decrease of river discharge was also observed during the 1980's for tropical rivers in the Gulf of Guinea (Mahé, 1991). In Côte-d'Ivoire, a drastic decrease of river discharge was observed in the early 1970s (Fig. 8) but no trend was evident after the building of dams on the rivers Bandama (1972) and Sassandra (1978). The annual means of the two components of the wind show a significantly increasing trend from 1966 to 1990 in both countries (Fig. 9). For the minor upwelling season, there is no significant trend for both components in both countries (Pezennec, 1994). In the major upwelling season, the two components show different trends: the zonal component shows a significantly increasing trend in both countries, but no trend could be observed for the meridian component. This difference would imply that the direction of the wind becomes closer to that of the equator.

As depicted in Figure 9, the annual means of the wind speed (resultant) show a significantly increasing trend in both countries (1966-1990). A similar trend is observed during the major upwelling season in both countries but no trend could be observed for the minor upwelling season (Pezennec, 1994). Bakun (1990) reported increasing wind speed in other upwelling areas and attributed this trend to the greenhouse effect.

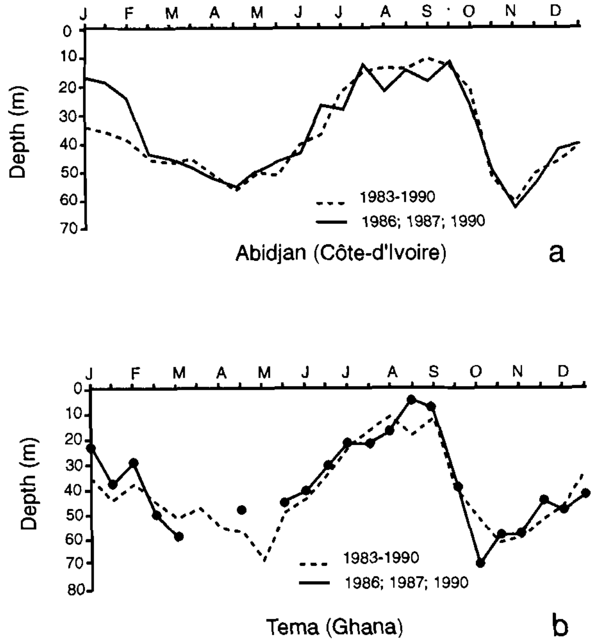


Fig. 7: Fortnightly depth of the 21°C isotherm off Abidjan (Côte-d'Ivoire) (a) and Tema (Ghana) (b).

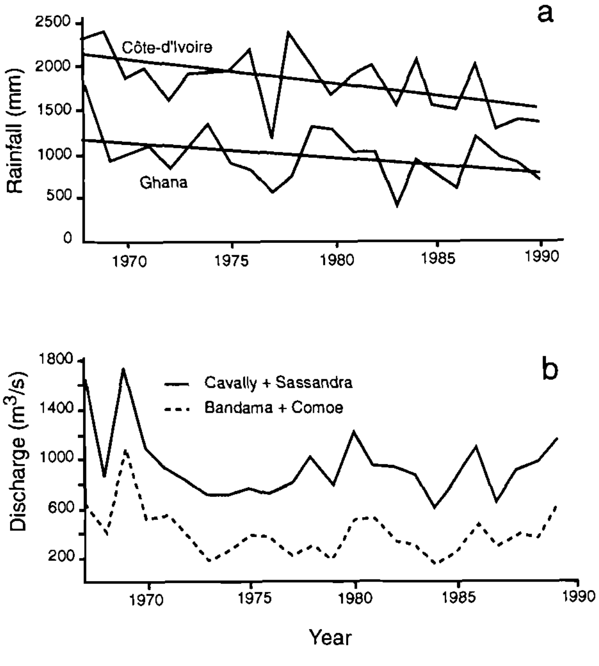


Fig. 8: a) Annual mean rainfall in the coastal areas of Côte-d'Ivoire (average for Tabou, Grand-Lahou and Abidjan) and Ghana (average for Takoradi and Tema); b) Annual means of river discharges in the Côte-d'Ivoire (sum of Bandama-Comoe and Cavally-Sassandra). The linear trends are least-squares estimates (Côte-d'Ivoire: $p=0.002$; Ghana: $p=0.03$)

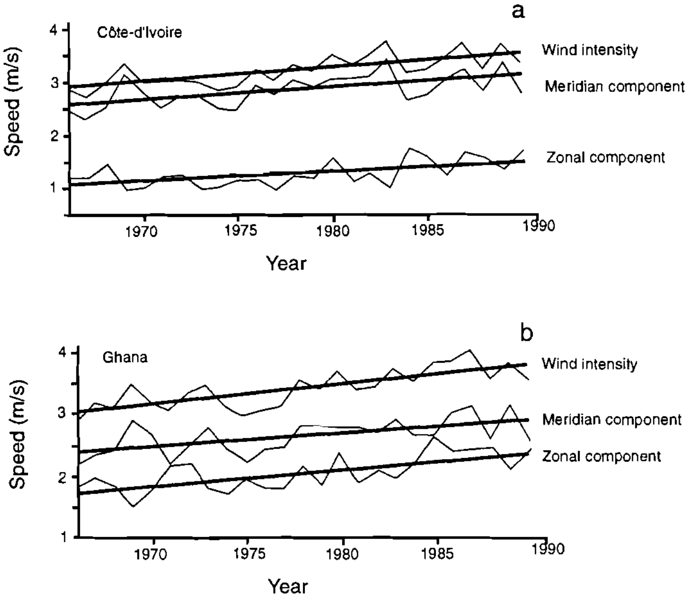


Fig. 9: Annual means of the wind components and wind intensity (resultant) off Côte-d'Ivoire and off Ghana and linear trends observed from 1966 to 1990 (Côte-d'Ivoire: Wind intensity p=0.0004; Meridian component p=0.018; Zonal component p=0.02. Ghana: Wind intensity p=0.00006; Meridian component p=0.011; Zonal component p=0.001).

4.5. Changes in relative upwellings intensities

The annual means of offshore sea surface temperatures sharply decreased between 1973 and 1976 in both countries, increased till the mid 1980s and decreased again, especially after 1987. The main point, however, is that the two upwelling seasons did not exhibit the same trends. Offshore temperatures recorded during the major upwelling season appear to have increased during the period under consideration, whereas those recorded during the minor upwelling season show an

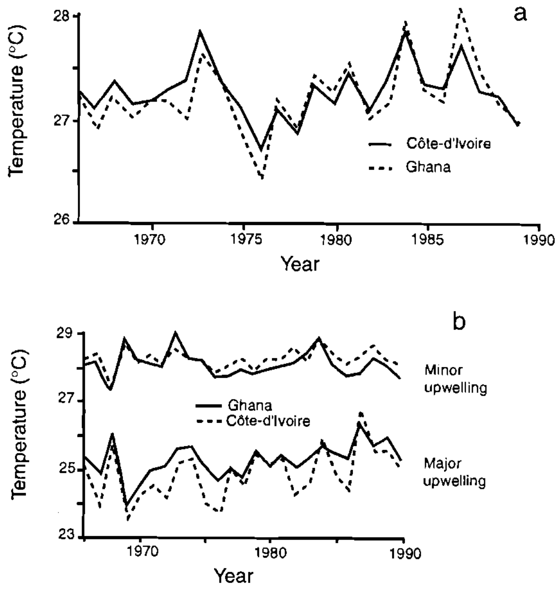


Fig. 10: a) Annual means of the offshore sea surface temperature off Côte-d'Ivoire and Ghana; b) annual means of the SST for the minor and major upwelling seasons (from COADS data).

opposite trend (Fig. 10). The result is that the difference between the intensity of the two upwelling seasons is decreasing with a significant trend since the early 1970s (Fig. 11). In both countries, the difference between the average temperature of the two upwelling seasons reduced on the average, by one degree between 1970 and 1990 (Pezennec and Bard, 1992).

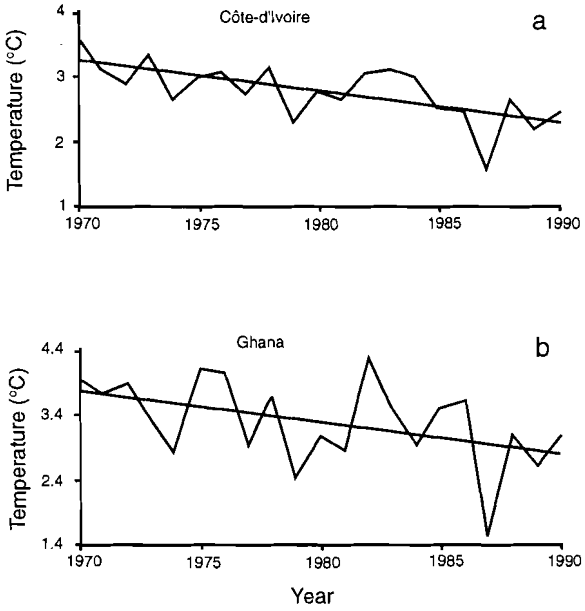


Fig. 11: Differences between the mean temperatures of the minor upwelling season (PSF) and the major upwelling season (GSF) from 1970 to 1990 (from COADS data), Côte-d'Ivoire (a), Ghana (b). The linear trends are least-squares method estimates (Côte-d'Ivoire p=0.0013; Ghana p=0.039).

DISCUSSION

The coastal region off Côte-d'Ivoire and Ghana is unique in the Guinea Current large marine ecosystem. The intensity of some of the large upwelling areas of the world have increased; this change may be related to global climatic change. Although some global climatic changes, such as an increase of wind speed and a decrease of rainfall have also been noticed in this region, these have apparently not affected the intensity of the upwelling. Rather, the observed local change is that the relative intensity of the two upwellings (major vs minor) of this region has changed.

ACKNOWLEDGMENTS

The DUSRU (Dynamics and Uses of Sardinella Resources from Upwelling off Ghana and Côte-d'Ivoire) program provided the means to have this work done. We thank the CEOS (Climate and Eastern Ocean Systems) project for sponsoring our participation in the Monterey meeting.

REFERENCES CITED

Arfi R., O. Pezennec, S. Cissoko and M. Mensah. 1991. Variations spatiale et temporelle de la résurgence ivoiro-ghanéenne. *In*: P. Cury and C. Roy (eds.). *Pêcheries ouest-africaines: variabilité, instabilité et changement*. ORSTOM, Paris: 162-172.

Bakun A. 1978. Guinea Current upwelling. *Nature*, 271:147-150.

Bakun A. 1990. Global climate change and intensification of coastal ocean upwelling. *Science*, 247: 198-201.

Bard F. X. and K. A. Koranteng (eds.). 1995. *Dynamics and Uses of Sardinella Resources from Upwelling off Ghana and Côte-d'Ivoire (DUSRU), Accra, 5-8 October, 1993*, ORSTOM, Paris 438p.

Binet D. 1982. Influence des variations climatiques sur la pêcherie des *S. aurita* ivoiro-ghanéennes: relation sécheresse-surpêche. *Oceanol. Acta*, 5: 443-452.

Binet D., E. Marchal and O. Pezennec. 1991. *Sardinella aurita* de Côte-d'Ivoire et du Ghana. Fluctuations halieutiques et changements climatiques. *In*: P. Cury and C. Roy (eds.). *Pêcheries ouest-africaines: variabilité, instabilité et changement*. ORSTOM, Paris, 320-342.

Colin C. 1988. Coastal upwelling events in front of the Ivory Coast during the FOCAL program. *Oceanol. Acta*, 11: 125-138.

Cury P. and C. Roy. 1987. Upwelling et pêche des espèces pélagiques côtières de Côte-d'Ivoire: une approche globale. *Oceanol. Acta*, 10: 347-357.

Houghton R.W. 1976. Circulation and hydrographic structure over the Ghana continental shelf during the 1974 upwelling. *J. Geophys. Res.*, 94 (4): 4816-4828.

Ingham M.C. 1970. Coastal upwelling in the northwestern Gulf of Guinea. *Bull. Mar. Sci.*, 20: 1-34.

Lamb P.J., R.A. Peppler, S. Hastenrath. 1986. *Nature*, 322: 238-240.

Le Loeuff P., E. Marchal and J.B. Amon Kothias. 1993. Environnement et ressources aquatiques de Côte-d'Ivoire. ORSTOM, Paris, T1: Le Milieu marin, 586p.

Mahé G. 1991. La variabilité des apports fluviaux au golfe de Guinée utilisée comme indice climatique. *In*: P. Cury and C. Roy (eds.) *Pêcheries ouest-africaines: variabilité, instabilité et changement*. ORSTOM, Paris: 147-161.

Marchal E. and J. Picaut. 1977. Répartition et abondance évaluées par échointégration des poissons du plateau continental ivoiro-ghanéen en relation avec les upwellings locaux. *J. Rech. Océanogr.*, 2: 39-57.

Mendelssohn R. and P. Cury. 1987. Fluctuations of a fortnightly abundance index of the Ivorian coastal pelagic species and associated environmental conditions. *Can. J. Fish. Aquat. Sci.*, 44: 408-428.

Mensah M.A. 1991. The influence of climatic changes on the coastal oceanography of Ghana. *In*: P. Cury and C. Roy (eds.) *Pêcheries ouest-africaines: variabilité, instabilité et changement*. ORSTOM, Paris: 67-79.

Merle J. 1978. *Atlas hydrologique saisonnier de l'océan Atlantique intertropical*. Travaux et Documents, ORSTOM, 82, 184 p.

Morlière A. 1970. Les saisons marines devant Abidjan. *Doc.Scient. Cent. Rech. Océanogr. Abidjan*, 2: 1-15.

ORSTOM/FRU. 1976. *Rapport du groupe de travail sur la sardinelle (S. aurita) des côtes ivoiro-ghanéennes, Abidjan, 28 juin-3 juillet 1976*, ORSTOM, 62 p.

Pezennec O. 1994. *Instabilité et changements de l'écosystème pélagique côtier ivoiro-ghanéen. Variabilité de la ressource en sardinelles : faits, hypothèses et théories*. Thèse de Doctorat. Océanologie biologique. Université de Bretagne Occidentale, Brest.

Pezennec O. and F.X. Bard. 1992. Importance écologique de la petite saison d'upwelling ivoiro-ghanéenne et changements dans la pêcherie de *Sardinella aurita*. *Aquat. Living Resour.*, 5: 249-259.

Picaut J. 1983. Propagation of the seasonal upwelling in the eastern equatorial Atlantic. *J. Phys. Oceanogr.*, 13: 18-37.

Sherman K., L. M. Alexander and B. D. Gold (eds.). 1991. *Food chains, yields, models, and management of large marine ecosystems*. Westview Press, 310 p.

Trends and Variability of Environmental Time Series along the Senegalese Coast

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ABSTRACT

The variability and trends of some environmental time series measured on the Senegalese coast are presented. Since the 1980s, wind speeds are increasing and since 1988, sea surface temperatures are decreasing. Nitrates, which are related to temperature, fluctuate notably during the upwelling periods. Salinity varies depending on many factors such as rainfalls which occur during the hot season. Phosphates and chlorophyll are also variable according to seasons and years. Seasonal variations predominate for the majority of the studied parameters.

RÉSUMÉ

La variabilité et les tendances observées dans certaines séries temporelles d'environnement mesurées sur les côtes sénégalaises sont présentées. Depuis les années quatre-vingt, les vitesses des vents augmentent et, depuis 1988, les températures de surface de l'océan diminuent. Les nitrates, qui sont liés à la température, fluctuent de façon notable pendant les périodes d'upwelling. La salinité varie en fonction de nombreux facteurs, comme les pluies qui ont lieu durant la saison chaude. Les phosphates et la chlorophylle sont aussi variables selon les saisons et les années. Les aspects saisonniers sont prédominants pour la plupart des paramètres étudiés.

INTRODUCTION

The environment of the Senegalese coast has been studied in different ways: on the one hand, sea surveys are undertaken at various times of the year; on the other hand samples are regularly taken off the coast. They constitute time series used for a routine monitoring of the hydro-climate.

Others methods such as the monitoring of sea surface temperatures by remote sensing and by ships of opportunity are others means of studying the environment.

Data have been processed in different studies (Berrit, 1962; Rossignol and Aboussouan, 1965; Rébert, 1978; Gallardo, 1981; Portolano, 1981; Teisson, 1982; Rébert, 1983; Touré, 1983). They have permitted to understand the hydrology of the Senegalese coast. The morphological contrast between the north and the south of Cap-Vert and the seasonal contrast, mainly due to the winds, are the main characteristics of the coast. Moreover, the temporal series collected from the coastal stations have shown other phenomena such as a North-South shift of the upwelling phenomenon on the fringe of the coast. Indeed the upwelling lasts longer in the South than in the North and seems to start sooner in the South (Teisson, 1982). However, because of the importance of the upwelling in the enrichment of the Senegalese waters, most of those works tend to study parameters such as temperature or wind. The other parameters, such as salinity and nutrient salts have so far attracted very little attention.

The aim of this note is to determine the variability and trend of the various parameters monitored from coastal stations. The wind will be also considered because of its impact on the dynamic of the upwelling.

1. MATERIAL AND METHODS

1.1. Choice and distribution of stations

The first coastal stations along the Senegalese coastline have been established in the 1950s. Rightaway, it appeared that the Senegalese coast should be divided into three zones (the Grande Côte in the North, the Cap-Vert area and the Petite Côte in the South). Thus, stations were established such as to cover these three sectors. From North to South, we have stations at Saint-Louis, Kayar, Yoff, Thiaroye, Gorée and Mbour (Fig. 1). They have progressively been established and consequently time series are available from ten to twenty years.

These stations were established to monitor the hydrology of the marine zone regularly, and at a low cost. The Cap-Vert stations, like all the others, were located such as to monitor the littoral. These stations, however, benefit from the proximity of the CRODT laboratory whose team of technicians can carry out on the spot sampling. This makes it possible to sample nutrient salts and phytoplankton in addition to the physical parameters.

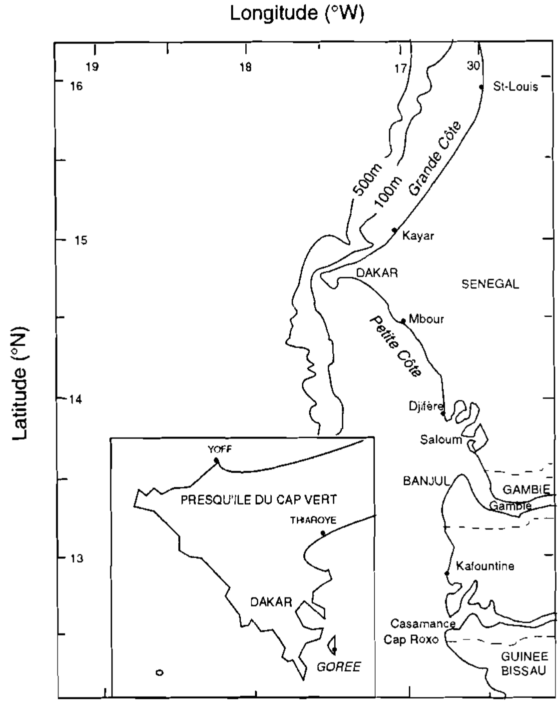


Fig. 1: Location of coastal stations (dots) off Senegal.

1.2. Frequency and mode of the sampling

Sampling at coastal stations is done with buckets. The temperature and salinity data are collected daily. Subsamples are collected in 200 ml glass bottles for salinity and 250 ml for chlorophyll measurements; for nitrates and phosphates, 50 ml bottles are used. The nutrient salt samples are taken weekly from two of the three Cap-Vert stations, i.e., from Gorée and Yoff. Thiaroye station is too polluted for these parameters to reflect what really happens in the open sea. Chlorophyll samples are taken every day at Yoff and Thiaroye and every week at Gorée. The time series of nutrient salts are very short (they only cover the last three years), whereas the salinity and temperature series cover all the stations for periods of up to thirty years. The wind data are gathered every three hours and come from the Dakar-Yoff meteorological station. These data have been collected for about thirty years.

1.3. Method

Temperatures are measured with a precision of 1/10th of a degree Celsius, using a mercury thermometer; a digital salinometer is used in the laboratory to determine salinity. The nutrient salt samples are kept at a cold temperature in chloroform as soon as they are taken. Estimation of nutrient salt levels is done using the method of Strickland and

Parsons (1972). Chlorophyll levels are estimated using a Turner 111 fluometer; when the chlorophyll concentration was very high, a Bausch-Lomb 2000 spectrophotometer was used.

2. RESULTS

2.1. Temperature

The temperature daily data show that there is little variability from one day to the next, except for the cold season, during which diurnal fluctuations of over 1°C are sometimes observed. The monthly mean temperature measured in one station for all the years vary according to seasons. The length of the cold season is variable and depends on the station considered.

At Mbour, the variations around the monthly median were relatively weak from 1959 to 1992 particularly during the hot season. The strongest fluctuation is observed in February. The cold season (below 24°C) goes from November to mid May and the minimum temperature is about 19°C. On the 'Grande Côte' along the north part of the coast, as well as at Cap-Vert, we observed higher variations at the beginning and at the end of the cold season, and during the transitional season (from October to December and from April to June). The minimum temperature are about 16°C at Saint-Louis and 17°C at Yoff. A progressive warming can be observed as one moves southward. During the hot season, the dispersion of the temperatures is higher in this zone than in Mbour. The cold season seems shorter than in Mbour and lasts from December to mid April. At any given station, the temperature gaps between the cold and hot seasons are very high (over 10°C). The highest difference is about 15°C. We also note that the annual mean temperature increases from North to South, that is from Saint-Louis to Mbour. This North-South tendency is, however, disturbed by the station of Thiaroye, which record lower temperature than at Yoff and Kayar. At all stations, the annual mean temperature (Fig. 2) clearly show periods of low temperatures from 1974 to 1977 and from 1985-1986. From 1988 on, a decrease is noticed which continues until 1991. In 1992, the temperatures increased again. The annual average temperatures are relatively high and vary from 1964 to 1970.

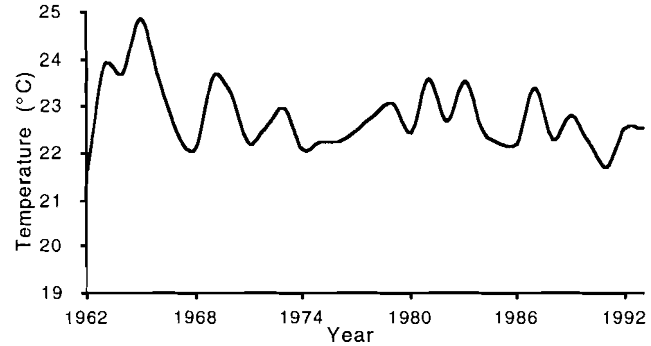


Fig. 2: Annual mean temperatures from 1962 to 1992 for coastal stations off Senegal.

2.2. Salinity

The daily salinities show a relatively important variability (up to 1‰). The evolution of monthly mean salinity is relatively stable between January and May, increases in June and reaches its maximum in July. Between August and September, a minimum of salinity is observed and the gaps between minimum and maximum salinity are smaller in the Cap-Vert stations, particularly during the cold season. They are important in Mbour and Saint-Louis. No North-South trend is noticed however. On the other hand, the decrease of average salinity is sharper and lasts longer at Saint-Louis than at the other stations. Between March and April, a slight decrease of salinity is observed at the stations of Mbour and Saint-Louis, whereas at Kayar and at Cap-Vert, this phenomenon does not occur. In fact, at Cap-Vert, between January and June, the salinity is hardly variable, but stays between 35 and 36‰. The seasonal variability of salinity is weaker than that of temperature. However, a clear prevalence of the average salinities occurs between September and December.

The annual average of the salinities shows that at Cap-Vert (Fig.4, Yoff and Thiaroye), from one station to the other, the salinity does not vary. On the Grande Côte, during the 1960s and 1970s, salinities increased from Saint-Louis to Kayar and became stable from the 1980s (Fig. 4). In the same way until 1983, the salinities at Mbour became closer to those at Saint-Louis (Fig.4). The annual mean for salinities at all stations (Fig.3), shows a progressive increase from the 1970s, and a maximum is observed in 1987.

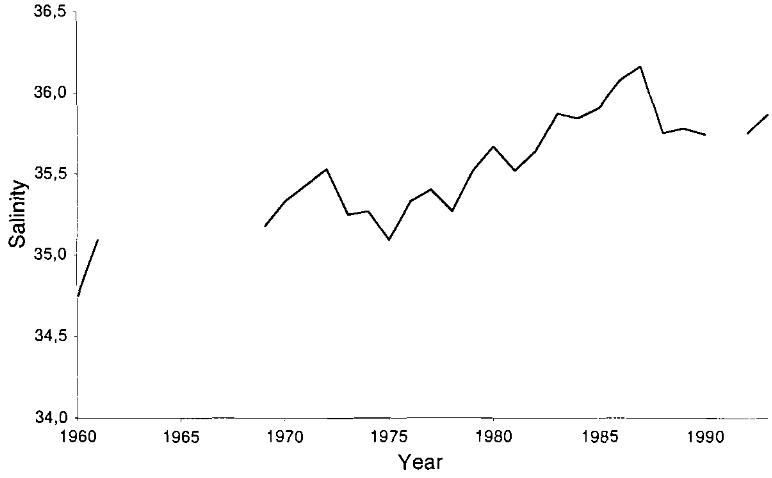


Fig. 3: Annual mean salinity at coastal stations off Senegal.

2.3. Winds

Analyses of wind data from the Senegalese coast have been presented by Rébert (1978), Portolano (1986), Roy (1989) and Roy (1992). Monthly wind mean speed (Fig. 5a) shows a progressive increase between January and April. From May, there is a decrease which reaches the minimum of August-September. The fluctuations of speed around the median are strong all throughout the year, the maxima and minima always being constant. The gap in relation to the median slightly diminishes from mid-June to mid-August. August has the highest extreme values and rather high average speeds.

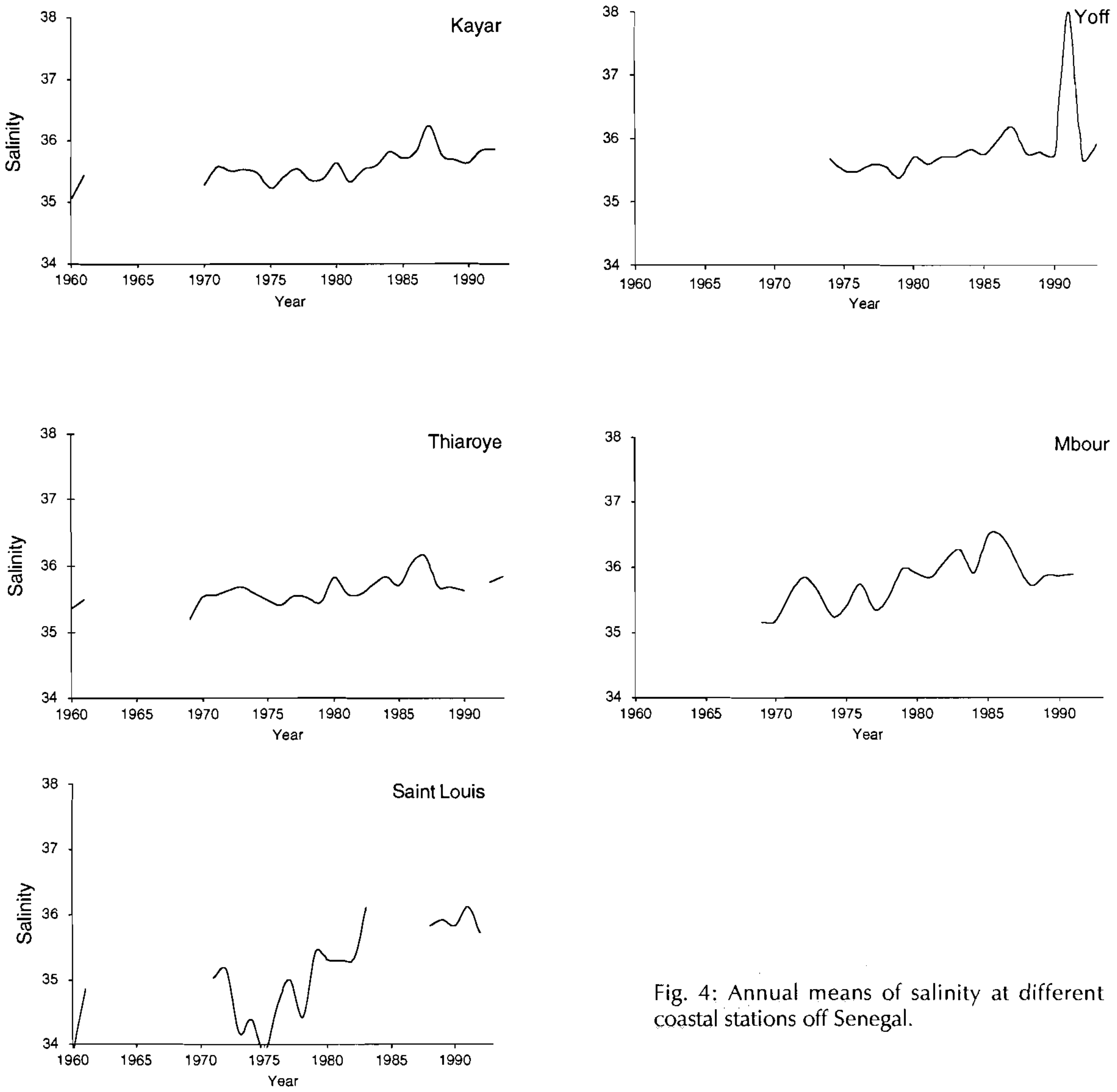


Fig. 4: Annual means of salinity at different coastal stations off Senegal.

The evolution of mean annual wind speed between 1964 and 1992 is presented in Fig. 5b. Note the peak in the early 1970s and the increase in the late 1980s - early 1990s.

2.3.1- The upwelling index

The Senegalese coastal upwelling strength can be determined using the normal component of the Ekman transport (Teisson, 1982). Because the orientation of the coast is different north and south of Cap-Vert, an upwelling index has been calculated for each of these areas using wind data from 1964 to 1991. This index is calculated using the equation :

$$IUC = rCd * V_2/2 * g * \sin (j) \qquad (1)$$

where:

r= air density;

Cd= rugosity coefficient;

V_2= square parallel to the coast wind component;

g = earth rotation angular speed;

j = latitude.

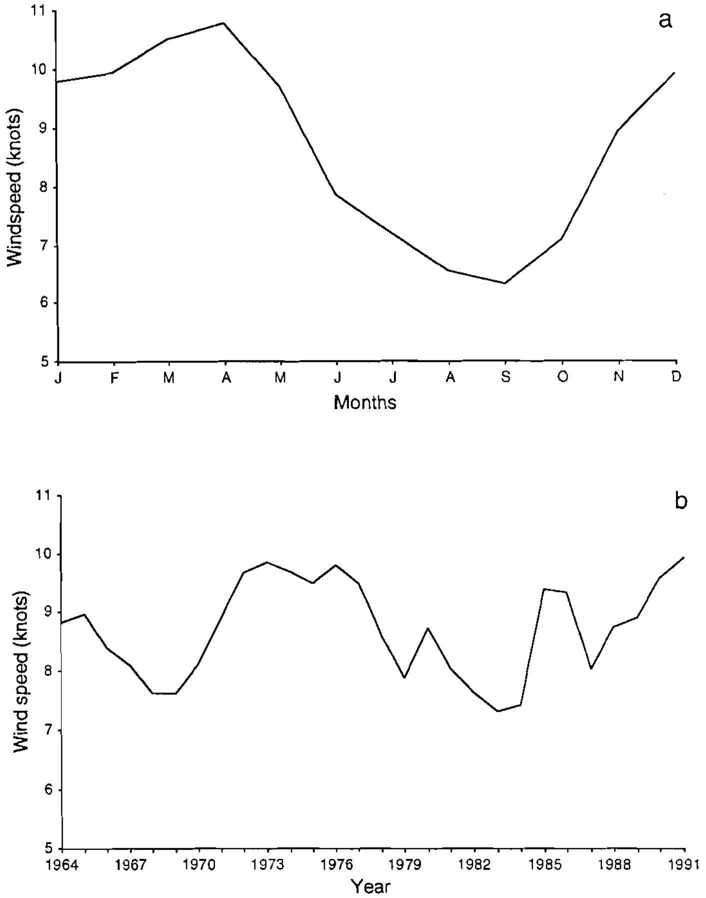


Fig. 5: Wind speed (in knots)
a) montly means; b) annual means.

This index depends, among other things, on wind intensity (Bakun, 1973). The monthly means of the upwelling index for all years 1964-1991 (Fig. 6a) show a strong variability. In June - September, the variability is weaker. In the southern zone, the monthly mean index is positive throughout the year (between 1.50 and 0.10), whereas in the North it is equal to zero or becomes negative in June - September. South of Cap-Vert, the mean index increases from January to April and from September to December. In the North, the peak is reached between March and April. Moreover, the mean indices observed in the South are higher than those in the North. The mean upwelling indices (Fig. 6b) show a period of strong upwelling from 1972 to 1977. The index was strong in 1985 and has been growing since 1988. The mean index was higher in the South during those years. However, it varies in the same way in the two zones. The upwelling indices calculated from wind data collected at sea by trade ships (Roy, 1992) are higher than those calculated from data collected at Yoff. They show that from 1971, the index started to increase and reached a peak in 1973. Starting from 1975, the index leveled off and remained high in the North as well as in the South. The North-South difference is relatively weak but the index is generally higher in the South.

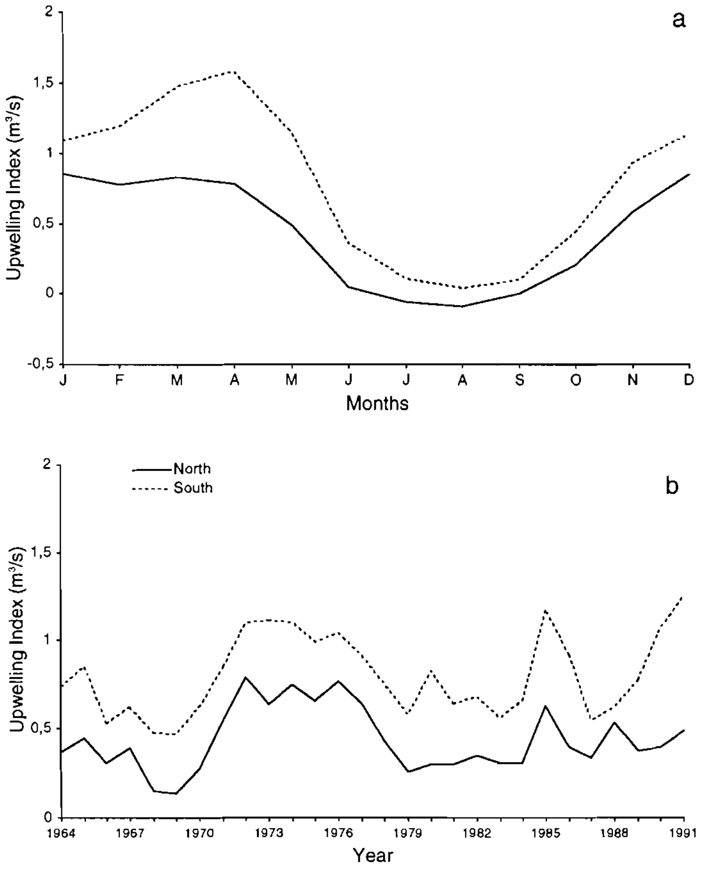


Fig. 6: Upwelling index (m^3/s) a) monthly mean for the areas north and south of Cap-Vert, Senegal; b) annual means.

2.4. Nitrate

Monthly mean nitrate (Fig. 7) increases from January to reach a peak in May. At Gorée the values get close to zero from August whereas at Yoff, the concentrations are generally higher. Monthly means show that maxima as well as concentrations vary from one year to another. At Gorée (Fig. 7a) concentrations measured between January and May 1991 are generally higher than those measured during the other years. The peak is reached in April and May. In 1992 the maximum at Gorée was measured in April and concentrations, although weak starting from June, were still noticeable throughout the rest of the year. They were generally higher than those of 1993. In 1993 the highest nitrate concentrations were measured in February at Gorée and were nearly zero between July and October. At Yoff (Fig. 7b) in 1991, nitrates reached a peak in June whereas in 1992 and 1993, this peak was observed in March and February respectively. The average concentrations measured in 1991 are generally higher than those of the other two years, and those of 1992 are higher than those of 1993 which become null between July and October. The variability around the mean is higher during the cold season and can reach 80% of the mean. The inter-annual variability is also rather marked at each station.

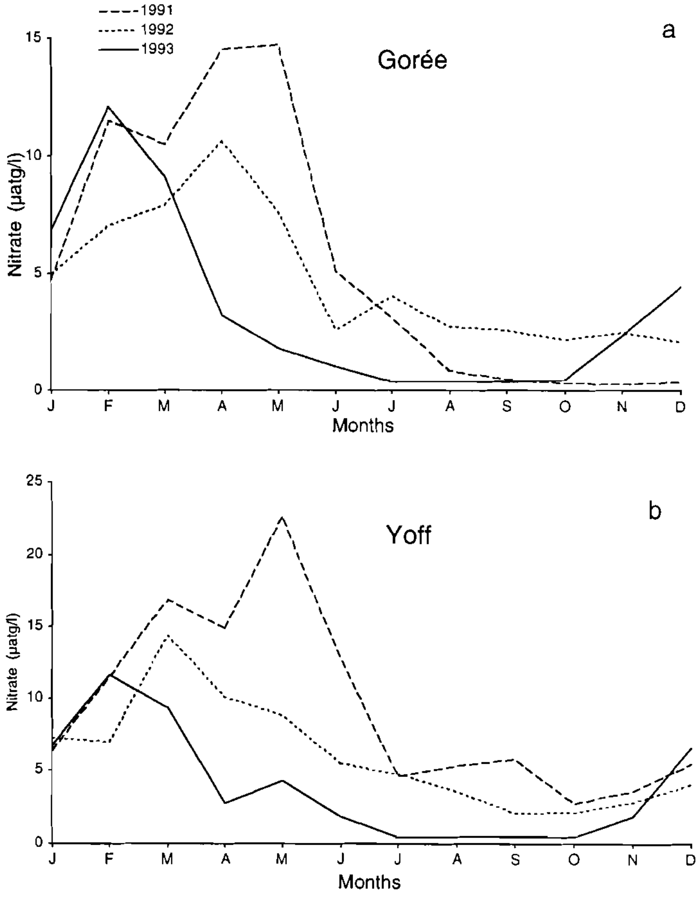


Fig. 7: Monthly means of nitrates in 1991, 1992 and 1993
a) at Gorée; b) at Yoff.

2.5. Phosphates

Monthly mean phosphate (Fig. 8) shows an increase in average values during the cold season, with a peak in March. Concentrations are lower from July to December, and the minimum occurs in August. Concentrations are higher at Gorée than at Yoff. The monthly means for each year and station show that while in Gorée (Fig 8a) the highest concentrations occurred from January to May in 1991 and 1993; in 1992, they occurred from August to November. Peaks were observed in February for the year 1993, in March for 1991 and in September for 1992. At Yoff (Fig. 8b), the highest phosphate concentrations were measured in May 1991, February 1993 and September 1992. At these two stations the measured concentrations were generally higher during the 1991 cold season. The variability around the mean is relatively high during the cold season; It can reach 36% of the mean, while the concentrations are lower and less variable during the hot season.

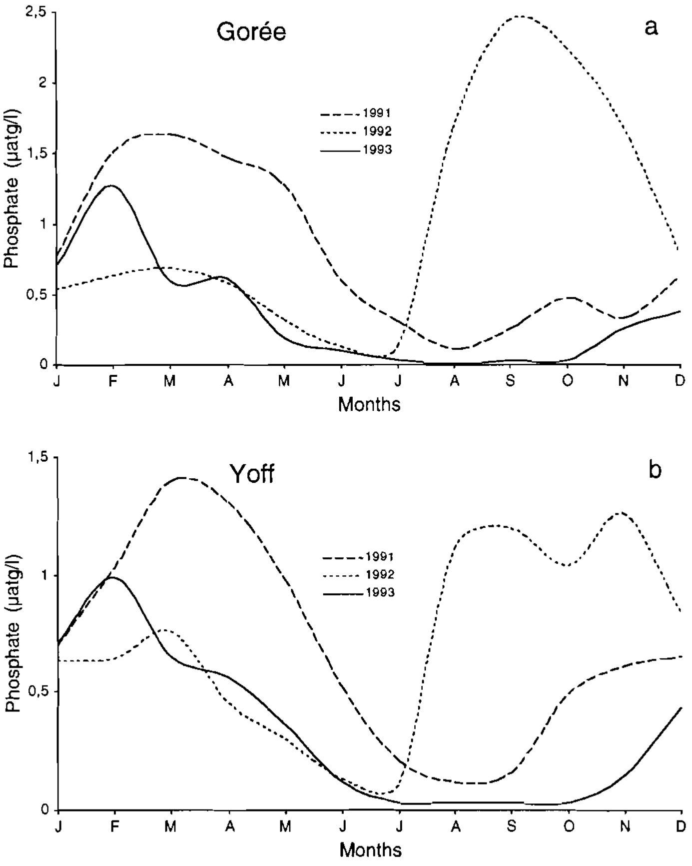


Fig. 8: Monthly means of phosphates in 1991, 1992 and 1993
a) at Gorée; b) at Yoff.

2.6. Chlorophyll

At the three stations of the Cap-Vert, monthly mean chlorophyll (Fig. 9), shows a great seasonal variability. In fact, two periods can be seen: from January to June, when high concentrations of chlorophyll can be measured at all stations; and from July to December when chlorophyll concentrations are extremely low. The highest peak for chlorophyll is measured in May at the various stations except at Thiaroye where a higher second peak appears as early as February.

At Yoff and at Gorée, chlorophyll concentrations are rather close and lower than at Thiaroye.

The evolution of the monthly means per station and per year shows that :

- at Gorée (Fig. 9a), there were higher concentrations in 1993, with a peak in May. In 1991 and 1992, the peaks were reached in May. A secondary peak occurred, however, in July 1992 and an important decrease of concentrations appeared from September; in 1991 this decrease occurred as early as July;

- at Yoff (Fig. 9b), chlorophyll concentrations were higher in 1993 than in the other years and, unlike the general mean the maximum was reached in July. In 1992, the maximum chlorophyll occurred in February, whereas in 1991 it was in May;
- at Thiaroye (Fig. 9c), the concentrations are higher than at the other stations. In 1991 the maximum was measured in May, while in 1992 two peaks were observed in April and June.

The intra-seasonal variation is generally stronger during the cold season and the inter-annual variability is high particularly at Thiaroye.

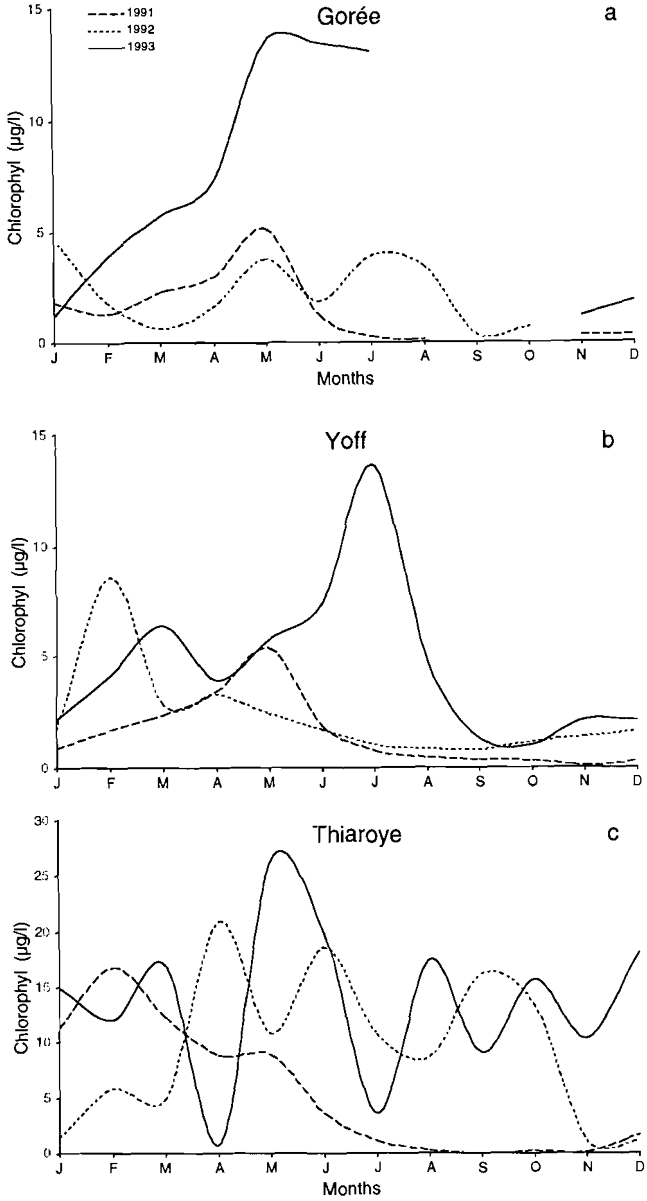


Fig. 9: Monthly chlorophyll concentration (µg/l) in 1991, 1992 and 1993 a) at Thiaroye; b) at Yoff; c) at Thiaroye.

DISCUSSION

Comparisons show that during the period 1964-1991, temperature and wind speed varied inversely through time. According to coastal upwelling indices, the upwelling has generally been weaker north of Cap-Vert according to the two wind data sources (Yoff station and ships of opportunity). However, the temperatures at Mbour and Saint-Louis recorded opposite signals. This may be explained by the fact that on the southern coast, the upwelling is situated at the same level as the continental slope, whereas in the northern zone, the upwelling takes place near the coast (Deme-Gningue *et al.*, 1990). Thus, lower temperatures are measured in this zone when the indices show that the upwelling is stronger on the southern coast.

The fact that the variation of temperatures is weaker at Mbour than near Saint-Louis and Yoff may be due to the remoteness of the upwelling sources in this area, compared to the two other areas. Towards south of Cap-Vert, the gradual increase of minimum temperatures may also be explained by this phenomenon; this confirms results obtained during the CIRSEN survey (Deme-Gningue *et al.*, 1990). The fact that temperatures recorded at Thiaroye and Gorée are lower than those measured at Yoff and Kayar stations, further north, may be explained by the orientation of the coast in that area and to a local phenomenon that concerns only the bay of Gorée (Teisson, 1982).

An analysis of seasonal variability of salinity, based on the division between the upwelling season and the hot (rainy) season is not very conclusive because, during the rainy season there is a period of strong decrease of salinities which increase rapidly afterward. The decrease in salinity at stations Thiaroye and Yoff from August to September and up to mid-October may be due to the arrival of the Guinean waters (Toure, 1983; Rébert, 1983). The fact that the rain water draining system is more dense at Thiaroye and Yoff than at Goree may explain why the salinity is higher at Gorée. In the same way, changes in rain patterns may be the cause for the gradual increase of salinities since the 1970s.

The concentrations of nutrient salts and phytoplankton biomass at coastal stations appears to be closely linked to the temperatures measured at those sites. In fact, a temperature-nitrate relation (T-NO3) can be clearly observed at Cap-Vert stations, and also at Yoff and Gorée. It is represented by a steep straight line which tends to later stabilize. In 1991 the straight line was between 15 and 21°C, with a more gentle inclination at those stations. According to those observations, the T-NO3 relation is not variable in space in a given year, and its shape is the same through time. Indeed, nitrates decrease quickly as temperatures increase and this up to a certain level which may vary from one year to another. We can also note that the 1991 upwelling was stronger than the 1992 one, as the temperatures were clearly lower in 1991. It seems that the gradient of the line T-NO3 is more gentle when the upwelling is weaker, and thus the threshold temperature increases.

The variability of the gradient of the T-NO3 relation may be linked to the evolution of the threshold temperature of the straight part of the curve, which may explain the gradient. Thus, variability, which according to Oudot and Roy (1991) and Bakun (1986) expresses the biological mechanisms of the ecosystem, only reflect the speed at which the waters are brought up to the surface. The gradient is more gentle when the speed is low. In fact, we can refer to the explanation of Rébert (1983) concerning upwelling waters which can be relatively warm and still rich in nutrient. According to Rébert (1983) the thermal response of the ocean in relation to wind variations should be around 2.5 days. Thus, a hypothesis which may explain this phenomenon is that the distance between the station and the source of the upcoming would cause a warming up of the waters before they reach the coast. This, combined with the proximity of the continent and the shallowness of the waters are factors which may explain the characteristics of our observations.

The evolution of temperatures and chlorophyll through 1991 shows that apart from Thiaroye station, the trade winds period is the richest in chlorophyll. At Yoff, as well as at Gorée, the chlorophyll peak is observed in May, whereas minimal temperatures are measured in February-March. On the opposite, at Thiaroye, the chlorophyll maximum is observed in November, a month of abnormally high upwelling index for the period considered. The temperature-chlorophyll relation (T-CHL) in 1991 at Thiaroye station looks like those of T-NO3. The threshold of the line would be at 22°C. For 1992 the relation T-CHL is different from that observed in 1991. A definite form which links the two parameters cannot be identified at any of the stations. The 1992 observation on the T-CHL relation conforms better to the T-CHL relation theories, because temperature is not the explanatory factor for chlorophyll concentrations. The year 1991 is not a typical case. The shape of the 1991 chlorophyll-temperature curve, which is the same as the shape of the T-NO3 curve at Thiaroye is best explained by the presence, at that station, of macrophytes whose chlorophyll, mixed with that of the phytoplankton, could influence the relationship (Dème-Gningue *et al.*, 1990). The chlorophyll-nitrate relation (CHL-NO3) is less simple than the one between temperatures and nitrates because nitrate is not the only important parameter for the development of phytoplankton. In 1991 and 1992, chlorophyll increased with nitrates to reach about 10 µg/l of nitrate and then decreased. This threshold, which was constant for 1991 and 1992 at Yoff and at Gorée may be variable depending on conditions of light and water stability. The work done at Cap-Vert stations permits to analyze the variability of the T-NO3 relation. It always has the same shape of a line whose slope varies from one year to the next. On the other hand the relation between the upwelling, the presence of nutritient salts and the development of phytoplankton is determined by nitrate increase coupled with temperature decreases. The threshold of this relation corresponds to the lull of winds and the start of the increase of chlorophyll concentration.

The correlation between the different parameters studied are significant only for temperature and nitrate. Nitrates and temperatures have a negative correlation which is weaker on a monthly basis than on a seasonal basis. On the contrary, the correlation between the station and the various parameters are all very weak. The nitrates concentrations at Yoff are on average higher than at Gorée. This can be explained by the location and physical environment of these stations. The station of Yoff is closer to the shore and further North.

REFERENCES CITED

Bakun A. 1973. Coastal upwelling indices, west coast of North America, 1946-1971. *U.S. Dept. Commer. NOAA Tech. Rep. NMFS SSRF*, 671, 103 p.

Bakun A. 1986. Definition of environmental variability affecting biological processes in large marine ecosystems. *In*: K. Sherman and L.M. Alexander (eds.). *Variability and management of large marine ecosystems*. AAAS selected symposium, 99:89-108.

Berrit G.R. 1962. Contribution à la connaissance des variations saisonnières dans le golfe de Guinée. Observations de surface le long des lignes de navigation. II. Etude régionale. *Cah. Océanogr. COEC*, 14 (9): 633-643.

Dème-Gningue I., C. Roy and D. Touré. 1990. Variabilité spatio-temporelle de la température, des nitrates et de la chlorophylle devant les côtes sénégalaises. *Doc. scient. CRODT*, 122.

Gallardo Y. 1981. On two marine ecosystem of Senegal, separated by a peninsula. *In*: J.C.J. Nihoul (ed.). 12th. Int. Liège Colloquium on Ocean Hydro-dynamics, Liège (Belgium), 1980. *Eco-hydro-dynamics*. Elsevier, Oceanogr. Sér., 32: 141-154.

Portolano P. 1981. *Contribution à l'étude de l'hydroclimat des côtes sénégalaises*. Rapp. interne CRODT/ORSTOM, vol. 1 (Texte), 68 p. vol. 2 (Fig.), 61p.

Portolano P. 1986. Analyses des séries vent-températures de la mer en surface des côtes sénégalaises. *Océanog. trop.*, ORSTOM, 21 (2): 205-227.

Oudot C. and C. Roy. 1991. Les sels nutritifs au voisinage de Dakar: cycle annuel moyen et variabilité inter-annuelle. *In:* P. Cury P. and C. Roy (eds.). *Pêcheries ouest-africaines: variabilité, instabilité, changement.* ORSTOM, Paris: 80-89.

Rébert J.P. 1978. Variabilité des conditions de surface dans l'upwelling ouest-africain. Comm. 100. Symposium sur le courant des Canaries: Upwelling et ressources vivantes. *Doc. scient. CRODT*, 67, 27p.

Rébert J. P. 1983. Hydrologie et dynamique des eaux du plateau continental sénégalais. *Doc. scient. CRODT*, 89, 99p.

Rossignol M. and M.T. Aboussouan. 1965. *Hydrologie marine côtière de la presqu'île du Cap-Vert. Contribution à l'étude de la productivité des eaux.* Publ. prov. ORSTOM. 2° partie, 166 p.

Roy C. 1989. Fluctuation des vents et variabilité de l'upwelling devant les côtes du Sénégal. *Oceanologica Acta*, 12 (4): 361-369.

Roy C. 1992. *Réponses des stocks de poissons pélagiques à la dynamique des upwellings en Afrique de l'ouest: analyse et modélisation.* Thèse de doctorat. Editions ORSTOM, coll. Etudes et Thèses, Paris.

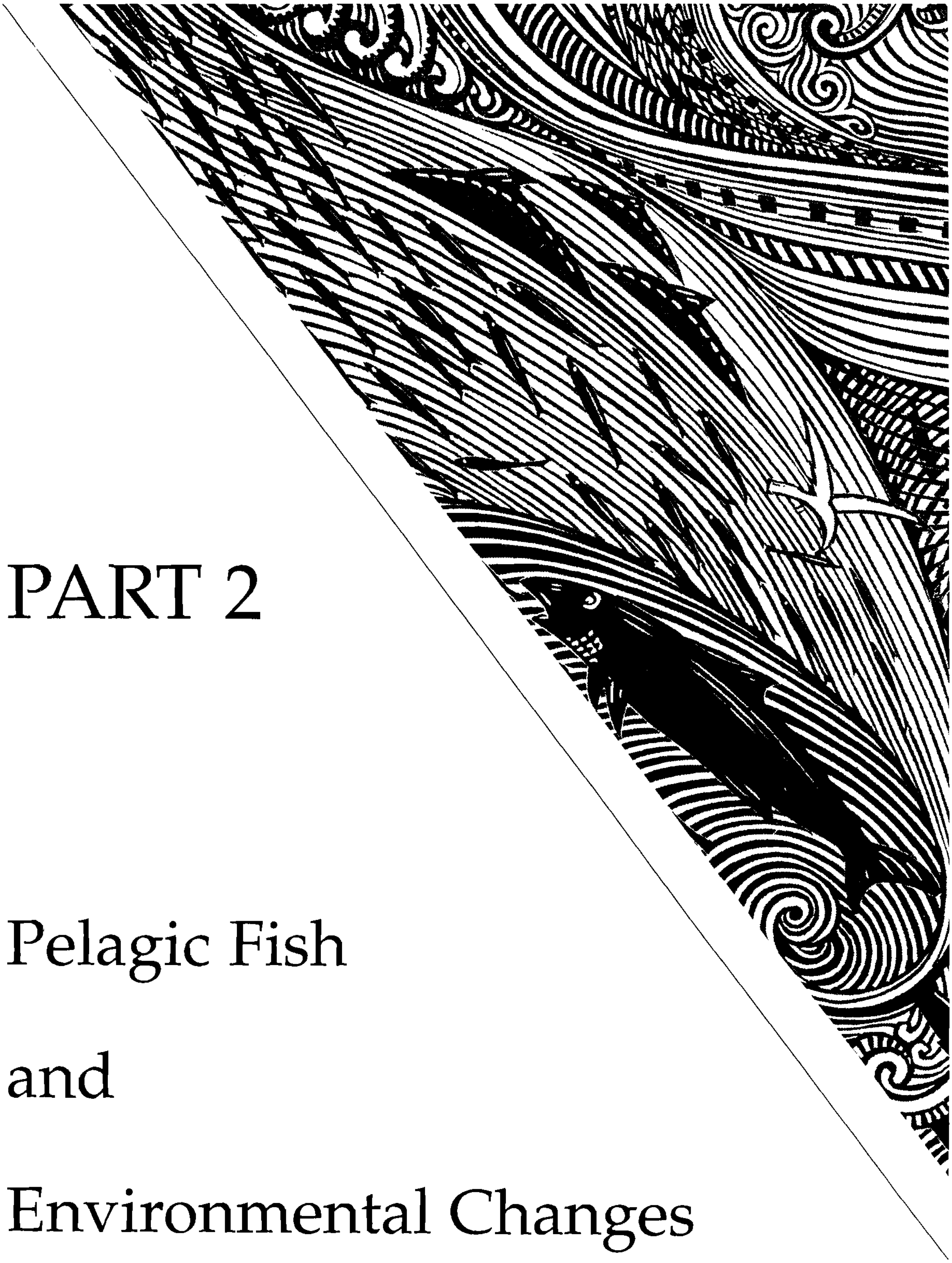
Strickland J.D.H. and T.R. Parsons. 1972. *A practical handbook of seawater analysis.* Fish. Res. Board of Canada Ottawa, 167, 2nd ed.

Teisson C. 1982. Application de la théorie d'Ekman à l'étude des courants et des remontées d'eau profondes le long des côtes sénégalaises. *Doc. scient. CRODT*, 106, 79 p.

Touré D. 1983. Contribution à l'étude de l'upwelling de la baie de Gorée (Dakar, Sénégal) et de ses conséquences sur le développement de la biomasse phytoplanctonique. *Doc scient. CRODT*, 93, 186p.

PART 2

Pelagic Fish
and
Environmental Changes



Food, Transport and Anchovy Recruitment in the Southern Benguela Upwelling System of South Africa

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ABSTRACT

Recruitment of the South African anchovy, *Engraulis capensis*, is related to two environmental indices. These are fish oil yields (measured as the oil-to-meal ratio from pelagic reduction factories) and south-easterly winds as measured at Cape Point lighthouse. The nature and appropriateness of these indices are discussed in terms of recent statistical studies on oil yields and modelling of advective processes on anchovy recruitment. The rationale for these relationships is that good oil yields are indicative of good food availability to the growing anchovy, whereas strong south-easterly winds yield poor (cool and turbulent) conditions for spawning and a greater risk of fish eggs and larvae being transported offshore into the deep ocean. In 1986 an intrusion of Agulhas water is believed to have upset both relationships, but they are still statistically significant over the entire time-period. Non-linear relationships between anchovy recruitment and south-easterly winds are also presented.

RÉSUMÉ

Le recrutement de l'anchois d'Afrique du Sud, *Engraulis capensis*, est étudié en fonction de deux indices environnementaux : les rendements en huile de poisson (mesurés par le rapport entre l'huile et la farine de poisson dans les usines de réduction de poissons pélagiques) et les vents du sud-est à Cape Point Lighthouse. La nature et le caractère approprié de ces indices sont discutés à l'aide de récentes analyses statistiques sur les rendements en huile et la modélisation des processus d'advection et leur action sur le recrutement de l'anchois. Le raisonnement afférent à ces relations est que de bons rendements en huile indiquent une bonne disponibilité en nourriture pour la croissance des anchois, tandis que de forts vents du sud-est procurent des conditions défavorables (froides et turbulentes) et un risque plus grand pour les œufs et larves d'être transportés vers le large dans l'océan profond. En 1986, on pense qu'une intrusion des eaux provenant du courant des Aiguilles est susceptible d'avoir perturbé ces deux relations, mais elles restent cependant toujours significatives durant toute la période de temps considérée. Des relations non linéaires entre le recrutement de l'anchois et les vents du sud-est sont aussi présentées.

INTRODUCTION

This paper relates anchovy (*Engraulis capensis*) recruitment in the southern Benguela Upwelling System to the variables of food and transport. This is accomplished by providing evidence showing that these variables are indeed important to anchovy recruitment in the region, and by showing that the long-term indices taken to represent food availability and transport are appropriate. Thereafter, both linear and non-linear regressions between these indices and anchovy recruitment biomass and recruitment numbers are undertaken.

The Benguela Upwelling System is one of the world's four major eastern ocean upwelling systems (Parrish *et al.*, 1983) extending from southern Angola to south of Cape Town. It can be divided into a northern and southern region on either side of the Lüderitz upwelling cell (Fig. 1), on the basis of differences in meteorology and oceanography (Shannon, 1985) and largely separate fish stocks (Crawford *et al.*, 1987). The southern region differs from other systems in that it is bounded on its poleward margin by a warm water system caused by topography (the Agulhas Bank) and Agulhas Current leakage, and therefore is subject to both South Indian and South Atlantic influences (Shelton *et al.*, 1985). Meteorologically it shows strong teleconnections with El Niño/Southern Oscillation (ENSO) cycles (Taunton-Clark, in prep.). The northern region is more affected by the oceanic "Benguela Niño" phenomenon (Shannon *et al.*, 1986).

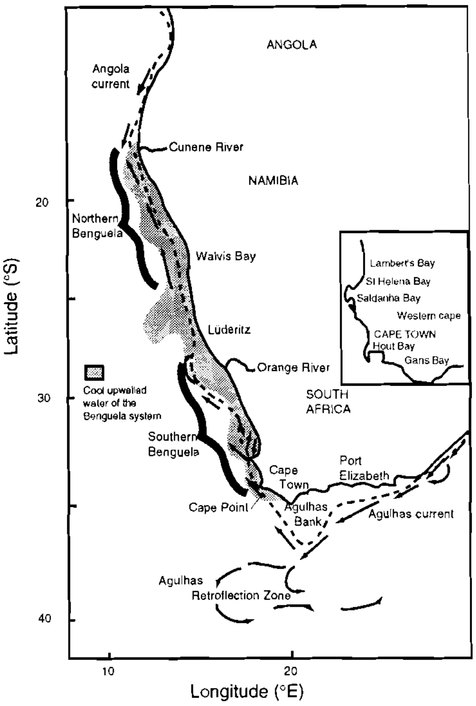


Fig. 1: The major currents off Southern Africa's west coast and the Benguela upwelling system showing the division into northern and southern regions, and the major fishing ports (adapted from Siegfried *et al.*, 1990).

The pelagic fishery in the south was dominated by anchovy from 1967 to 1993, following a period of dominance by sardine *Sardinops sagax* (Schülein *et al.*, 1995). Extensive multidisciplinary research into the recruitment processes of anchovy has been undertaken subsequent to direct acoustic surveys of the resource, which commenced in 1984, showing the stock to be both larger and more variable than previously thought (Hampton, 1987). In particular, the anchovy recruitment failure of 1989 was closely examined and postulated to be due largely to a lack of food for spawning adults during the peak spawning period in that year (Hutchings and Boyd, 1992). However, the study by the latter authors also identified larval transport and growth of recruits as potentially important variables. Bloomer *et al.* (1994) investigated the prediction of recruitment by means of a rule-based model and emphasized the role of turbulence and larval transport, as affected by winds in the spawning and transport regions respectively. Cochrane and Hutchings (1995) have recently re-examined a larger list of environmental variables influencing recruitment of the southern anchovy stock.

The pelagic fishery of the northern Benguela, centered at Walvis Bay, was initially dominated by catches of sardine for a quarter of a century until 1977. Anchovy, although caught since 1970, were only dominant from 1978 to 1984, apart from a single good recruitment in 1987. The life history of anchovy in the northern system is similar to that off Peru and California, in terms of upwelling providing food, but also bringing about losses of spawning products. In addition, the region is subject to strong interannual oceanic advection events called Benguela Niños (Stander and De Decker, 1969; Shannon *et al.*, 1986; Boyd *et al.*, 1987), which severely restricted productivity and led to an anchovy recruitment failure in 1984 (Boyd *et al.*, 1985).

Direct field evidence of a food limitation for anchovy in the Benguela system is hard to obtain and therefore various proxies for feeding, such as the oil content of pelagic fish from commercial landings, as well as oocyte atresia of spawners in the spawning season, have been used as surrogates. The former data set of oil yields covers both the northern and southern Benguela since 1951 (Fig. 2), and has recently undergone statistical analysis for seasonality, trend, anomalous years and coherence between ports (Schülein *et al.*, 1995). In the present study, we follow-up the work of Schülein *et al.* (1995) and use oil-to-fishmeal ratios of pelagic fish landings as an index of feeding.

The other variable which we address is transport, with the index used being restricted to the southern Benguela, namely south-easterly winds at Cape Point during the anchovy spawning season. However, the rationale for selecting transport as an important variable, and its apparent correspondence with south-easterly winds, is supported by extensive simulations done for this study using a computer model developed by Nelson and Shannon (1994). This model, fully described by Shannon (1995), utilizes four years of current measurements on the South African shelf (Boyd and Oberholster, 1994) to obtain a mean flowfield, and computes anchovy egg production based on seven years of spawner distributions. Batches of anchovy eggs are released and transport is simulated through the mean flowfield, upon which various perturbations are superimposed.

1. ENVIRONMENTAL INDICES AND DATA SOURCES

1.1. Oil-to-meal ratios of pelagic fish in the northern and southern Benguela (Schülein *et al.*, 1995): an index of feeding

Oil-to-meal data are collected on a monthly basis from pelagic fish reduction factories at seven ports from Walvis Bay in Namibia to Gans Bay on the Cape south coast. The time-series for the four Western Cape ports (excluding Cape Town and Gans Bay- see Fig. 1) are also averaged into a single index (as shown in Fig. 2).

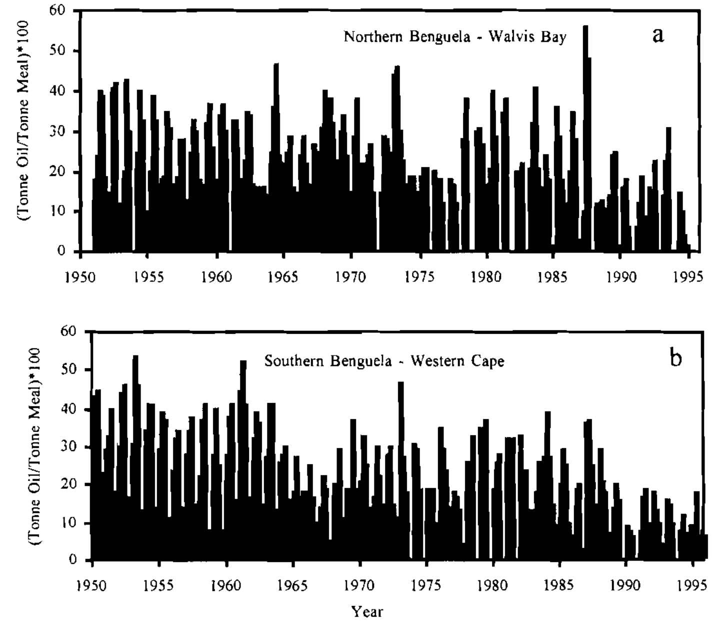


Fig. 2: Monthly oil-fishmeal ratios (tonne oil x 100/tonne meal) in the northern (a) and the southern Benguela systems (b) (after Schülein *et al.*, 1995).

The monthly data were fitted with a Fourier (sine/cosine) model to take into account seasonality (and the fact that data were not available for all months of the year), and either a long-term linear trend or year factors showing anomalous years (Fig. 3). The coherence between ports was investigated by correlating the residuals resulting from fitting autoregressive models to the year factors from the different ports.

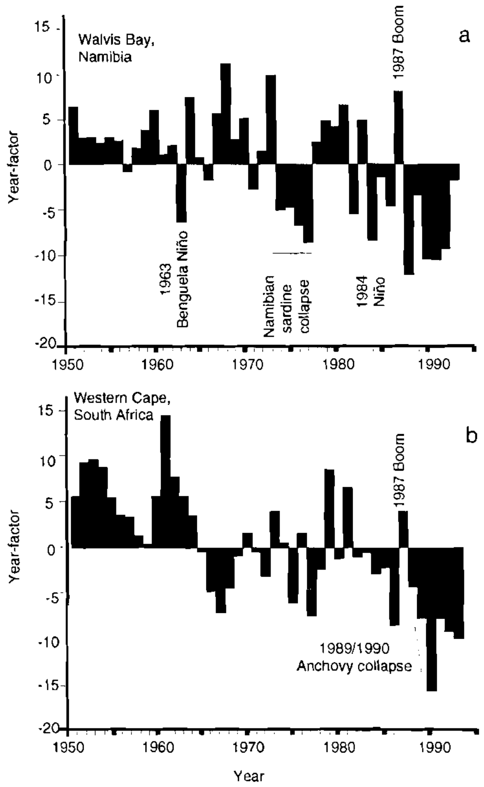


Fig. 3: Oil yield year-factors from the northern (a) and the southern Benguela systems (b), 1951-1993 (adapted from Schülein *et al.*, 1995).

Schülein *et al.* (1995) report a strong seasonal signal in oil-to-meal ratios, ranging from 37% of the amplitude at Walvis Bay to between 43 and 50% at the ports of the Western Cape. The peaks in the phases off the Western Cape show a high degree of coincidence moving southwards with the arrival of recruits in the catches (Hampton, 1987). The degree of coincidence of years of high and low oil yields in the Benguela system is of much interest in assessing the scale of spatial coherence of the phenomena, such as was done for sea surface temperature by Taunton-Clark and Shannon (1988). Coherence between Walvis Bay in the northern Benguela and the average for the western Cape ports over the period 1951 - 1993 is statistically significant (r=0,51). However, Gans Bay (on the Cape south coast and subject to Agulhas Bank hydrology) only showed weak coherence with the closely adjacent Benguela system ports (see Fig. 1), underscoring the different ecosystem forcing between it and the Benguela region. Northern/southern coherence values were not high, with the common variance explained being approximately 25%. This level of coherence is thought to be caused by the occurrence of both Benguela wide signals (e.g., 1987) as well as oceanic events such as Benguela Niños (Shannon *et al.*, 1986), which are mainly restricted to the northern region and are associated with reduced productivity (e.g., 1963 and 1984; Stander and De Decker, 1969; Boyd *et al.*, 1985).

Despite the evidence resting mainly on the studies of the Benguela Niño events in the north and the 1989 collapse in the south, Schülein *et al.* (1995) argue that the oil-to-fishmeal time-series is an index reflecting the successful feeding of the pelagic fish stocks and therefore the ecological health of the ecosystem.

1.2. Transport of anchovy eggs and larvae in the southern Benguela: does modelling suggest transport that affects recruitment?

In the southern region, the transport of anchovy eggs and larvae from their spawning ground on the Agulhas Bank to the Cape west coast nursery grounds is due to equatorward alongshore transport in a frontal jet system (Bang and Andrews, 1974; Crawford, 1980; Shelton and Hutchings, 1982; Boyd *et al.*, 1992; Hutchings and Boyd, 1992) (Fig. 4). This well-described process has recently been modelled using an averaged and interpolated Acoustic Doppler Current Profile (ADCP) flowfield for transport (Fig. 5). This flowfield was recently adjusted by minus 3° in current direction to counteract an incorrect offset for ADCP transducer alignment for part of the study period (when the offset was 2° instead of -2° or -3°). Currents incorporated were predominantly bottom-referenced, allowing simple correction. The biological processes incorporated in the model are listed in Appendix A. Runs with this model, including percentage-wise strengthening and reduction of the East/West orientated components of the (uncorrected) flowfield, suggested little variability in anchovy year-class strength attributable to variation in transport processes (Crawford *et al.*, 1995). This result was viewed with some sceptism on account of the importance attached to transport in the descriptive studies referred to above, and because there already exists some evidence of an inverse relation between anchovy recruitment and the strength of upwelling winds in the spawning region, although not the transport region (Bloomer *et al.*, 1994).

In 1994, the ENSO high phase coincided with strengthened SE (upwelling) winds after three years of below-average winds during its low phase (Fig. 6), and it coincided with the worst anchovy recruitment since measurements began in 1984 (and possibly in two decades). Environmental causes were sought and the advection model and its application were examined more critically. In the first instance, modifications to the flowfield were made to tune results to obtain a more realistic spatial distribution of recruitment and advective losses using the extensive 1991 spawner distribution. The 'weakness' of the original (uncorrected) flowfield was viewed as the complete absence of advective losses west of Cape Agulhas. Hence,

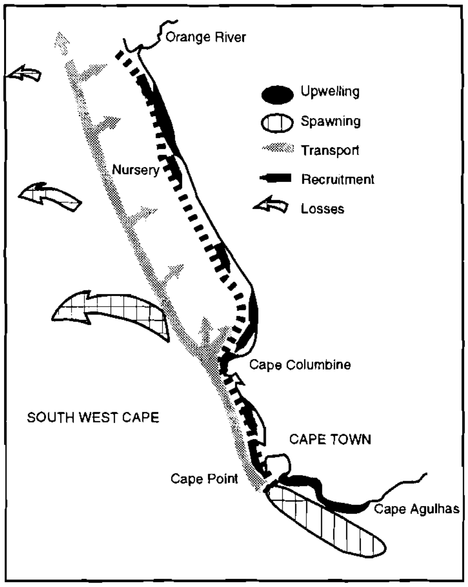


Fig. 4: The various life history stages of the anchovy *Engraulis capensis* in the southern Benguela (after Hutchings and Boyd, 1992).

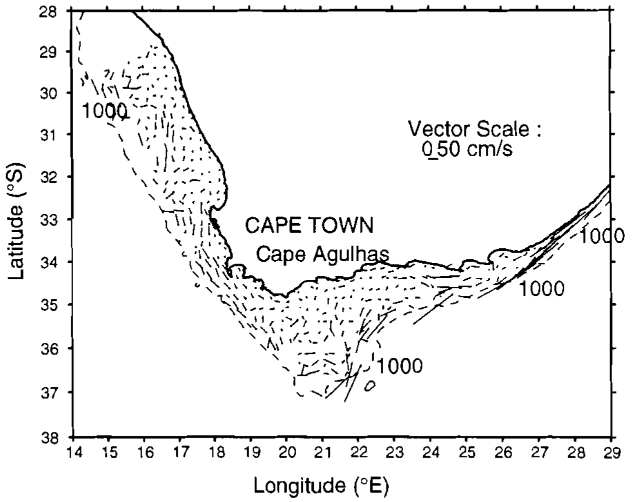


Fig. 5: Currents at 30 and 50 m depth for spring and summer, measured by Acoustic Doppler Current Profiler on *F.R.S. Africana* from November 1989 to March 1993 (during austral spring and summer), and upon which the flowfield in the model was based. Note that , in this figure, the vectors are 3° biased in a positive sense. The currents flow away from the dot.

mainly westward advection was added until greater spatial realism in the distribution of recruits and losses was considered to have been achieved. At the time, justification for this process was the fact that most of the ADCP flow field data had been collected during the El Niño years of 1990/91 - 1992/93, which show a greater amount of onshore (NW) winds than do non-El Niño years (Fig. 6). In addition, flow above the 30 - 50 m reference depths may well have been directed more offshore because of the direct influence of upwelling winds causing Ekman drift in the upper layer. The 3° (generally onshore) offset of the uncorrected field would also have played a small role. The development of a modified flowfield (relative to the uncorrected one), as described by Shannon (1995), was eventually accomplished by adding velocity components as shown in Figure 7. This done, the model was run using seven actual spawner distributions under the following flowfields: 1) the uncorrected flowfield, 2) the corrected flowfield and 3) the field based on additions to the uncorrected flowfield. Differences can be seen in Table 1. The results are similar for both the uncorrected and corrected flowfields (mean difference between the two recruitment values is 1.3%, although a paired t-test showed the difference to

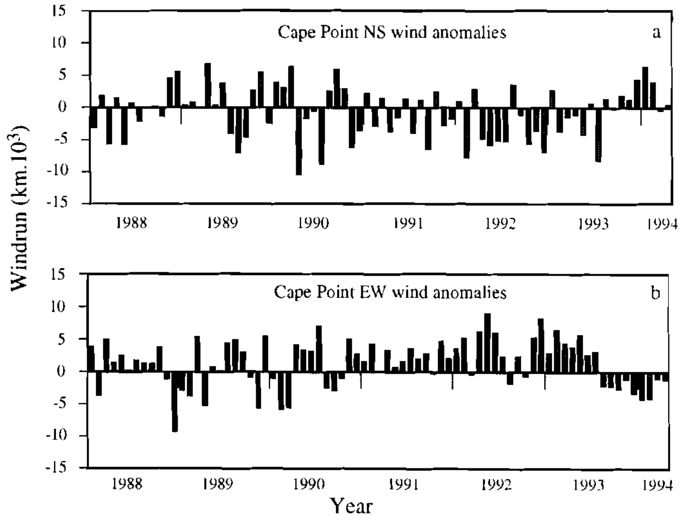


Fig. 6: Monthly N/S (a) and E/W (b) wind anomalies at Cape Point from January 1988 to April 1994. Positive anomalies indicate stronger winds from the south and west.

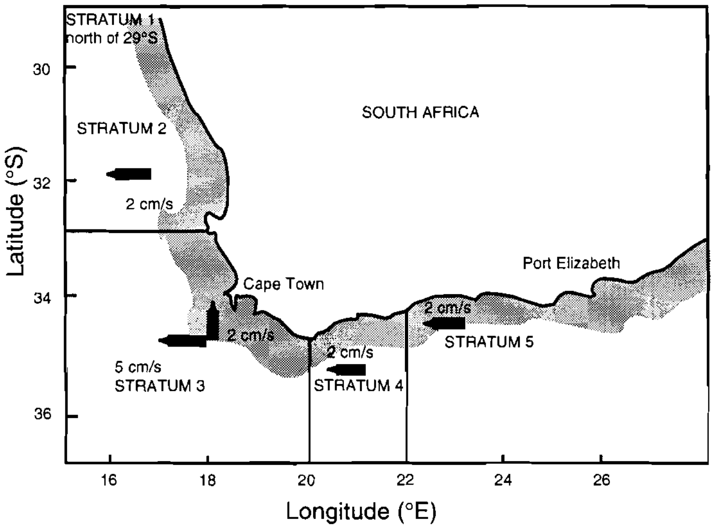


Fig. 7: Modifications to the uncorrected ADCP velocity field shown in Fig. 5 and used in the simulation of transport under non-El Niño conditions (during which higher advective losses could be expected).

be significant at the 5% level - the corrected field yielding slightly lower recruitment than the uncorrected field). The modified field resulted in markedly smaller or poorer recruitment but also substantially more variability in recruitment numbers, which now vary by a factor of two and indicate transport to be important variable in the recruitment process.

Spawning/ Recruitment	'Uncorrected' 'Reduced' advection scenario	'Corrected' 'Reduced' advection scenario	Modified advection scenario
1986/87	470	468	122
1987/88	475	461	179
1988/89	420	420	139
1989/90	469	465	135
1990/91	484	484	214
1991/92	441	431	200
1992/93	473	464	219
Seven years mean	462	456	173
Standard deviation of mean	23	23	40
Coefficient of variation (%)	5	5	23

Table 1: Summary of recruitment results (numbers x10^9) from application of anchovy model to various flowfields (see text).

1.3. Anchovy recruitment

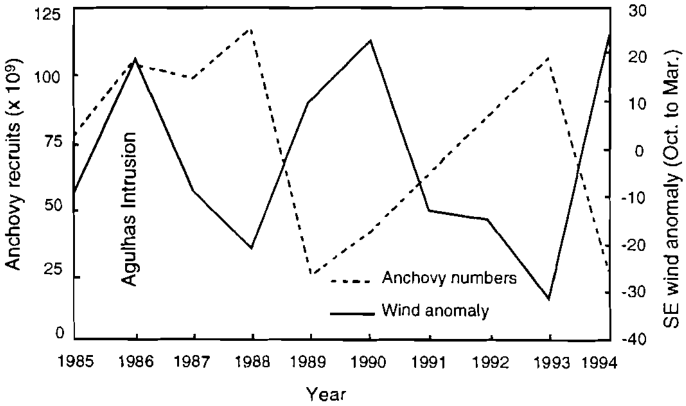
Recruitment numbers and biomass were estimated from hydro-acoustic surveys (Hampton, 1992 and 'Pelagic Working Group documents of the Sea Fisheries Research Institute') conducted since 1984 between Cape Agulhas and the Orange River. The present study uses these survey estimates directly for correlation with the environmental indices, in contrast to Cochrane and Hutchings (1995) who used population model estimates of recruitment.

2. LINEAR CORRELATION OF ANCHOVY RECRUITMENT WITH INDICES OF TRANSPORT AND FOOD

The recruitment numbers from acoustic surveys were found to vary by a factor of five and also relate inversely to the SE wind record (Fig. 8). Similar relationships had been proposed previously by various authors (e.g., Boyd (ms), Cochrane and Hutchings, 1995), but the statistical significance of this specific correlation was established by the 1994 data point (even when the 1986 outlier was included). This outlier corresponded to an intrusion of Agulhas Current water as far as southern Namibia (Shannon *et al.*, 1990) which, despite strong SE winds, could have restricted advective losses. If this point is excluded, the correlation is even more 'significant', as shown in Figure 9. The general division into two groups, namely poor recruitment and average-to-good recruitment, as well as the outlying good recruitment, can clearly be seen in this figure.

This result had a feedback effect on the way the advection model was viewed. Instead of searching for a single flowfield representative of average conditions, the possibility of the different flowfields shown in Table 1 pertaining to various years in a flip-flop scenario within the period 1987-1993, as shown schematically in Table 2, was now favoured. The latter table shows results using only the corrected and the modified ADCP flowfields. In particular 1989, but also 1990 and 1992 were years of high advective loss (Shannon *et al.*, in press), the former two coinciding with moderate to high SE winds, whereas 1987, 1988, 1991 and 1993 were years of low advective losses. This did not match the model completely, because high advective losses were also shown by the model following the extensive spawning of 1991/1992. Nevertheless, because of non-linear mortality, these losses did not reduce recruitment to the same extent as in 1988/1989 and 1989/1990.

Fig. 8: Time-series of the numbers of anchovy recruits (billions) measured during winter hydro-acoustic surveys and the cumulative October to March SE wind anomaly measured at Cape Point, 1985-1994.



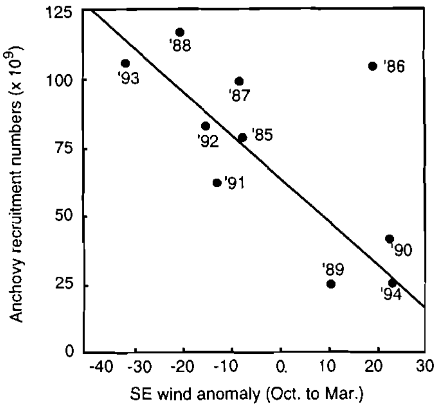


Fig. 9: Correlation between anchovy recruit numbers and the spring/summer SE wind anomaly at Cape Point. The line is drawn excluding the 1986 data point (see text), although the correlation coefficients are given for this point excluded ($r=-0.88$; $n=9$; $p<0,005$), as well as for it being included, ($r=0.65$; $n=10$; $p<0,05$).

Spawning/ Recruitment	(Corrected) 'Reduced' advection scenario (numbers x10^9)	Modified advection scenario	Observed trends (Figures 8 and 9)
1986/87	468*	122	Low SE wind - High recruitment
1987/88	461*	179	Low SE wind - High recruitment
1988/89	420	139*	High SE wind - Offshore spawning Low recruitment
1989/90	465	135*	High SE wind - Low recruitment
1990/91	484*	214	Low SE wind
			High number of recruits
1991/92	431*	200	Low SE wind - good spawning and recruitment on central Agulhas Bank
1992/93	464*	219	Very low SE wind - High number but low biomass of recruits

*: suggested flowfield domain

Table 2: Summary of recruitment results from application of the model to two different flowfields (see text) and comparison with observed wind and recruitment, and inferred flip-flop scenario.

The conclusion of the modelling and correlation exercises (Fig. 8 and 9, Table 2) is that advective losses could indeed have a significant influence on anchovy recruitment numbers in the southern Benguela during periods of strong SE winds coinciding with the global signal of ENSO high phase. Local SE winds appear implicated in the process, as shown in the regression in Figure 9 (excluding the 1986 data point), with the 1986 outlier showing the occasional strong affect of oceanic advection.

The food index, namely the oil-to-meal ratios for the Western Cape, was correlated against anchovy recruitment biomass, also from the acoustic surveys, from 1985 to 1994. This resulted in a significant relationship, even when only the first four months of the year are used (Fig. 10). The correlation (r=0.69, n=10, Fig. 11) also shows the potential for oil yields to be used as a mid-season predictor of total recruitment biomass. Annual data could also be used as a proxy for recruitment in longer-term studies, because linear regression of recruitment biomass against mean annual oil yields and "year-factors" yielded r values of 0.74 and 0.72 respectively, although these indices could not be used in any predictive sense. The pelagic fish catches from the Western Cape west coast ports largely exclude the spawning fish, which are mainly found on the Agulhas Bank, although some spawning sardine are caught, as well as adult red-eye and juvenile horse mackerel, particularly in the first few months of the year.

Fig. 10: Time-series of the biomass of anchovy recruits measured during winter hydro-acoustic surveys (thousand tonnes) and the oil-to-fishmeal ratio between January and April from western Cape ports (excluding Gans Bay).

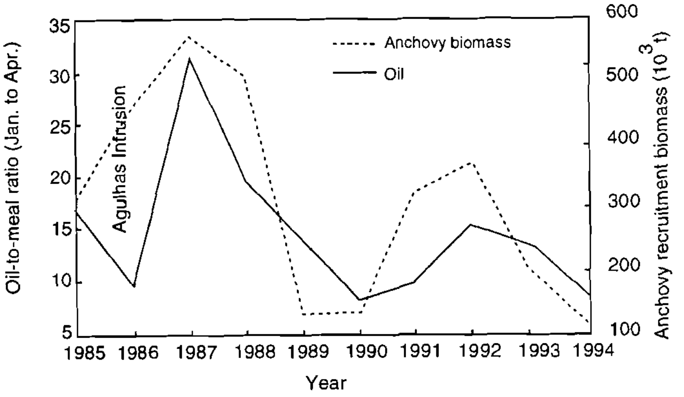
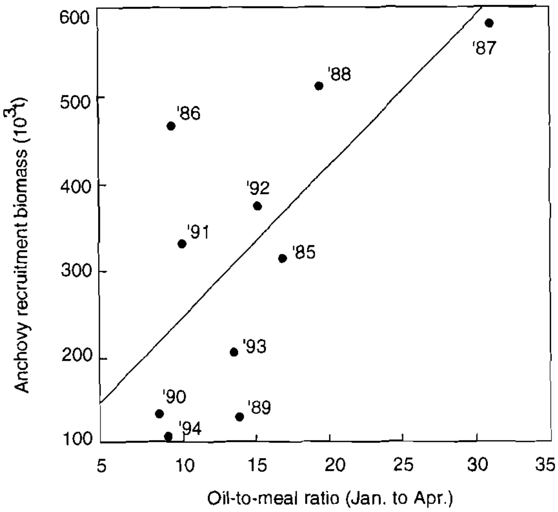


Fig. 11: Correlation (r=0.69; n=10; p<0.05) between the oil-to-fishmeal ratio from January to April and the biomass of anchovy recruits measured during winter hydroacoustic surveys (thousand tonnes).



3. NON-LINEAR RELATIONSHIPS

In terms of Optimal Environmental Window (OEW) models (Cury and Roy, 1989), the 1993 data point, with high numbers but an even lower biomass of recruits, is the only one that would appear to lie to the left of the dome. Recruitment in all other years falls either in the centre or to its right. This was tested using ACE methods (Cury *et al.*, 1995), with the anchovy biomass data being related to the wind index. The result is shown in Figure 12a. When numbers were considered, the transformation was basically linear for both variables, resulting in virtually the same negative relationship (Fig. 12b). However, an ACE regression of anchovy biomass against both wind and oil yield (not shown here) suggested that the positive relationship against oil-yield was dominant.

Additionally, in OEW models the factors of upwelling wind and food abundance are held to be positively correlated (i.e., more wind, more food). However, the wind and oil data presented here showed an insignificant inverse relationship when correlated linearly. This suggests that, in this southern Benguela model, the food and wind indices are not tightly coupled and that oil yield is acting more as a proxy for recruitment. Therefore, SE winds could possibly be the dominant independent factor, but both wind and food indices are nevertheless still subject to being overruled by oceanic advection in certain years such as 1986.

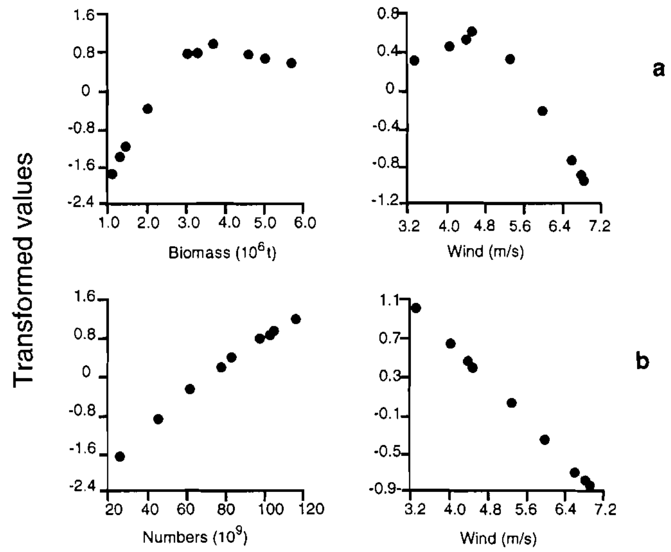


Fig. 12: Plot of the ACE transformation of anchovy recruit (a) biomass and (b) numbers and mean SE winds (m.s^{-1}) from October to March in the southern Benguela.

DISCUSSION

The South African anchovy fishery relies mainly upon catching the annual recruitment run, and TACs are based upon hydroacoustic estimates of recruitment undertaken in the middle of the fishing season. (Hampton, 1992). However, advance knowledge of recruitment would be of great value (Cochrane and Starfield, 1992).

In relating environmental factors to fish recruitment there is often the problem of which came first, the index which correlates with recruitment or the rationale for choosing a suitable index. In this instance, we were fortunate, but also restricted, in having a single, long time-series of fish oil-to-meal ratios which could be used as a food index and an appropriate long term wind record which appears to tie in with transport. Rationale involved choice of the temporal and spatial averaging in producing the indices.

The approach we took here with regard to the oil data differs fundamentally from previous studies (e.g., Cochrane and Hutchings, 1995) which looked at the oil yields of the previous year as a potential predictor of the recruitment the next year. (Such studies argued that high oil yields operating through adults having sufficient lipid reserves would lead to successful spawning and thereafter to good feeding for juveniles). By choosing oil-yields from the pre-recruitment period (although from fish of commercial size), we delay any forecast but hopefully make the relationship more robust. Both approaches do have problems, however. In order to justify using oil-yields to indicate likely future spawning success, the fishery would have to target on these spawners to a far greater extent than the SA pelagic fishery does. On the other hand by using the oil data from largely before the beginning of the season to indicate recruitment (as done here) we implicitly suggest a common favourable environment for adults of various species and anchovy pre-recruits.

With regard to the wind index, the transport rationale is generally given an equal or lesser rating than wind-driven turbulence, as described by Lasker (1975, 1978). We do not exclude the possibly important effect of turbulence on recruitment, but rather show that advective losses arising from the position of spawners in the flowfield can, and perturbations of the surface flowfield attributable to winds could, lead to a good proportion of the observed recruitment variability. The recruitment of anchovy, and possibly other pelagic species, could be investigated in the future by using the model to simulate transport under different flowfield scenarios, which could arise as a result of a changing global climate. Future work could build upon the use of oil-yield data as a proxy for anchovy recruitment and investigate the relationship of this variable, as dependent upon SE winds, using a longer time-series.

Lastly, it should be mentioned that, although SE winds can be strongly implicated in the anchovy recruitment failure during 1994 (through transport and/or turbulence), additional factors have been proposed by some of our colleagues. These include the possibly poor condition of young spawners and the sharp divide between very cool upwelled and warm Agulhas water in the spawning area, leading to fish being relatively far offshore in a small region of favourable temperatures. This anomalous year merits a study in its own right, particularly because it was studied by means of eight consecutive monthly cruises throughout the spawning season as part of the South African Sardine and Anchovy Recruitment Prediction programme. This programme also addresses the sardine, the spawning biomass of which had, by late 1994, reached the same as that of anchovy for the first time in over 25 years. Whilst the increase in sardine, resulting from conservative management plus unknown environmental cues is to be welcomed, it may affect the relationship between oil-yield data and anchovy recruitment, if anchovy are no longer the main contributor to the pelagic reduction plants.

ACKNOWLEDGMENTS

G. Nelson is acknowledged and thanked for constructing the anchovy transport model used in this study, and for his guidance in the project. We are grateful to L. Underhill for his statistical advice in the oil-yield project which forms part of this paper. The Benguela Ecology Programme is thanked for funding enabling A.J. Boyd to attend the First International CEOS meeting held in California in September 1994, and at which this paper was presented.

APPENDIX: MODELLING TRANSPORT OF CAPE ANCHOVY, *ENGRAULIS CAPENSIS*, OFF THE COAST OF SOUTH AFRICA

This model was developed by G. Nelson and L.J. Shannon of the Sea Fisheries Research Institute, Cape Town, in order to address the following questions:

(1)How does the interannual variation in spatial distribution of spawners influence recruitment and the spatial distribution of young-of-the-year anchovy?

(2)What are the effects of altered advection on anchovy recruitment?

The oceanic area around South Africa was divided into quarter-degree (latitude and longitude) blocks, to which spawner biomass and current data were allocated based on two data sets, namely Acoustic Doppler Current Profile (ADCP) data and November spawner biomass survey data. Each simulation involved selection of one of the historical spawner distributions between 1986 and 1992. Egg production in each block was then calculated from the spawner biomass measured there in that year, for each day within the spawning season (October - March). Egg production also depends on the fraction of females spawning each day of the spawning season, the number of eggs spawned per female per batch and the female ratio. Transport of reproductive products was simulated on an hourly time-scale from time of spawning until recruitment to the purse-seine fishery, assumed to take place after six months. Monte Carlo simulation of eddies and filaments and of smaller-scale diffusion was also included in the model. Numbers of anchovy were reduced by hourly mortality owing to factors other than advection. Batches crossing the offshore boundaries beyond where anchovy survive were considered to be lost to the system. Differential mortality, predation and swimming capability (of older juveniles) were omitted from this application of the model.

REFERENCES CITED

Bang N. D. and W. R. H. Andrews. 1974. Direct current measurements of a shelf-edge frontal jet in the southern Benguela system. J. Mar. Res., 32(3): 405-417.

Bloomer S. F., K.L. Cochrane and J. G. Field. 1994. Towards predicting recruitment success of anchovy *Engraulis capensis* Gilchrist in the southern Benguela system using environmental variables: a rule-based model. *S. Afr. J. Mar. Sci.*, 14: 107-119.

Boyd A. J., J.D. Hewitson, I. Kruger and F. Le Clus. 1985. Temperature and salinity trends off Namibia from August 1982 to August 1984, and their relation to plankton abundance and the reproductive success of pelagic fish. *Coll. Scient. Pap. Int. Comm. SE. Atl. Fish.*, 12(1): 53-60.

Boyd A. J., J. Salat and M. Masó. 1987. The seasonal intrusion of relatively saline water on the shelf off northern and central Namibia. *In*: A.I.L. Payne, J.A. Gulland and K. H. Brink (eds). The Benguela and comparable ecosystems. *S. Afr. J. Mar. Sci.*, 5: 107-120.

Boyd A. J., J. Taunton-Clark and G. P. J. Oberholster. 1992. Spatial features of the near-surface and midwater circulation patterns off western and southern South Africa and their role in the life histories of various commercially fished species. *In*: A.I.L. Payne, K.H. Brink, K.H. Mann and R. Hilborn (eds.). Benguela trophic functioning. *S. Afr. J. Mar. Sci.*, 12: 189-206.

Boyd A. J. and G. P. J. Oberholster. 1994. Currents off the west and south coasts of South Africa. *S. Afr. Shipp. News Fishg. Ind. Rev.*: 26-28.

Cochrane K. L. and A.M. Starfield. 1992. The potential use of predictions of recruitment success in the management of the South African anchovy resource. *S. Afr. J. Mar. Sci.*, 12:891-902.

Cochrane K. L. and L. Hutchings. 1995. A structured approach to using biological and environmental parameters to forecast anchovy recruitment. *Fish. Oceanogr.*, 4(2): 102-127.

Crawford R. J. M. 1980. Seasonal patterns in South Africa's western cape purse-seine fishery. *J. Fish Biol.*, 16(6): 649-664.

Crawford R. J. M., L.V. Shannon and D. E. Pollock. 1987. The Benguela ecosystem. 4. The major fish and invertebrate resources. *In*: M. Barnes (ed.). *Oceanography and marine biology. An annual review*. Aberdeen, University Press, 25: 353-505.

Crawford R. J. M., L.J. Shannon and G. Nelson. 1995. Environmental change, regimes and middle-sized pelagic fish in the south-east Atlantic Ocean. *Sci. Mar.*, 59 (3-4): 417-426.

Cury P. and C. Roy. 1989. Optimal environmental window and pelagic fish recruitment success in upwelling areas. *Can. J. Fish. Aquat. Sci.*, 46 (4): 670-680.

Cury P., C. Roy, R. Mendelssohn, A. Bakun, D.M. Husby and R. H. Parrish. 1995. Moderate is better: exploring nonlinear climatic effect on Californian anchovy (*Engraulis mordax*). Climate change and fish population. Beamish, R. J. (ed.) *Can. Spec. Publ. Fish. Aquat. Sci.*, 121: 417-424.

Hampton I. 1987. Acoustic study on the abundance and distribution of anchovy spawners and recruits in South African waters. *In*: A.I.L. Payne, J.A. Gulland and K. H. Brink (eds.). The Benguela and comparable ecosystems. *S. Afr. J. Mar. Sci.*, 5: 901-917.

Hampton I. 1992. The role of acoustic surveys in the assessment of pelagic fish resources on the South African continental shelf. *In*: A.I.L. Payne, K.H. Brink, K.H. Mann and R. Hilborn (Eds.). Benguela trophic functioning. *S. Afr. J. Mar. Sci.*, 12: 1031-1050.

Hutchings L. and A. J. Boyd. 1992. Environmental influences on the purse seine fishery in South Africa. *Investigación Pesq.*, Santiago, 37: 23-43.

Lasker R. 1975. Field criteria for survival of anchovy larvae: the relation between inshore chlorophyll maximum layers and successful first feeding. *Fishery Bull.*, Wash., 73: 453-462.

Lasker R. 1978. The relation between oceanographic conditions and larval anchovy food in the California Current: identification of factors contributing to recruitment failure. *Rapp. P.-v. Réun. Cons. int. Explor. Mer*, 173: 212-230.

Parrish R. H., A. Bakun, D.M. Husby and C. S. Nelson. 1983. Comparative climatology of selected environmental processes in relation to eastern boundary current pelagic fish reproduction. *In*: G.D. Sharp and J. Csirke (eds.). Proceedings of the Expert Consultation to Examine Changes in Abundance and Species Composition of Neritic Fish Resources, San José, Costa Rica, April 1983. F.A.O. *Fish. Rep.*, 291(3): 731-777.

Schülein F. H., A.J. Boyd and L. G. Underhill. 1995. Oil-to-meal ratios of pelagic fish taken from the northern and the southern Benguela system -seasonal patterns and temporal trends, 1951-1993. *S. Afr. J. Mar. Sci.*, 15: 61-82.

Shannon L. V. 1985. The Benguela ecosystem. 1. Evolution of the Benguela, physical features and processes. *In*: M. Barnes (ed.). *Oceanography and marine biology. An annual review.* Aberdeen, University Press, 23: 105-182.

Shannon L. J. 1995. *Modelling environmental influences on year-class strength of Cape anchovy Engraulis capensis off South Africa*. M.Sc. thesis, University of Cape Town.

Shannon L. V., A.J. Boyd, G.B. Brundrit and J. Taunton-Clark. 1986. On the existence of an El Niño-type phenomenon in the Benguela system. *J. Mar. Res.*, 44(3): 495-520.

Shannon L. V., J.J. Agenbag, N.D. Walker and J. R. E. Lutjeharms. 1990. A major perturbation in the Agulhas retroflection area in 1986. *Deep-Sea Res.*, 37(3): 493-512.

Shannon L.J., G. Nelson, R.J.M. Crawford and A.J. Boyd. In press. Possible impacts of environmental change on pelagic fish recruitment: modelling anchovy transport by advective processes in the southern Benguela. *Global Change Biology.*

Shelton P. A. and L. Hutchings. 1982. Transport of anchovy, *Engraulis capensis* Gilchrist, eggs and early larvae by a frontal jet current. J. Cons., *Cons. int. Explor. Mer*, 40(2): 185-198.

Shelton, P. A., Boyd, A. J. and M. J. Armstrong. 1985. The influence of large-scale environmental processes on neritic fish populations in the Benguela Current system. *Rep. Calif. Coop. Oceanic Fish. Invest.*, 26: 72-92.

Siegfried W. R., R.J.M. Crawford, L.V. Shannon, D.E. Pollock, A.I.L. Payne and R. G. Krohn. 1990. Scenarios for global-warming induced change in the open-ocean environment and selected fisheries of the west coast of southern Africa. *S. Afr. J. Mar Sci.*, 86:281-285.

Stander G. H. and A. H. B. De Decker. 1969. Some physical and biological aspects of an oceanographic anomaly off South West Africa in 1963. *Invest. Rep. Div. Sea Fish. S. Afr.*, 81, 46p.

Taunton-Clark J. and L. V. Shannon. 1988. Annual and interannual variability in the south-east Atlantic during the 20th century. *S. Afr. J. Mar. Sci.*, 6: 97-106.

Taunton-Clark, J. In prep. Coastal wind variability at Cape Point and Cape Columbine on the South African southwest coast.

Sardine and other Pelagic Fisheries Changes Associated with Multi-Year Trade Wind Increases in the Southern Canary Current

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ABSTRACT

Two periods of high abundance and southward spreading of sardines (*Sardina pilchardus*) and accompanying changes of other pelagic fish are described through the landings of an industrial fishery off Sahara and Mauritania. In the mid-1970s, the catches increased six-fold, exceeding 600 000 t in 1976-1977, then they decreased to 200 000 t, before rising again, in 1989-1990, to the same level. Afterwards, eastern bloc fishing effort was severely reduced and the catch dropped. Wind and sea surface temperature series obtained from ships-of-opportunity show that each of these booms followed a multi-year intensification of the northeasterly trades and upwelling.

An explanatory hypothesis is proposed, which relies on the alongshore and cross shelf circulation and on patterns primary of secondary production rate. In strong upwelling and fast offshore advective situations, primary production prevails and can feed large populations of sardine which thrive on phytoplankton. While in weaker upwelling areas, counter-currents acting as large scale retention loops, improve the transfer of primary production to zooplankton and favor zooplankton filter feeders (*Sardinella*, *Trachurus*) and small predators (*Decapterus*, *Scomber*).

During the trade wind strengthening periods, increases in the southward circulation and Ekman upwelling modify the ecosystem so that sardines colonize newly upwelled waters, overwhelm other species and widen their range up to Senegal. While in relaxation intervals, the decline of sardine leads to the dominance of sardinella, horse mackerel and mackerel.

Correlation analysis show that the yearly catches of sardine lag two years behind the alongshore wind stress. This means that larval and young fish survival is improved by increases of wind induced upwelling. Comparing catches to the monthly wind stress shows that strong wind always favors recruitment except during the first three months of larval life where the detrimental effect of the offshore losses overwhelms the improvement of feeding conditions.

RÉSUMÉ

Les données de captures d'une pêcherie industrielle établie au large du Sahara et de la Mauritanie permettent de décrire deux périodes de forte abondance et d'expansion de la sardine (*Sardina pilchardus*) vers le sud, ainsi que les changements concomittants qui se sont produits parmi les autres espèces pélagiques. Dans le milieu des années 70, les prises ont été multipliées par six jusqu'à dépasser 600 000 t en 1976-1977, puis elles ont diminué jusqu'à 200 000 t avant de retrouver en 1989-1990 le même niveau. Ensuite l'effort de pêche des pays de l'Est a été fortement réduit et la prise s'est effondrée. Les données de vent et de température de surface recueillies par les navires marchands montrent que chacune de ces expansions a suivi un renforcement de plusieurs années des alizés et de l'upwelling.

Une hypothèse explicative est proposée, basée sur les schémas de circulation parallèle et perpendiculaire à la côte et sur le rapport des productions primaire et secondaire. Dans des situations d'upwelling intense et de forte advection vers le large, la production primaire l'emporte et peut alimenter de grandes populations de sardines phyto-planctonophages. Au contraire, dans les régions d'upwelling faibles, des contre-courants agissent comme des boucles de rétention et augmentent le temps de résidence des eaux au dessus du plateau, ce qui améliore le transfert de la production primaire vers le zooplancton et favorise donc les filtreurs de zooplancton (*Sardinella, Trachurus*) et les prédateurs (*Decapterus, Scomber*).

Pendant les périodes de renforcement du vent, l'accroissement de la circulation vers le sud et l'intensification des upwellings d'Ekman modifie l'écosystème de telle façon que les sardines colonisent les eaux nouvellement remontées et étendent leur aire de répartition jusqu'au Sénégal. Cependant, dans les intervalles de relaxation, le déclin des sardines conduit à la dominance des sardinelles, chinchards et maquereaux.

Des calculs de corrélation montrent que les prises annuelles de sardine suivent la courbe de l'intensité du vent avec un retard de deux ans. Ce qui signifie que la survie des larves et des jeunes poissons est améliorée par l'upwelling induit par le vent pendant les deux premières années de leur vie. La comparaison des prises aux tensions de vent mensuelles montre que le vent favorise le recrutement à toutes les périodes de l'année, sauf pendant les trois premiers mois de la vie larvaire où l'effet négatif de l'entraînement au large prévaut sur l'amélioration des conditions trophiques.

INTRODUCTION

Clupeoid fish, and particularly sardines, are well known to be highly variable resource and the analysis of scales records from anoxic sediments showed that large variations in stock size have occurred before the development of fisheries (Soutar and Isaacs, 1974). On the other hand, similarities between the fluctuations of several sardine fisheries, in different oceans, suggest that climatic factors, at a quasi-planetary scale, might control these populations (Cushing, 1982).

Stock increases in density are frequently associated with geographic spreading, as the case of the north eastern Atlantic sardine. The northern boundary of *Sardina pilchardus* is approximately the entrance of the British Channel (Southward *et al.*, 1988). During the 1950s, the French sardine fishery was bountiful and large quantities of sardine were caught all the way to the North Sea. The fishery of Northern Morocco was then considered as most southern fishery for this species. However, at the same time (1953), the regular occurrence of small number of *S. pilchardus* was established in Mauritanian waters (Cadenat and Moal, 1955), and some individuals were occasionally caught as south as Dakar (Fréon, 1988). During the 1960s catches from the North Sea to the Gulf of Biscay declined. Also, at the end of the 1960s, a strong southward extension of the sardines occurred in the Canary Current (Fig. 1) leading to the emergence of a new fishery off the Western Sahara, which had been initially directed towards horse mackerels (*Trachurus spp.*), mackerels (*Scomber japonicus*) and scads (*Decapterus ronchus*), (FAO, 1985, 1990). The sardine catches, mainly due to eastern bloc trawlers, (Fig 2) increased quickly from 80 000 to 650 000 tonnes, then decreased below 200 000 t during the late 1970s and early 1980s. Again, in the late 1980s, catches reached approximately the level of the preceding maximum (FAO, 1990). But, from 1992 onwards, political changes and economic problems led the eastern bloc countries to dramatically reduce their fishing effort and, consequently, the catch has declined considerably (FAO, 1994).

An apparent relationship between the southwards expansion of sardine, the strong catch increase and a drop in sea surface temperature was noticed by Domanovsky and Barkova (1976) and Fréon (1988). The latter equally observed a change in

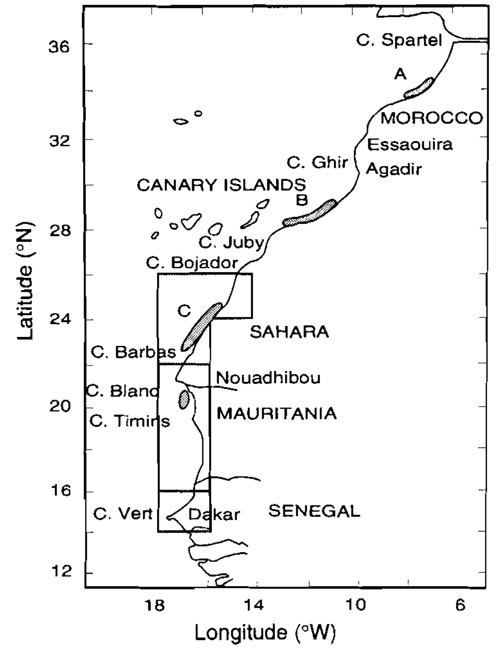

Fig. 1: Location of the spawning areas of stocks A, B, C (shaded), (from FAO, 1985) and of Banc d'Arguin (south of Cape Blanc). These areas are henceforth called 'Sahara', 'Mauritania' and 'Senegal'. The SST and wind data presented here stem from these areas.

the specific composition of the pelagic catch, and hypothesized probable causes for these changes. Also, a review of ecological knowledge in this area led Binet (1988) to explain how the trade wind acceleration increased offshore and southwards surface transport, enhanced the primary/secondary production rate, favoring phytoplankton feeders and the southwards expansion of temperate species.

Thus, the second boom of the sardine fishery, south of 26°N, during the late 1980s, following another multi-year strengthening of the trade winds and concomitant with a new southward expansion of this species all the way to Senegal, is of particular interest, as it corroborates the previous hypotheses. This paper generalizes these through a hypothesis linking trade winds and pelagic fisheries, from a literature review, then presents the climate and fishing changes observed along the north west coast of Africa, from 26°N to 14°N, during the last three decades.

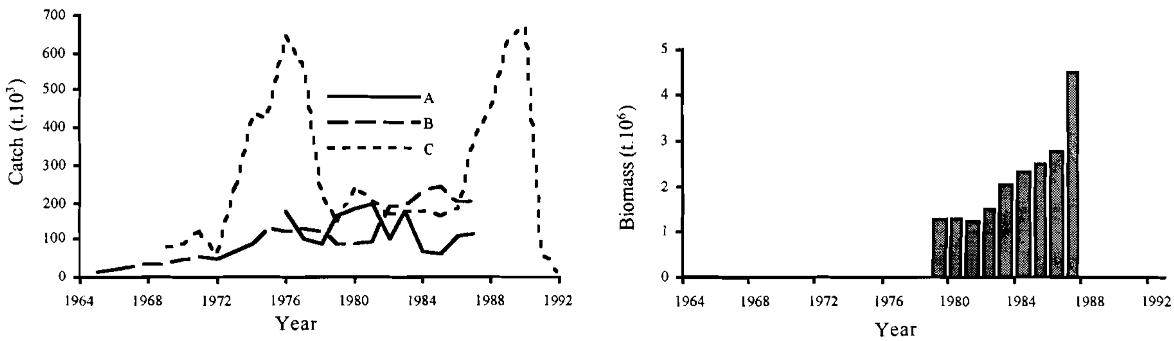

Fig. 2: Sardine catch of stocks A, B and C (see Fig. 1), Biomass of the stock C computed from a VPA. After FAO (1990 and 1994).

1. HYDRODYNAMICS AND PRODUCTION CHANGES INDUCED BY CHANGES IN WIND STRENGTH

An increase in trade wind velocity strengthens Ekman upwelling, offshore and southwards transport and could explain the settlement of *Sardina pilchardus* beyond its usual range, by enhancing the drift towards southern areas and in modifying the ecosystems such that sardines can overwhelm other pelagic species (Binet, 1988).

1.1. Alongshore circulation

Along the northwestern coast of Africa, surface transport is driven by currents that are usually equatorward: the Canary Current and the Guinea Current. Under this surface layer, a poleward counter-current, situated near the edge of the shelf, sinks progressively from the Bay of Biafra (where it is still a surface current) to Morocco. The core of this poleward circulation is located between 25 and 60 m depth, off Côte-d'Ivoire (Lemasson and Rébert, 1973), 50-100 m off Senegal (Rébert, 1983), 100-200 m off Banc d'Arguin, 200-300 m north of Cape Blanc, 400-500 m at 25°N and 500-1000 m between 30 and 34°N (Mittelstaedt, 1982, 1983) (Fig. 3).

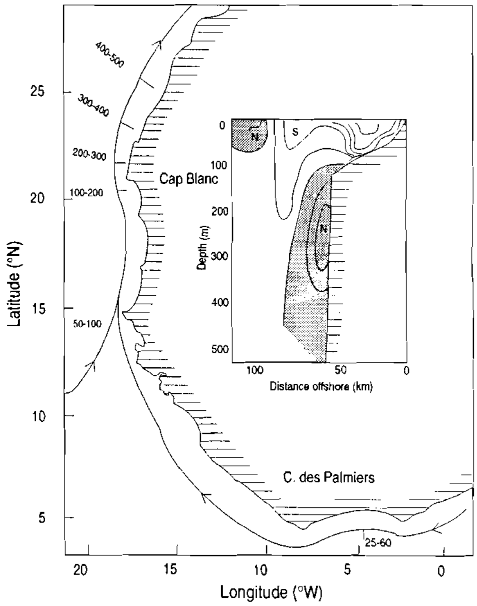

Fig. 3: Depth of the subsurface circulation (in m) along the coast of Northwest Africa. The polewards current progressively sinks north of Cape Blanc. The insert shows the alongshore components of the current (northwards and southwards, in cm/s), along a cross-shelf transect, north of Cape Blanc (21° 40'N). After Mittelstaedt (1982), Lemasson and Rébert (1973) and Teisson (1983).

However, the surface circulation fluctuates and seasonal reversals are known from Mauritania to the Bay of Biafra. On the shelf, between Cape Timiris and Cape Blanc, the flow is essentially wind-driven, and enhanced by a southward jet of 10 to 20 cm/s. However, offshore, a counterflow moves northwards opposite to the wind (Fig. 3). Inshore, there is also a superficial countercurrent, during summer and autumn (Mittelstaedt, 1976). The variability of the currents over the shelf and the slope is mainly determined by the interactions between the wind-driven flow and the countercurrent (Mittelstaedt *et al.*, 1975). Off

Saint-Louis du Sénégal (16°N), Catewicz and Siwecki (1985) found that currents in both northwards and southwards directions take the place of the general equatorward transport from June to November, in relation with seasonal interruption of the trade-wind. The velocities are low and the direction variable from June to August, while, during the following months, the current flows southwards and is faster. Teisson (1983) showed, similarly that during periods of strong trades, there is a fast southward flux, from the shore to beyond the continental slope, while during weak trades, a slow southwards vein flows in the middle of the shelf, between two northwards counter currents (Fig. 4).

Finally, a northward flow occurs along the Northwest African coast, due to the large-scale pressure gradient; however on the shelf, this effect is masked when the trade winds are strong enough to maintain the equatorward flow. The offshore undercurrent and the inshore near-surface countercurrent thus appear to be one and the same current system (Mittelstaedt, 1982).

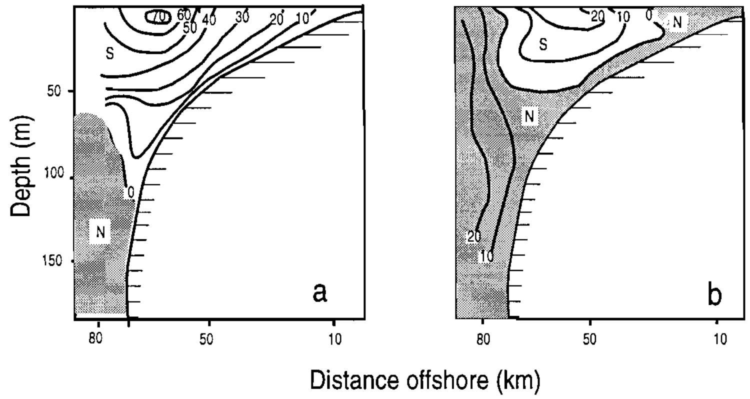

Fig. 4: Current section across the Senegalese shelf, at 14°N. North-South components (cm/s) during (a) strong trades and (b) weak trades, (from Teisson, 1983).

1.2. Upwelling and cross shelf circulation

There is no superficial countercurrent along the coast of Western Sahara, where the upwelling pattern is reduced to a two-cell system (Fig. 5a). In the coastal cell, the residence time of water in the euphotic layer, over the shelf is short, about 10 days (Jacques and Tréguer, 1986).

Off Mauritania, the cross circulation due to the coastal upwelling system is more complex. It has a horizontal diameter of 50 to 100 km (twice the shelf width), depending on the strength of the local winds. The most intense ascending motions occur at the shelf break, between 100 m and 150 m. The water masses rising up along the slope are trapped by the subsurface onshore flow of the compensation layer and upwelled on the shelf, close to the coast (Mittelstaedt *et al.*, 1975). The near-surface offshore flow ranges vertically over 15 m near the Banc d'Arguin to about 50 m at 20 km further seaward. Within the compensation layer, the upwelling waters come from the North at shallower depth and from the South at lower depths, due to the poleward-flowing current. (Mittelstaedt, 1982).

To explain these complex features, Mittelstaedt (1982) proposes a three-cell pattern, consisting of a strong inshore upwelling and of a weak offshore divergence, separated by a convergence over the slope (Fig. 5b). The subsuperficial waters of the undercurrent may rise in the onshore as in the offshore upwellings while the surface waters of the countercurrent may be involved in the upwelling circulation of the shelf by downwelling along the convergence zone and rising along the slope in the compensation layer. The existence of an occasionally closed inshore upwelling circulation cell makes it possible for some of the upwelled water to recirculate in two to three weeks. Mittelstaedt (1982) computes the residence time of the water on the shelf to one month, starting from the entry of subsurface water on the shelf and ending when the surface layer leaves the shelf, after having passed two upwelling cycles. This pattern associates vertical and horizontal recycling with the latter, an anticyclonic cell, probably being the more effective.

Off Mauritania, complex hydrographic patterns, including a countercurrent near the surface enables the recycling of water, both vertically and horizontally, in a manner different from that off the Sahara (Fig. 5).

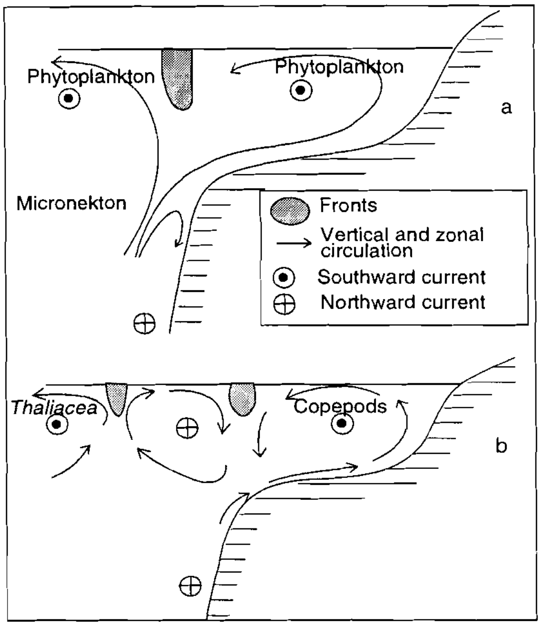

Fig. 5: Pattern of the cross shelf circulation off Sahara, 25°N (a) and Mauritania, 18°N (b). After Jacques and Tréguer (1986), Mittelstaedt (1982) and Weikert (1984).

1.3. Balance between phyto and zooplankton productions

Phytoplankton production can quickly follow a nutrient enrichment of the euphotic layer, provided that turbulence has sufficiently decreased. Off Morocco, Grall *et al.* (1982) observed a lag of 4 to 10 hours between the maximum wind impulse and the arrival of deep water at the surface. Chlorophyll then increases 6 hours after the wind relaxes, and stratification begins. Indeed, phytoplanktonic cells need only a few hours for division. Thus, maximum chlorophyll areas are situated very close to the core of upwelling plumes. Frequently, a large part of this primary production is lost for consumption by herbivores, on ends in dead ends. In some areas, large swarms of *Thaliacea* can exploit quickly the huge amount of biomass produced, because Salps and doliolids may short-circuit sexual reproduction and multiply very quickly by budding. Cladocerans too, can reproduce parthenogenetically and ensure a rapid utilization of the primary production. However, the bulk of the zooplankton is made of Copepoda, whose life cycles are much too long (2 to 4 weeks in tropical seas) to ensure an efficient transfer of a bloom of primary production to secondary production. This is probably the reason why zooplankton is not very abundant in regions of strong upwellings.

Along the north western coast of Africa, the maxima of zooplankton and of phytoplankton are closely matched in areas with weak, seasonal upwelling, while there is mismatch in permanent strong upwellings.

Off Morocco, Grall *et al.* (1974) measured the rate ATP/Chl*a*, (roughly equivalent to the sum of autotrophs plus heterotrophs, divided by chlorophyll *a*). This rate was lowest near the core of the plume and increased southward, to a maximum 60 nautical miles from the core. In the two-cell upwelling system off Sahara, there are only small copepods over the shelf. The strongest zooplankton biomasses are found offshore (Vives, 1974; Hargreaves, 1978; Weikert, 1984; Olivar *et al.*, 1985), contrarily of what is currently observed. Larger species (notably Euphausiacea) live off the shelf (Blackburn, 1979). On the contrary, south of Cape Blanc (Mauritania), larger zooplankton biomasses are found on the shelf, or nearby (Alcaraz, 1982).

The seasonal maxima of phytoplankton and zooplankton occur approximately at the same time in Mauritania (south of Cape Timiris), off Dakar and Abidjan, while off Morocco, the phytoplankton and zooplankton peaks are dissociated (Fig. 6).

This probably means that when the residence time of zooplankton near the bloom of phytoplankton is too short, the copepods are not able to transform efficiently the primary production into eggs and to lay these near the richest phytoplankton areas. This is so mainly because phytoplankton is concentrated in the euphotic layer, while zooplankton,

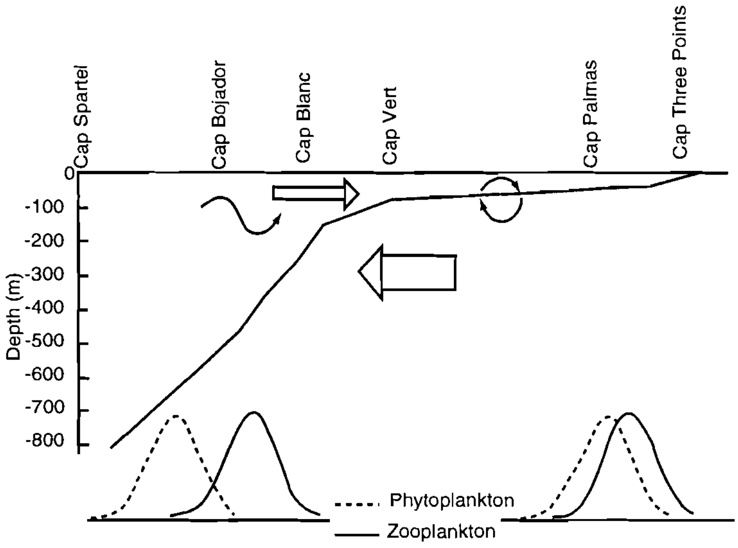

Fig. 6: Surface and subsurface circulation along the West Africa (broad arrows). Mean depth of the subsurface polewards circulation. Zooplankton drift is related to ontogenetic vertical migration (sinusoid and circular arrows). South of Cape Vert, ontogenetic migration can retain zooplankton populations in high primary production areas, because the undercurrent brings back older stages near their hatching place; phytoplankton and zooplankton annual cycles are matched. North of Cape Blanc, the polewards current sinks deeper and ontogenetic migration of most copepod species cannot retain them in the most productive areas; moreover the residence time of waters over the shelf is short and high zooplankton biomasses are found offshore. In coastal areas the zooplankton peak lags several months after the phytoplankton bloom (adapted from Binet, 1988, 1991).

distributed over the whole water column, is scattered by the currents. The efficiency of transformation of phytoplankton into animal biomass is low and the zooplankton seasonal maximum lags behind the phytoplankton bloom. However, certain copepods perform an ontogenetic migration; the young stages remain near the surface, while the older stages dwell in a deeper, opposite current. This behaviour can retain the population in a given area, or at least weakens its dispersion (Binet and Suisse de Sainte-Claire, 1975; Binet, 1977). Vertical migrations, when coupled to an appropriate currents system, are probably the reason why maxima of phyto- and zooplankton do occur at the same time in moderate upwelling areas, where offshore transport is slow or where two opposite currents are superposed (Binet, 1988, 1991), (Fig. 6).

We may reasonably suppose that the complex hydrological mechanisms enabling the water to recirculate in upwelling cells or slowing southward and offshore transports, lengthen the residence time of zooplankton near productive areas and improve the energetic transfer from primary to secondary production. It appears that in the strongest upwelling areas (Morocco, Sahara), where no subsurface layer counter acts the southwards transport, the upwelling leads mainly to a phytoplanktonic production. Off Mauritania on the other hand, as long as the countercurrent is not too deep, recirculating cells and vertical migrations enhance zooplankton production. The same, occurs, a fortiori, on the shelves off Senegal and Côte-d'Ivoire, where the countercurrent comes close to the surface.

Off Mauritania, the northwards surface transport develops when the trade winds relax, while the southwards transport strengthens and spreads up to Senegal during strong northerly periods. Then, phytoplankton production is probably favored instead of the zooplankton, and a shift of the upper levels of the food webs, from zooplankton-feeders to phytoplankton feeders, becomes likely.

1.4. Pelagic fish feeding and spawning

Clupeids are microphagous and most feed on zooplankton. Nevertheless, diatoms, and to a lesser extent dinoflagellates, are regularly consumed by Californian sardine along with zooplankton (Lewis, 1929). In the Canary Current, the contribution of phytoplankton to stomach contents of *Sardina pilchardus* is far from being negligible (Nieland, 1980) and this species frequently schools near diatoms blooms. Moreover, Cushing (1978) notes that the digestive tract of *S. pilchardus* is longer than that of strictly zoophagous clupeoids, which enables this species to digest phytoplanktonic cells. On the contrary, *Sardinella* spp. are mainly zooplankton filter-feeders, *Trachurus* spp. are only zooplankton feeders and *Decapterus rhonchus* and *Scomber japonicus* are predators. Thus, *Sardina pilchardus* can feed on phytoplankton and colonize newly upwelled waters, where secondary production is weak; this contrasts with the others species which tend to occur in the more mature ecosystems at the boundaries of the upwellings.

Along the northwestern coast of Africa, *Sardina pilchardus* has three main spawning areas (Fig. 1) corresponding to the three stocks A, B (north of Cape Juby) and C (south of Cape Juby). Reproduction does not occur in the strongest upwelling areas, between Essaouira and Cape Ghir and the larvae are less abundant between Cape Barbas and Cape Blanc where offshore advection is very strong. In the C stock (Sahara), the spawning area spreads between Cape Bojador and Cape Barbas (26° to 22°N). Off Cape Blanc *S. pilchardus* spawns from the center to the edge of the shelf. Eggs are distributed over the first 60 m, but after hatching, most larvae occur in the first 30 m (John *et al.*, 1980; John, 1985). Some of the deeper eggs are driven shoreward by the return circulation, then drift south westwards. The main spawning period is in October-December, a secondary spawning bout occurs in April-May. Concentrations of spawners appears to be associated with small turbulent eddies in autumn and winter (Barkova and Domanevskaya, 1990), the seasons during which wind speeds are at their minimum.

Egg production is regulated by a thermic threshold and starts at temperature ranging from 15 to 17°C. Thus, spawning cannot happen in the very center of an upwelling. In weak upwellings, eggs tend to be abundant over the entire shelf, while in strong upwellings, eggs tend to occur over the shelf break, in warmer waters (John *et al.*, 1980). This regulating mechanism improves odds for the larvae to find a suitable environment for their development.

Sardinella aurita is another abundant pelagic fish from the intertropical belt including West Africa. It inhabits coastal waters, seasonally enriched by upwellings, and also spawns in Mauritania. The Banc d'Arguin and coastal region south of Cape Timiris include nurseries. The main reproduction season is in July-October, when the upwelling declines (Conand, 1977). *S. aurita* feeds mainly on zooplankton (Nieland, 1982).

Thus, while all of these species can live in upwelling, the feeding and reproductive strategies of *Sardina pilchardus* give it a better ability to colonize newly upwelled waters. On the other hand, any strengthening of southwards transport and correlated weakening of northwards surface currents, favours the settlement of new populations of sardine south of their usual latitudinal range and weakens the northwards migration of *Sardinella* spp.; and any cooling of the shelf waters favours temperate species (sardine) against tropical ones (sardinella).

2. DATA SETS

2.1. Climatic observations

Winds and sea surface temperatures (SST) were obtained from the international network of ships-of-opportunity. These raw data were processed for the entire tropical Atlantic basin to determine monthly fields of pseudo-wind stress[1]. The database was started in 1964 and is continuously updated (Picaut *et al.*, 1985; Servain *et al.*, 1987; Servain and Lukas, 1990). The monthly values of wind stress and SST are calculated in 5° longitude by 2° latitude quadrangles. An objective analysis method is then used to create a 2° x 2° gridded monthly data base. Afterwards, the calculated data of the nearshore squares were averaged in three larger latitudinal strips, herafter called 'Sahara', 'Mauritania' and 'Senegal' to allow comparisons with the available fisheries statistics (Fig. 1, Table 1).

To obtain time series of a wind-induced upwelling index, monthly values of alongshore wind stress were computed. In Sahara region the wind vector was projected onto the shoreline direction. In other areas, where the coastline is assumed to be North-South, we used the southwards component of the wind stress. Climatologies were computed for the different areas (Fig. 7 a,b,c).

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[1] *The wind stress vector is the product of the density of air, the drag coefficient, the wind velocity vector and the absolute value of observed wind speed. The pseudo wind tress, hereafter named "wind stress" is equal to the product of the last two terms (wind velocity vector by absolute value of the wind speed).*

Areas	Latitude range (°N)	Longitude range (°W)	Coast direction (°N)
'Sahara'	22 - 26	14 -16 and 16 - 18	208
'Mauritania'	1° - 22	16 - 18	180
'Senegal'	14 - 16	16 - 18	180

Table 1: Geographical areas in which wind stress and SST from the database of J. Servain were averaged (these areas do not correspond to political entities).

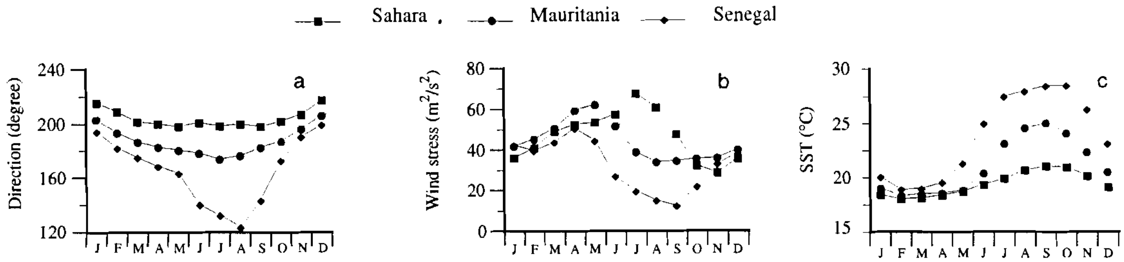

Fig. 7: Climatology from the ships of opportunity (database of J. Servain, 1964-1993): a) Wind direction, b) Alongshore wind stress, c) sea surface temperature.

2.2. Fisheries statistics

From 1964 to 1987, the catches in 'zone C', (26°N to 19°N, i.e., approximately from Cape Bojador to Cape Timiris), were obtained by WECAF working groups (FAO, 1990). *Sardina pilchardus* appeared in this area from 1969 onwards. The bulk of the catch was made up by eastern bloc countries, mainly the Soviet Union and including the former German Democratic Republic (GDR; Fig. 8). Boats were large pelagic trawlers (RTMA, BMRT and RTMS) and purse seiners associated to carriers (FAO, 1990).

Catches of mackerel (*Scomber japonicus*), scad (*Decapterus rhonchus*), Atlantic horse mackerel (*Trachurus trecae*), Cunene horse mackerel (*T. trachurus*) and *Sardinella* spp. from 1964 up to 1981 are known from a broad latitudinal range, corresponding to the WECAF divisions 34.1.3 and 34.3.1, (9°N to 26°N) (*in* Fréon, 1988).

From 1979 up to 1992, all pelagic catches made in the Mauritanian EEZ and off Western Sahara were collected by the Centre National de Recherches sur l'Océanographie et les Pêches (CNROP), Nouadhibou and compiled during the November 1993 working group held at Dakar (FAO, 1994).

Total catch of sardine was preferred to catch per unit of effort (CPUE) as an index of long term abundance variations because some effort data were missing or difficult to standardize and especially because the use of CPUE has proved to be hazardous to assess the abundance of highly variable pelagic resources. Fish are non randomly distributed, they frequently aggregate and their CPUE remains stable even when abundances decline. The fishing effort dramatically dropped after 1990 (Fig. 8).

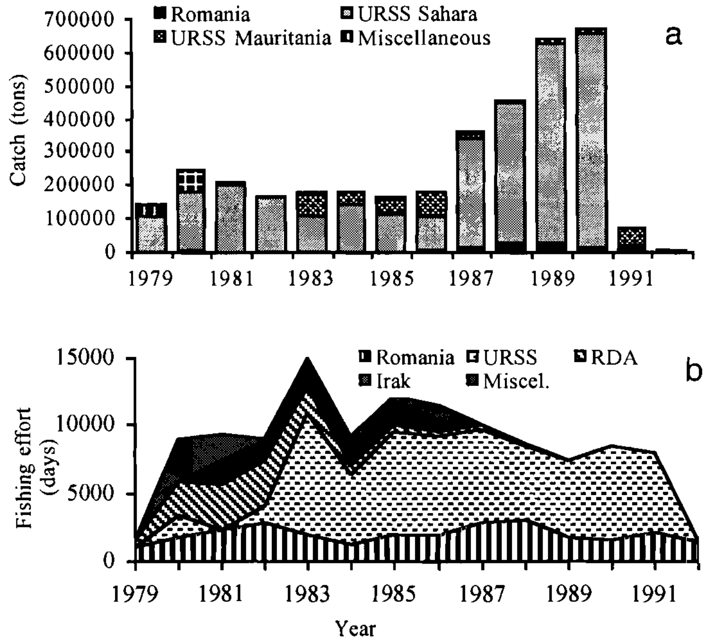

Fig. 8: Data on the sardine fishery: a) sardine catch off Mauritania and Sahara by different countries (1979-1992); b) fishing effort by different countries off Mauritania (1979-1992).

Available data do not allow a clear separation between what has been fished off Mauritania and off Sahara. The Romanians fished only off Mauritania since 1979, meanwhile the Soviet fleet operated mainly off Sahara. As the Soviet catch largely exceeds all others, we compared the whole catch made off Mauritania and Sahara to the alongshore wind stress recorded off Sahara. The differences between the two sardine catch series, during their overlapping period, are small, compared to the peaks observed in 1976-77 and in 1989-90. Thus, we created a composite catch series including the first data set for the 1969-78 period and the second one, from 1979 onwards (Fig. 2). The dramatic decrease of the Soviet fishing effort after 1991 led us to discard the values of 1991 and 1992 from the correlation versus wind stress (section 4.4), as they probably did not reflect a real decrease in stock abundance.

The fishing strategy and the seasonal variations of availability of the different species off Mauritania were studied based on the mean monthly CPUEs of the Romanian fleet (1979-1992).

Off Senegal, *Sardina pilchardus* is caught only by small scale fisheries. It has been previously recorded as a very rare species (Fréon, 1988; Fréon and Stequert, 1979) and appeared in the small scale fishery statistics only in 1991. Unfortunately *Sardina pilchardus* is not appreciated by Senegalese consumers and, due to its low price (5 FCFA/kg), fishers do not target this species. Thus, its real abundance is not well known.

3. CLIMATE

3.1. Wind stress and SST climatologies

The meridional migration of the Intertropical Convergence Zone (ITCZ, which separates the northern and southern trade wind systems) determines wind and SST seasonal variations. ITCZ moves from a near equator latitude, during boreal winter, to a northern position, around 15°N on the coast and 20°N in the continent, during boreal summer. The northeasterly trade winds blow all over the year along the Saharan coast, while along the Senegal, winter and spring northerly alternate with variable, frequently westerly winds from June to October (Fig. 7a). The average wind speed increases from the south to the north, reaching their maxima in April to July, from the Senegal to the Sahara (Fig. 7b).

Along the northwestern coast of Africa, upwelling is considered to be a basically wind-driven process (Wooster *et al.*, 1976). Indeed, almost all correlations between monthly values of alongshore wind stress and SST are negative (Fig. 9). The only exceptions are found off Senegal, in July, August and September, during the monsoon season (Fig. 7). Nevertheless, it is of interest to notice the weakness of the correlation in summer and winter, in the three areas. These weak correlations probably mean that SST depends not only on local winds but also on remote events carried southwards by the Canary Current (Rébert, 1983). Wooster *et al.* (1976) observe that the field of offshore Ekman transport and those of coastal temperature anomalies are basically similar. However, a discrepancy occurs between 20° and 25°N, where the coastal temperature anomaly continues through the last quarter of the year even though the offshore transport has decreased significantly. That probably means that cold upwelled waters are strongly advected from the north at this time. Then the waters of the Saharian shelf are probably more mature (in an ecological sense) than waters that have been just upwelled and thus, more suitable for the feeding of early larvae.

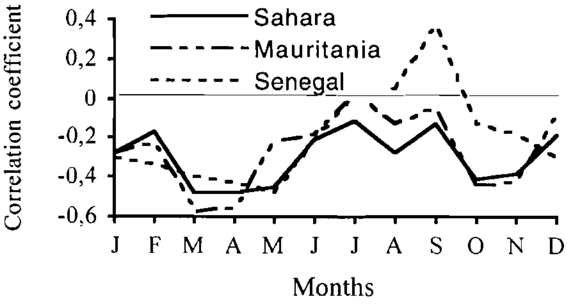

Fig. 9: Correlations between monthly values of alongshore wind stress and sea surface temperature. Negative correlations indicate Ekman upwelling.

3.2. Changes during the last three decades

Then we consider the alongshore wind stress (ASWS) series as a broad scale proxy for upwelling intensities. From 1964 up to 1993, ASWS (Fig. 10) and SST (Fig. 11) show roughly inverted patterns. Positive anomalies of ASWS (upwelling favorable) occurred at approximately the same time in the three study areas : from 1971 to 1975, in 1986 and from 1991 onwards. Strong negative anomalies of SST were clearly associated to the first two events, while period of strong winds in the early 1990s corresponds only to a slight cooling.

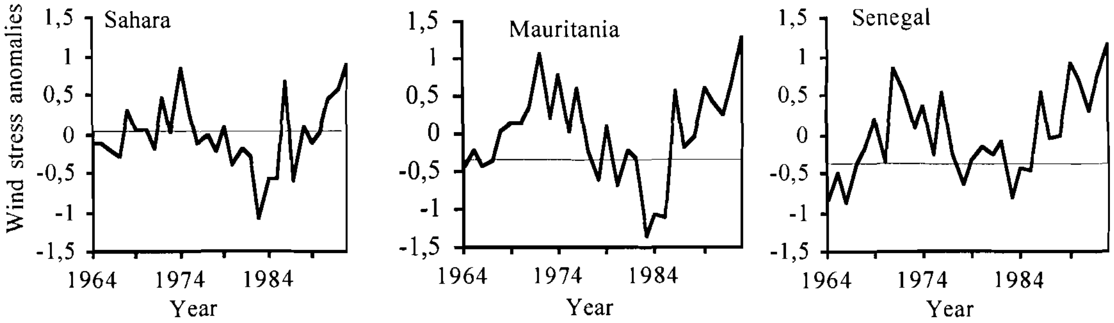

Fig. 10: Normalized series of alongshore mean annual wind stress anomalies (1964-1993). The wind stress is parallel to 208° off Sahara, and is southwards off Mauritania and Senegal.

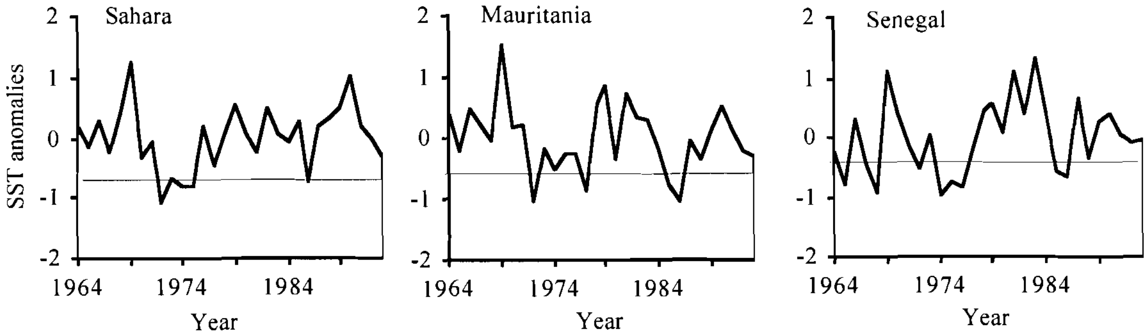

Fig. 11: Normalized series of mean annual sea surface temperatures anomalies, 1964-1993.

4. SMALL PELAGIC FISHERIES

4. 1. Southwards spreading of Sardine

The fishery for *Sardina pilchardus* in northern Morocco is relatively recent, as it began only during the 1920s (Belvèze, 1984). The fishing area progressively spread southwards, into what has been called zone A (32° to 30°N), (Belvèze, 1984). Occasional occurrence of small sardines was recorded farther south, in the Baie du Lévrier (near

Nouadhibou) as early as 1923 by Monod. In June 1941, Spanish trawlers caught some small specimens (7-8 cm) off the Cape Blanc; in September 1952, a stomach of *Orcynopsis unicolor* provides another record. In 1953, the regular presence of sardine in the Baie du Lévrier was established by beach seine sampling from April to July (Cadenat and Moal, 1955). All were of small sizes (7 to 12 cm) but they reached sexual maturity and the catch of very small fish (3 cm) proved that a population has established itself. Furnestin (1955) attributed the small size of these fish to a low growth rate in the southern limit of their province, and he thought that no commercial yield was foreseeable in this area.

From 1965 a second fishery developed between 29° and 27°N (zone B), then a third, south of 26°N, after 1969 (zone C). Catches of several tons were obtained in the Baie du Lévrier and north of Cape Blanc in 1972 and 1973 (Maigret, 1974). The southern boundary of the sardine fishery was estimated at 28°N in 1966, 21°N in 1970 and 18°N in 1973 (Domanovsky and Barkova, 1976). In 1974 some sardines were caught off Senegal (Conand, 1975; Boëly and Fréon, 1979). Then the schools came back northwards and the species almost disappeared from Mauritanian waters in 1982-83.

However, from 1984 the species was again fished off the Banc d'Arguin (20°N) and a new southward displacement appeared to begin (FAO, 1985). Indeed, the Senegalese small scale fisheries caught 77 t of *Sardina pilchardus* in 1991, and 1100 t in 1994, mainly by purse-seines. During a short period of the winter 1994, sardines were the main species caught in certain beaches south of Cape Vert, (Petitgas, pers. comm.). The present expansion of *Sardina pilchardus* in Senegalese waters is by no means comparable with the preceding scarce records. The rare records of sardine concerned mainly young fish, caught in waters between 16°C and 19°C, during the cold season, although, in 1954 and 1976, young fish were fished in the Bay de Gorée, in 25°-28°C waters (Fréon, 1988). On the contrary, the beach seine sampling, between January and March 1994, proved that the schools were made of 20-23 cm ripe sardines, weighing 100-130 g. Remote sensing thermographs indicate a strong cooling of superficial waters during the winters from 1986 onwards (except 1990). In 1986 and 1994, surface cold waters spread southwards from the Mauritania to southern Senegal (Demarcq, this vol.). This cooling may be responsible of the exceptional abundance of sardine south of Dakar. In the course of May 1994, the species was also caught in the bottom nets of the small scale fisheries, and it disappeared soon after, probably escaping in deeper waters as the warm season was advancing. On the contrary, the first months of 1995 were rather warm and no sardine was reported.

Although the Senegalese catch was very limited until 1994, it has clearly demonstrated, twice in twenty years, a southwards spreading of the geographical range of the sardine, following, one or two years later, the huge catch off Sahara in 1976-1977 and in 1989-1990. Moreover, each of these peaks was approximately in phase with a strengthening of the trade winds.

4.2. Seasonal pattern of catches and CPUE off Sahara and Mauritania

Seasonal and spatial distribution of pelagic catches can be used to infer ecological preferences of different fish species. The fishing strategy, i.e. the distribution of fishing days north and south of Cape Timiris, was approximately the same for the Soviet and Romanian fleets (Fig. 12). Most of the effort was in the south from April to June, then the boats moved northwards until the end of the year. This shift of the fishing boats is related to the seasonal displacement of the strongest upwelling. Chavance *et al.* (1991) observed that the fleet mainly worked in the region of the steepest SST gradients. Indeed, *Trachurus* spp. are the main catch of pelagic trawlers and this fishing strategy enables a regular yield of either of the two main *Trachurus* species. On the 1985-1991 Romanian catch averages (Fig. 13), the CPUE of the temperate species

T. trachurus highest during winter and almost null in summer, while the tropical *T. trecae* was mainly fished in the southern area, all along the year. Chavance *et al.* (1991) noted that the two peaks of yield correspond respectively to arrival of spawning concentrations of each of these two species into Mauritanian waters.

The seasonal patterns of CPUE for *Decapterus rhonchus* and *Scomber japonicus* differ from the preceding (Fig. 13). The higher catches occur after the maximum upwelling period. The seasonal changes in CPUE are related to temperature optima and feeding regimes. Phytoplankton predominates during period of maximum upwelling intensity, while heavier concentrations of zooplankton are delayed until wind stress and offshore transport relax (See Section 1.3). *S. japonicus* and *D. rhonchus* having a carnivorous diet avoid the newly upwelled waters, more than do *Trachurus* spp.

The tropical species *Sardinella aurita* and *S. maderensis* are more abundant during the summer non-upwelling period and higher concentrations of these two species are encountered south of Cape Timiris (Fig. 13).

The best catches of *Sardina pilchardus* clearly come from northern Mauritania, though the fishing effort of Romanians and Soviets were roughly equivalent in north and south areas (Fig. 12). The best fishing months were January-May and, secondly November-December. In other words, sardine was mainly fished during its two spawning seasons, and the catch were almost null from June to September, during the warmer period.

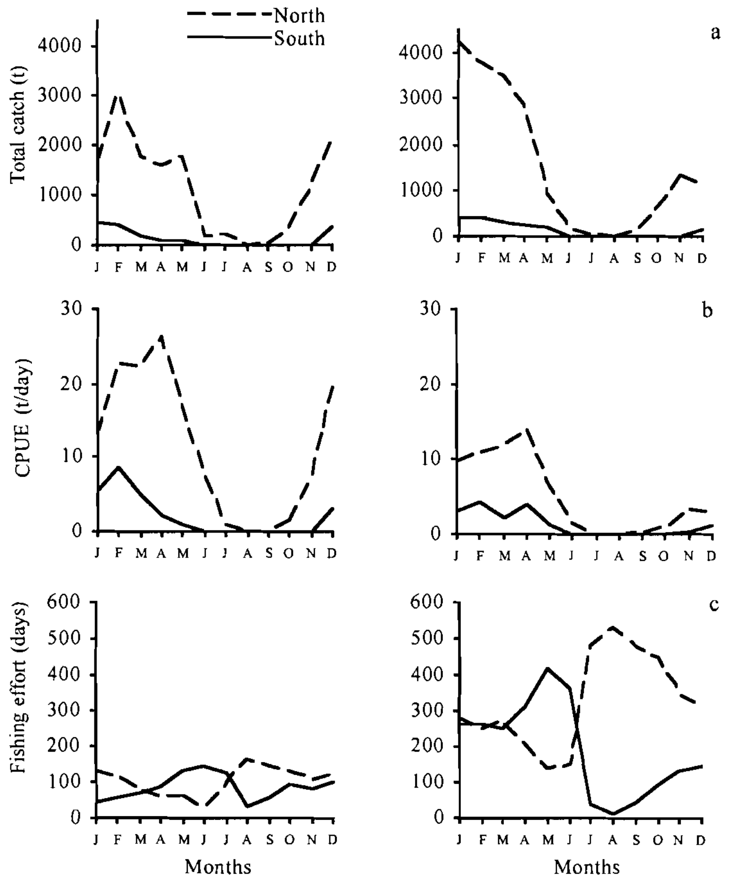

Fig. 12: Seasonal features of the Romanian (left) and Sovietic (right) sardine fisheries off Mauritania, North and South of 19°N:
a: total catch;
b: catch/effort;
c: fishing effort.

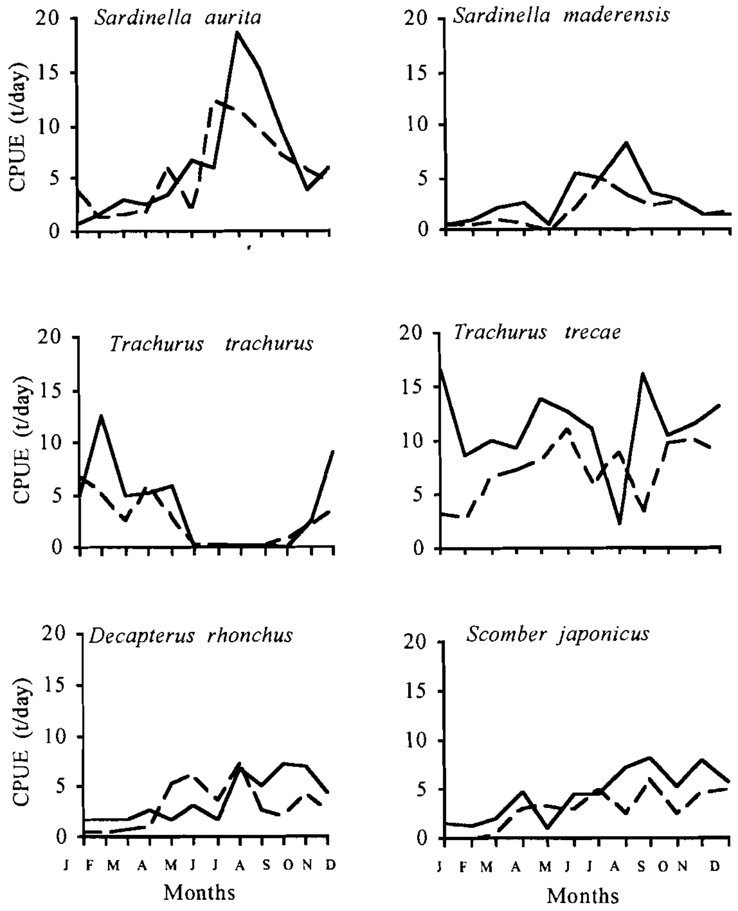

Fig. 13: Seasonal variation of catch per unit of effort (t/day) of the Romanian fishery off Mauritania (1979-1992) for *Sardinella aurita, S. maderensis, Trachurus trachurus, T. trecae, Decapterus rhonchus* and *Scomber japonicus*, off northern and southern Mauritania.

4.3. Changes in species dominance

A change in the relative abundance of pelagic species during the mid 1970s wind event was described by Fréon (1988) and Binet (1988). While the sardine landings were growing, the relative abundance of mackerels (*Scomber japonicus*), horse mackerels (*Trachurus* spp.), jack mackerels (*Decapterus rhonchus*) and *Sardinella* spp. were diminishing (Fig. 14). The new data set (1979-1992) shows a basically similar pattern. After the 1970s wind event, the proportion of sardine decreased, the catches were again dominated by *Trachurus* spp and *Decapterus*. Then, the 1986 ASWS peak was followed by a several year increase of *Sardina pilchardus* at the expense of the other species, up to 1989. These changes closely resemble those which happened 10 years earlier.

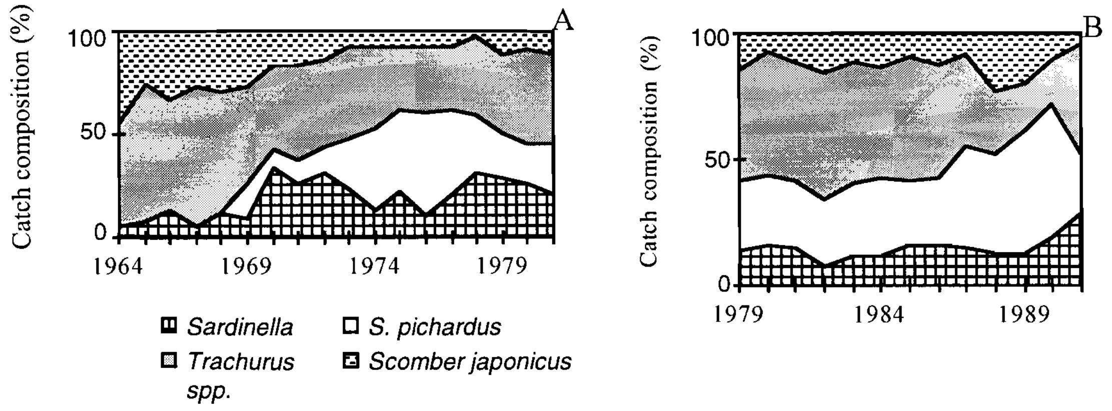

Fig. 14: Changes in the species composition of pelagic catches in the 9°-26°N area (left), from Fréon (1988) and Binet (1988); and off Mauritania (right), from FAO (1994).

4.4. Wind - sardine recruitment relationships

A linear correlation was sought between the time series of wind stress and sardine catch off Sahara and Mauritania (1969-1990), (Fig. 15). These were first calculated between annual values of ASWS and sardine catches. The best correlation is obtained between the annual catch and the wind of the previous years (Table 2). Assuming that catch variability reflects - to a certain extent - changes in the stock abundance, these correlations mean that if sardines are mainly recruited at two years old, the recruitment is favoured by increase, in the wind, induced upwelling during the first yearof life of the fish, and the result appears in the fishery two years later. According to Barkova (*in* FAO, 1990) stock biomass began to increase slowly in 1982, and quickly from 1987 (Fig. 2), that is only one year after the 1986 wind strengthening.

Year	year n	year n-1	year n-2	year n-3
r	0.126	0.242	0.354	0.237

Table 2: Correlations between the yearly catch of sardine (Sahara and Mauritania) and the alongshore wind stress between 22° and 26°N.

Then, in order to identify the season whose climate determines recruitment levels, the regressions were calculated between the annual catches and the twelve monthly ASWS series, with time lags ranging from zero to two years (Fig. 15). The correlations are weak, but positive for the largest part of the year. Negative values are observed only in May, July, August and particularly December. The coherence of these results has some significance. If the spawning periods are in October-December and April-May, strong winds when larvae are less than three months old, negatively affect their survival; on the other hand, strong winds during the rest of the year improve survival. In other words, strengthening of Ekman upwellings are beneficial to the food web and to sardine feeding, insofar they do not occur within the very first months after spawning of sardine.

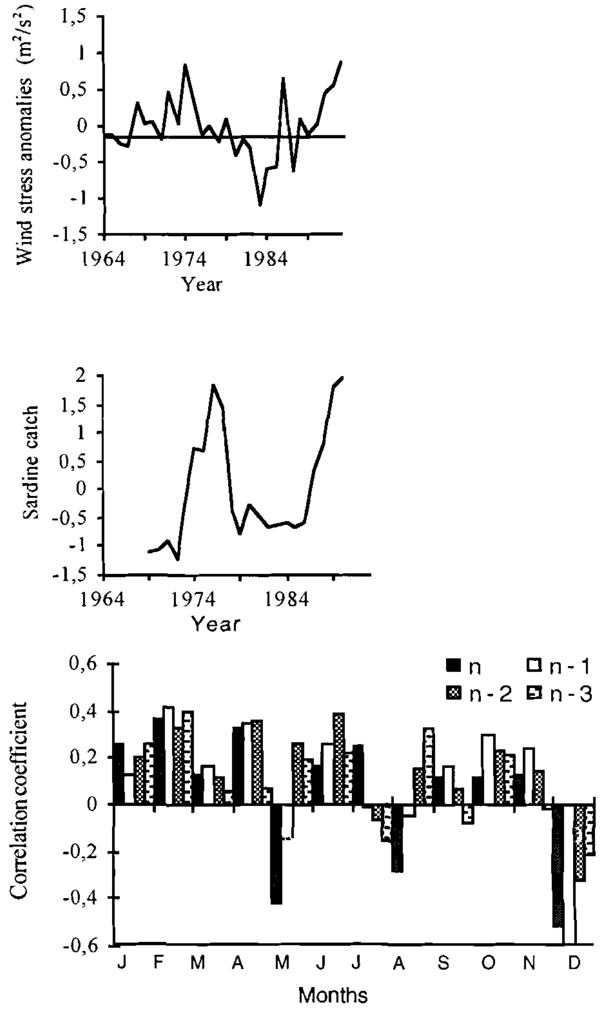

Fig. 15: Analysis of sardine recruitment: a) standardized anomalies of alongshore wind stress; b) total sardine catch off Sahara and Mauritania (1969-90); c) correlations between the annual sardine catch off Sahara and Mauritania and monthly alongshore wind stress, for time lags from 0 to 3 years.

CONCLUSION

In the southern part of the Canary Current a large fishery has developed off the Western Sahara, based on a sardine population, (stock C), which was absent before 1965. Two southwards expansions of this sardine occurred at 23 years interval. *Sardina pilchardus* was fished off Mauritania, where large industrial fleets were exploiting it and off Senegal, where moderate numbers were caught by the small-scale fishery. Southwards extensions are correlated to multi-year periods of trade wind strengthening which occurred in 1972-75, in 1986 and from 1991. We described likely environmental changes associated to the new climate pattern: intensification of upwelling regime, southward transport, and decline of SST. Phytoplankton production was probably boosted as well, but not matched by zooplankton grazing, due to the brevity of the residence time of waters over the shelf. Thus, sardines larvae were strongly advected towards the south and, as adult sardines are able to feed on phytoplankton, they were favoured instead of the zooplankton feeders, or the carnivorous small pelagic fish.

Off Northwest Africa, sardines spawn during the whole year, with a distinct maximum in winter. In the Cape Blanc area, larvae were abundant at SST between 16° and 17°C, scarce at temperature above 18°C and absent when the SST exceeded 21°C (John *et al.*, 1980). These authors described an absence or scarcity of larvae in 1968, 1970 and 1972, during weak or absent upwelling, while they record high catches of larvae in 1974, 1975 and 1977. These fluctuations are in good agreement with the changes of upwelling intensity, and corroborate the correlations we found between recruitment and annual wind stress.

However, spawning is limited by temperatures below 15.5°C (John *et al.*, 1980), and during strong upwellings, eggs are only found in small number over the shelf break. The negative correlation we found between catch and ASWS, during the spawning period, probably means that during early life, the advective losses are more deleterious for the larval survival than food limitations. This is in contrast to other parts of the year, when strong upwellings enhance the food content of coastal waters and the survival of young sardines.

In the Canary Current, the drift of fish larvae is basically directed southwards. Lloris *et al.*, (1979) propose a biological cycle of a demersal fish (*Pagellus acarne*) based on a latitudinal separation of adults (northern, upstream group) and juveniles (southern, downstream group). Eggs and larvae released by the adults drift southwards and lead to the southern group. The reverse link between young and adult is assumed to be a countercurrent migration off the edge of the shelf. (This return migration might be helped by the deep northwards current). The life span of *Sardina pilchardus* eggs is 2 to 4 days, while larvae may reach up to 9 weeks (John *et al.*, 1980). Along a transect parallel to the coast, from Morocco to Mauritania, the larger larvae were found in the south, indicating the direction of their drift. However, John *et al.* noted that, in 1977, the southern drift of near-surface larvae may be an exception due to the strong upwelling rather than a regular feature.

However, during the last decades of strong upwellings, a general trend to a southwards extension of the geographical ranges of pelagic species has occured (Ehrich *et al.*, 1987). Thus, we may reasonably suppose that the southwards circulation was enhanced and northwards surface transport inhibited during these windy years. It became unlikely for juvenile tropical fish to settle north of Cape Blanc. On the contrary, during wind relaxation periods, the slowing of alongshore and cross shelf circulations lengthen the residence time of water over the shelf, improves food web transfers and favours carnivorous fish. The decrease of northerlies enables a northwards surface transport and a colonization of the Mauritanian shelf by tropical species.

The first records of a species, out of its usual range, are generally from isolated individuals, which can be considered as vagrants, according to Sinclair (1988). If these vagrants are numerous enough, and if they encounter good environmental conditions, including circulation features enabling a complete life cycle on the shelf, their offsprings may initiate a new, self-sustaining population. The recent history of cod settlement off West Greenland, from larvae advected from the Iceland, is a similar example (Dickson and Brander, 1993). Thus, the southward extension of sardines from Morocco to Senegal, during the last decades, probably went off through the successive settlement of spawning areas, heading to self sustaining populations off Cape Bojador-Cape Barbas, Cape Blanc-Cape Timiris and possibly on the Senegalese Petite Côte, south of Cape Vert. This colonization was probably facilitated by the heavy exploitation of other fish stocks.

It required 20 years at least, between the first spawning, observed in 1950, in the Baie du Lévrier (Mauritania) and the first industrial fishing in 1970. Maigret (1974) noted that the three years preceding the first landings in Nouadhibou were especially cold. The first observations of *Sardina pilchardus* in Senegalese waters, previously reported by Fréon (1988), concerned young individuals probably carried by the southward circulation. In 1977 some ripe specimens were caught and again in 1994. Thus, it seems that a new population is settling south of Cape Vert, but due to lack of observation in 1995, we cannot confirm it. Although a Senegalese sardine fishery looks very unlikely in the future, let us remind that to Furnestin (1955) a regular sardine fishery off Mauritania was quite improbable.

It is satisfying to see that the same ecological relationships held during three decades and that chaotic dynamics did not prevail against them. The reasons are probably because upwellings are young ecosystems where any strengthening of Ekman pumping increases offshore transport, stops the maturation, and resets all the ecosystem, preventing chaotic evolution.

According to the 50 years wind stress time series compiled by Bakun (1990, 1992), it seems that the present climatic change was beginning at least 50 years ago. If, according to Bakun, this increase in the eastern boundaries trade winds is due to the increased contrast in temperature between heated land masses and the oceans, in relation to the 'greenhouse effect', we may expect a continuation and a strengthening of these phenomena during the coming years. Probably, the strengthening will not be regular but fluctuating, and we can expect a continuation of the alternance of sardine and horse mackerel-sardinella periods, with more frequent sardine periods.

REFERENCES CITED

Alcaraz M. 1982. Zooplankton biomass and its relation to total particulate carbon and nitrogen off northwest Africa. *Rapp. P.-v. Réun. Cons. int. Explor. Mer*, 180: 270-273.

Bakun A. 1990. Global climate change and intensification of coastal ocean upwelling. *Science*, 247: 198-201.

Bakun A. 1992. Global greenhouse effects, multi-decadal wind trends, and potential impacts on coastal pelagic fish populations. *ICES Mar. Sci. Symp.*, 195: 316-325.

Barkova N.A. and M.V. Domanevskaya. 1990. *Utilisation des informations satellitaires pour l'étude des particularités de répartition de la sardine dans l'Atlantique centre-est.* ICES, C.M. 1990/H9. 12 p.

Belvèze H. 1984. *Biologie et dynamique des populations de sardine (Sardina pilchardus Walbaum) peuplant les côtes atlantiques marocaines et propositions pour un aménagement des pêcheries.* Thèse Univ. Bret. occident., 532 p.

Binet D. 1977. Cycles biologiques et migrations ontogéniques chez quelques copépodes pélagiques des eaux ivoiriennes. *Cah. ORSTOM, sér. Océanogr.*, 15 : 111-138.

Binet D. 1988. Rôle possible d'une intensification des alizés sur le changement de répartition des sardines et sardinelles le long de la côte ouest africaine. *Aquat. Living Resour.*, 1: 115-132.

Binet D. 1991. Dynamique du plancton dans les eaux côtières ouest africaines : écosystèmes équilibrés et déséquilibrés. *In*: P. Cury et C. Roy (eds.). *Pêcheries ouest-africaines: variabilité, instabilité et changement.* ORSTOM, Paris: 117-136.

Binet D. and E. Suisse de Sainte-Claire. 1975. Contribution à l'étude du copépode planctonique *Calanoides carinatus* : répartition et cycle biologique au large de la Côte-d'Ivoire. *Cah. ORSTOM, sér. Océanogr.*, 13 : 15-30.

Blackburn M. 1979. Zooplankton in an upwelling area off northwest Africa : composition, distribution and ecology. *Deep-Sea Res.*, 26, 1 A: 41-56.

Boëly T. and P. Fréon. 1979. Les ressources pélagiques côtières. *In*: J.P. Troadec and S. Garcia (eds.). Les ressources halieutiques de l'Atlantique centre-est. 1ère partie : les ressources du golfe de Guinée, de l'Angola à la Mauritanie. *FAO Doc. tech.*, 186, 167 p.

Cadenat J. and R. Moal. 1955. Note sur la sardine (*Sardina pilchardus* Walbaum) de la région du cap Blanc. *Rapp. P.-v. Cons. int. Explor. Mer.* 137: 21-23.

Catewicz Z. and R. Siwecki. 1985. On the currents in the coastal zone of African shelf off Saint-Louis. *Oceanologia*, 21: 59-75.

Chavance P., Y. Loktionov and M. Mahfoud. 1991. Importance des saisons de transition hydrologique et impact des anomalies climatiques sur l'activité d'une flottille industrielle pélagique en ZEE mauritanienne. *In*: P. Cury et C. Roy (eds.). *Pêcheries ouest-africaines: variabilité, instabilité et changement.* ORSTOM, Paris: 246-258.

Conand F. 1975. *Distribution et abondance des larves de clupéidés au large des côtes du Sénégal et de la Mauritanie en septembre, octobre et novembre 1977.* ICES, CM 1975/J 4, 9p.

Conand F. 1977. Oeufs et larves de la sardinelle ronde (*Sardinella aurita*) au Sénégal : distribution, croissance, mortalité, variations d'abondance de 1971 à 1976. *Cah. ORSTOM, sér. Océanogr.*, 15: 201-214.

Cushing D.H. 1978. Upper trophic levels in upwelling areas. *In*: R. Boje and M. Tomczak (eds.). *Upwelling ecosystems*. Springer-Verlag: 101-110.

Cushing D.H. 1982. *Climate and Fisheries*. Academic Press, London, 373 p.

Dickson R.R. and K.M. Brander. 1993. Effects of a changing wind field on cod stocks of the North Atlantic. *Fisheries Oceanography*, 2 (3/4): 124-153.

Domanovsky L.N. and N.A. Barkova. 1976. *Some pecularities of sardine (Sardina pilchardus Walb.) distribution and spawning along the northwest Africa*. ICES. CM 1976/J6, 6, 15 p.

Ehrich S., H.C. John and P. Westhaus-Ekau. 1987. Southward extension of the reproductive range of *Macroramphosus scolopax* in the upwelling area off north-west Africa. *In*: A.I.L. Payne, J.A. Gulland and K.H. Brink (eds). The Benguela and comparable ecosystem. *S. Afr. J. Mar. Sci.*, 5: 95-105.

F.A.O. 1985. Rapport de la troisième réunion du groupe de travail ad hoc sur la sardine *Sardina pilchardus* (Walb.). *COPACE/PACE Séries*, 85/39, 157 p.

F.A.O. 1990. Rapport des groupes de travail ad hoc sur la sardine et sur les chinchards et les maquereaux dans la région nord du COPACE. *COPACE/PACE Series*, 90/50, 372 p.

F.A.O. 1994. Rapport du groupe de travail ad hoc sur les sardinelles et autres espèces de petits pélagiques côtiers de la région nord du COPACE. Dakar 1993, *COPACE/PACE Series*, 91/58, 295p.

Fréon P. 1988. *Réponses et adaptations des stocks de clupéides d'Afrique de l'ouest à la variabilité du milieu et de l'exploitation. Analyse et réflexion à partir de l'exemple du Sénégal.* Ed. de l'ORSTOM, Coll. Etudes et Thèses. Paris. 287 p.

Fréon P. and B. Stéquert. 1979. Note sur la présence de *Sardina pilchardus* (Walb.) au Sénégal: étude de la biométrie et interprétation. *Cybium* (3ème sér.), 6: 65-90.

Furnestin J. 1955. Remarques sur quelques caractères de la sardine de Mauritanie (*Sardina pilchardus* Walbaum). *Rapp. P.-v. Cons. int. Explor. Mer*, 137: 24-25.

Grall J.R., P. Laborde, P. Le Corre , J. Neveux, P. Tréguer and A. Thiriot. 1974. Caractéristiques trophiques et production planctonique dans la région sud de l'Atlantique marocain. Résultats des campagnes CINECA-CHARCOT I et III. *Téthys*, 6 (1-2): 11-28.

Grall J.R., P. Le Corre, et P. Tréguer. 1982. Short-term variability of primary production in coastal upwelling off Morocco. *Rapp. P.-v. Réun. Cons. int. Explor. Mer*, 180: 221-227.

Hargreaves P.M. 1978. Relative abundance of zooplankton groups in the northwest African upwelling region during 1968 and 1972. *In*: R. Boje and M. Tomczak (eds.). *Upwelling ecosystem*. Springer-Verlag: 62-72.

Jacques G. and P. Tréguer. 1986. *Ecosystèmes pélagiques marins*. Masson, 243 p.

John H.-C. 1985. Horizontal and vertical distribution patterns of fish larvae off NW Africa in relation to the environment. *Int. Symp. Upw. W. Afr., Inst. Inv. Pesq. Barcelona*, 1: 489-512.

John H.-C., U.J. Bohde and W. Nellen. 1980. *Sardina pilchardus* larvae in their southernmost range. *Arch. Fisch Wiss.*, 31 (2): 67-85.

Lemasson L. and J.P. Rébert. 1973. Les courants marins dans le golfe ivoirien. *Cah. ORSTOM, sér. Océanogr.*, 11: 67-96.

Lewis R.C. 1929. The food habits of the California sardine in relation to the seasonal distribution of microplankton. *Bull. Scripps Instit. Oceanogr.*, 2 (3): 155-180.

Lloris D., J. Rucabado, J. Lleonart and P. Rubies. 1979. Adaptaciones de los organismos frente a variaciones ambientales sostenidas: *Pagellus acarne* como modelo de ciclo vital en el afloramiento del NW de Africa. *Inv. Pesqu.*, 43 (2): 479-490.

Maigret J. 1974. La sardine sur les côtes de Mauritanie (*Sardina pilchardus* Walb.). *Bull. I.F.A.N.*, 36 A (3): 714-721.

Mittelstaedt E. 1976. On the currents along the northwest African coast south of 22° North. *Dt. hydrogr. Z.*, 29 (3): 97-117.

Mittelstaedt E. 1982. Large-scale circulation along the coast of northwest Africa. *Rapp. P.-v. Réun. Cons. int. Explor. Mer*, 180: 50-57.

Mittelstaedt E. 1983. The upwelling area off northwest Africa. A description of phenomena related to coastal upwelling. *Prog. Oceanog.*, 12: 307-331.

Mittelstaedt E., D. Pillsbury and R.L. Smith. 1975. Flow patterns on the northwest African upwelling area. *Dt. hydrogr. Z.*, 28: 145-167.

Nieland H. 1980. *Die Nahrung von Sardinen, Sardinellen und Maifischen vor der Westküste Afrikas*. Berichte aus dem Inst. für Meereskunde. Univ. Kiel, 75, 137 p.

Nieland H. 1982. The food of *Sardinella aurita* (Val.) and *Sardinella eba* (Val.) off the coast of Senegal. *Rapp. P.-v. Réun. Cons. int. Explor. Mer*, 180: 369-373.

Olivar M.P., P. Rubiès and J. Salat. 1985. Zooplankton biomass in upwelling regions off northwest and southwest Africa. *Int. Symp. Upw. W Afr., Inst. Inv. Pesq. Barcelona*, 1: 471-477.

Picaut J., J. Servain, P. Lecomte, M. Séva, S. Lukas and G. Rougier. 1985. *Climatic atlas of the tropical Atlantic wind stress and sea surface temperature 1964-1979*. Univ. Bret. Occident. Brest, 467 p.

Rébert J.P., 1983. Hydrologie et dynamique des eaux du plateau continental sénégalais. *Doc. scient. Cent. Rech. Océanogr. Dakar-Thiaroye*, 89, 99p.

Servain J., M. Séva, S. Lukas and G. Rougier. 1987. Climatic atlas of the tropical Atlantic wind stress and sea surface temperature: 1980-1984. *Ocean-air Interactions*, 1: 109-182

Servain J. and S. Lukas 1990. *Climatic atlas of the tropical Atlantic wind stress and sea surface temperature : 1985-1989*. Océans tropicaux Atmosphère globale. IFREMER, ORSTOM, JIMAR, 133 p.

Soutar A. and J.D. Isaacs. 1974. Abundance of pelagic fish during the 19th and 20th centuries as recorded in anaerobic sediment off the Californias. *Fish. Bull.* (U.S.), 72: 257-273.

Southward A.J., G.T. Boalch and L. Maddock. 1988. Fluctuations in the herring and pilchard fisheries of Devon and Cornwall linked to changes in climate since the 16th century. *J. Mar. Biol. Assoc.* U.K., 68: 423-445.

Sinclair M. 1988. *Marine populations: an essay on population regulation and speciation*. Washington Press, Seattle and London. 252 p.

Teisson C. 1983. Le phénomène d'upwelling le long des côtes du Sénégal. Caractéristiques physiques et modélisation. *Arch. Cent. Rech. Océanogr. Dakar-Thiaroye*, 123.

Vives F. 1974. Le zooplancton et les masses d'eau des environs du cap Blanc. *Téthys*, 6 (1-2): 313-318.

Weikert H. 1984. Zooplankton distribution and hydrography in the Mauritanian upwelling region off northwestern Africa, with special reference to the calanoid copepods. *Meeresforch.*, 30: 155-171.

Wooster W.S., A. Bakun and D.R. Mc Lain. 1976. The seasonal upwelling cycle along the eastern boundary of the North Atlantic. *J. Mar. Res.*, 34: 131-141.

Climate Dependent Fluctuations of the Moroccan Sardine and their Impact on Fisheries

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ABSTRACT

The Moroccan Atlantic sardine (*Sardina pilchardus*) stocks have undergone some changes of abundance and distribution range during the past five decades. A long-term increase in Moroccan coastal upwelling intensity between 1950s and mid-1970s due to an increase in trade winds intensity is suggested to have induced this long-term fluctuation of sardine. The implications for the Moroccan sardine fisheries are discussed.

RÉSUMÉ

Les stocks de sardines marocaines atlantiques (*Sardina pilchardus*) ont connu des changements d'abondance et de distribution depuis les cinq dernières décennies. Un accroissement à long terme de l'intensité de l'upwelling côtier marocain entre les années 50 et le milieu des années 70 dû à l'accroissement de l'intensité des alizés est suggéré comme ayant induit cette fluctuation à long terme de la sardine. Les implications pour les pêcheries de sardine marocaine sont discutées.

INTRODUCTION

The Moroccan Atlantic coast, extending from the Gibraltar Strait (36°N) to Cape Blanc (21°N), is one of the world's four major coastal upwelling systems. In this area, catches are composed of small coastal pelagics similar to those encountered in other coastal upwelling systems, with the difference that they are dominated by the European sardine (*Sardina pilchardus*).

Previous studies have stressed instability as an inherent feature of coastal pelagic stocks, and its dramatic consequences for the fisheries (Sharp and Csirke, 1983; Pauly and Tsukayama, 1987; Wyatt and Larrañeta, 1988; Kawasaki *et al.*, 1991; Cury and Roy, 1991; Payne *et al.*, 1992). The abundance of coastal pelagic fish stocks varies considerably in time, and there is evidence, from paleoecological studies, that major variations have occurred before the beginning of the exploitation (Soutar and Isaacs, 1974). Many authors drew attention to the remarkable similarity in long-term catches of some widely separated stocks (Kawasaki, 1983, 1992; Lluch Belda *et al.*, 1989, 1992). Long-term catch fluctuations are accompanied by changes in stocks' geographical ranges (Crawford and Shannon, 1988; Junkera, 1986; Lluch Belda *et al.*, 1989, 1992; MacCall, 1990). These major long-term changes of abundance and geographical distribution are generally attributed to climatic changes (Kawasaki, 1983; Binet, this vol.; Demarcq, this vol.).

Sardine constitutes the backbone of the pelagic fishing industry in Morocco since the 1920s. Sardine distribution have undergone some changes since the 1960s which forced the small scale fisheries to move their base of operation. Consequently, the shrinkage of the traditional fishing area had a serious impact on the Moroccan pelagic industry. This paper describes these changes and presents an attempt to explain these long-term fluctuations in sardine stocks.

1. LONG-TERM CHANGE IN THE DISTRIBUTION OF SARDINE CATCHES

1.1. Sardine distribution pattern

The Atlantic sardine is divided into three stocks along the Northwest African coast (Fig. 1): a small northern stock between Cape Cantin and Gibraltar Strait, a central stock between Cape Cantin and Cape Bojador and a southern stock from Cape Bojador to Cape Blanc.

The three stocks of Atlantic sardine off Morocco (Northern, Central, Southern) are exploited in four fishery areas (Fig. 1). For the central stock, a zone A, from Safi to South of Agadir is distinguished from a zone B, from Sidi Ifni and Laâyoune, and which is exploited by Moroccan and Canarian boats. The southern stock is exploited by the fleet from eastern Europe.

These stocks carry out seasonal migrations along the coast within the limits of their geographical range. They concentrate in spawning areas for reproduction, but spread out during the upwelling season. These movements have a minor effect on

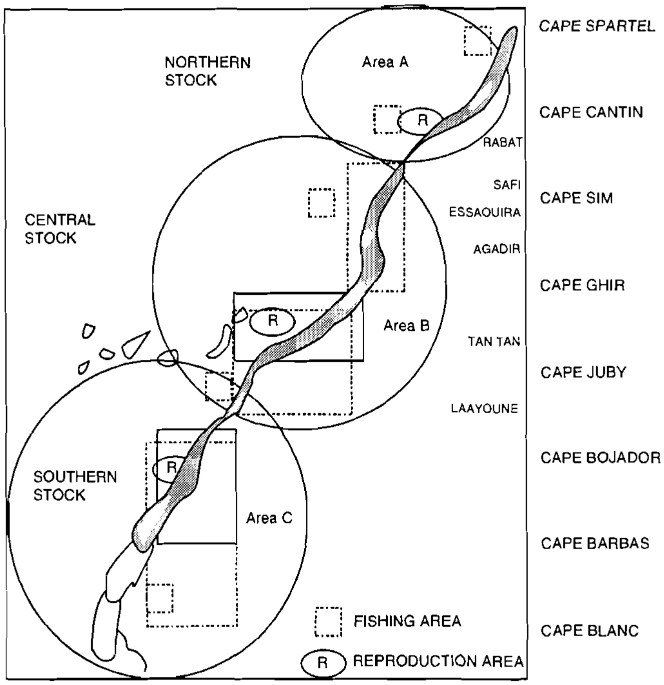


Fig. 1: Distribution pattern of the Moroccan sardine stocks and of their spawning (solid lines) and fishing grounds (dotted lines).

the central stock fisheries in areas B and for the southern stock, but they are important for the fishery in area A where the boats have a limited range of action. The availability of sardine in area A depends on the extension of the central stock that migrates every spring and summer from the southern end of the range.

1.2. Stock and catch trends

1.2.1- Brief history of the fishery

The exploitation of the Moroccan sardine developed chronologically from the north to the south. Small European fishing boats (Spanish, Portuguese and French) started fishing in the 1920s, in the areas of Larache, Casablanca and El Jadida. By the end of the 1930s, the fishery extends to Safi and Agadir. Other fisheries developed afterwards in the south. The Soviet Union fleet started exploiting the southern stock in the late 1950s, and a Canarian fishery in area B of the central stock developed in the 1960s. In the 1980s, Moroccan fisheries extended to area B of that same stock. The long-term catch of sardine along the Moroccan Atlantic coast from 1936 to 1990, is presented on Figure 2. It shows a gradual increase with peaks of great abundance in the mid-1970s and the late 1980s. As might be seen, the relative importance of the Moroccan sardine stocks increase towards the south (Fig. 3a, b, c). The central stock provides the bulk of the catch.

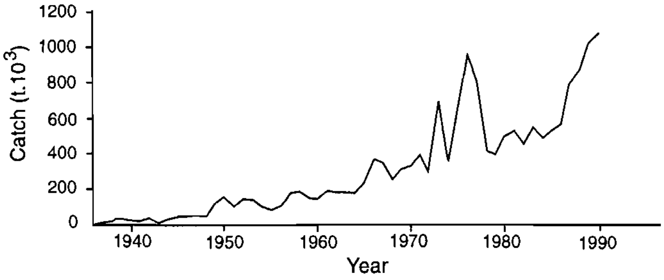


Fig. 2: Catch of Moroccan sardine along the Atlantic coast, 1936 to 1990.

1.2.2- Northern stock (Cape Spartel - Cape Cantin)

Little is known about the small northern stock. The only available information comes from catch statistics. Sardine catch decreased in the north between 1936 and 1960, probably because fishing effort moved south. This decrease was followed by a relative increase in the 1960s that strengthen during the 1970s and 1980s (Fig. 3a). One cannot, however, ascribe this increase simply to an increase in fish stock abundance.

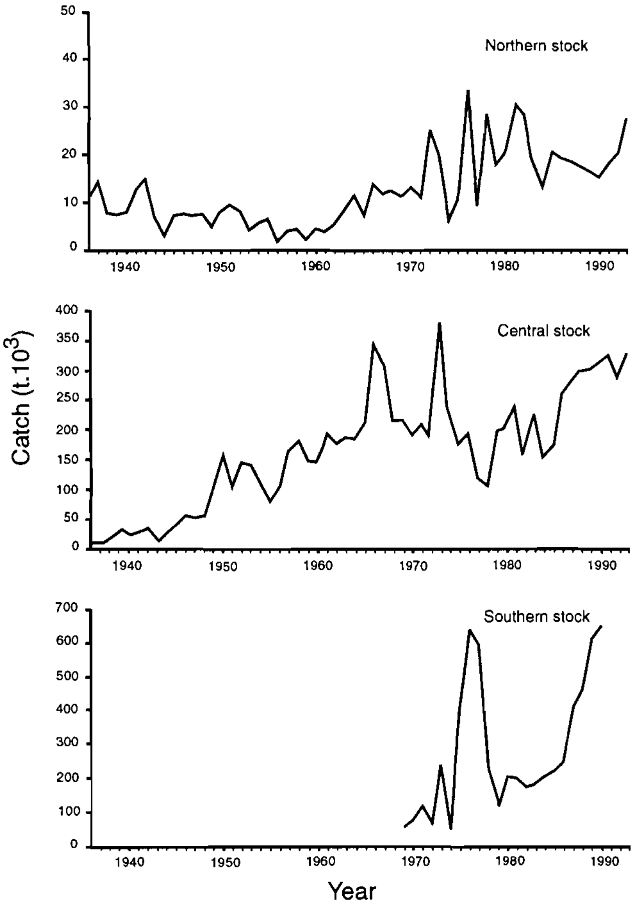


Fig. 3: Annual catch of sardine from the northern, central and southern stocks off Morocco.

1.2.3- Central stock (Cape Cantin - Cape Bojador)

Overall catches from the central stock increased gradually from the beginning of the fishery in area A to the late 1960s and then fluctuated around 250 000 tonnes (Fig. 3b). The analysis of the sardine landings in area A (Fig. 4) shows that after a period of increase lasting until 1965 and relative stability (except for two exceptionally good years 1966 and 1973), a decrease occurred. Towards the end of the 1980s and the beginning of the 1990s, catch level in the area reached the lowest observed values since the end of the 1940s. On the other hand, the Spanish catch in the B area showed a regular increase in 1976-77, then stabilized around 100 000 t per year (Fig. 5b). This stabilization coincided with the decline of the Moroccan catch in area A. This decline incited the Moroccan to extend fishing effort southward to zone B, where Moroccan landings are still increasing (Fig. 5b).

Fig.4: Sardine landings in the Moroccan traditional fishing area Central Stock, Area A from 1936 to 1993.

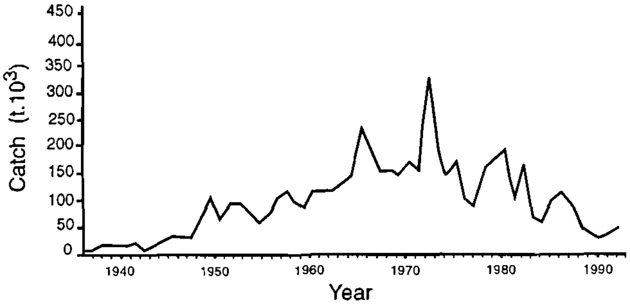
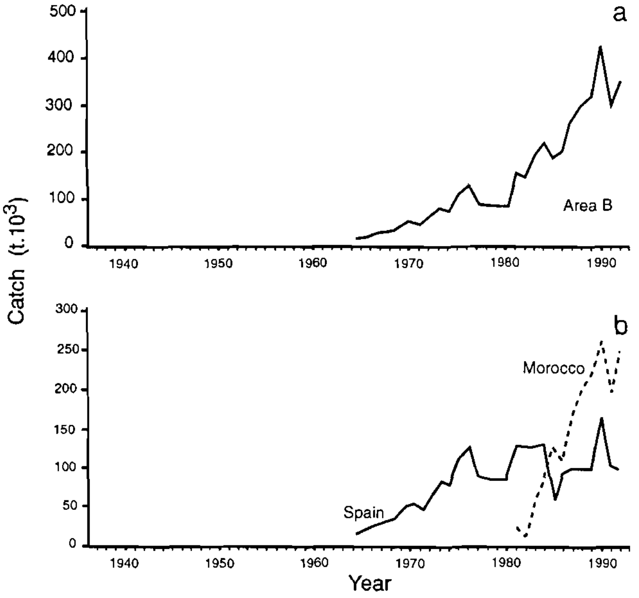


Fig. 5: Catch of sardine in fishing area B (a) total catch; (b) catch of the Spanish and Moroccan fleets.



The CECAF Ad hoc Working Group on Sardine (FAO, 1985) concluded that an important decrease of central stock abundance occured from 1971 to 1976. Abundance then increased in 1977 and then decreased again from 1986 onwards (FAO, 1990). According to the acoustic estimations of *R.V. Dr Fridtjof Nansen* carried out in December 1986, August 1989 and January-February 1992, the central sardine stock seems to have drastically decreased, from 1.5 million t in 1986 to 320 000 t in 1992. Recruitment has widely varied since the early 1970s. Average recruitment of 1968 and 1969 were followed by the relatively strong year class in 1970 which dominated in the catch until 1974. Recruitments declined afterward, except for 1978,1980 and 1982 (Fig. 6).

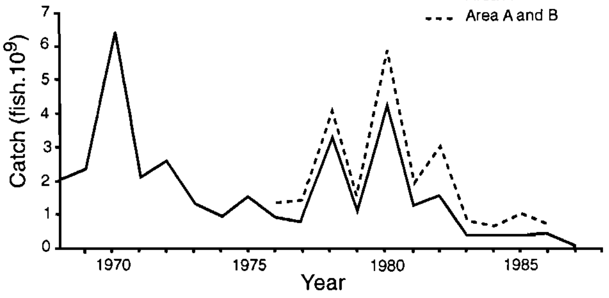


Fig. 6: Catch (0 + 1 year class) from the central stock (juveniles+recruits) (from Belvèze, 1984 and other sources).

Analysis of catch data in different ports of area A shows that the decline of sardine catch started in 1967 in the northern port of Safi then spread southward after 1973 to the ports of Essaouira and Agadir (Fig. 7). Overall, it appears that there has been a southward shift of location of the central sardine catches. In regard to the schoaling behavior of the sardine, it is likely that as its abundance declined, the central stock contracted its range towards the spawning area (Kifani and Gohin, 1992).

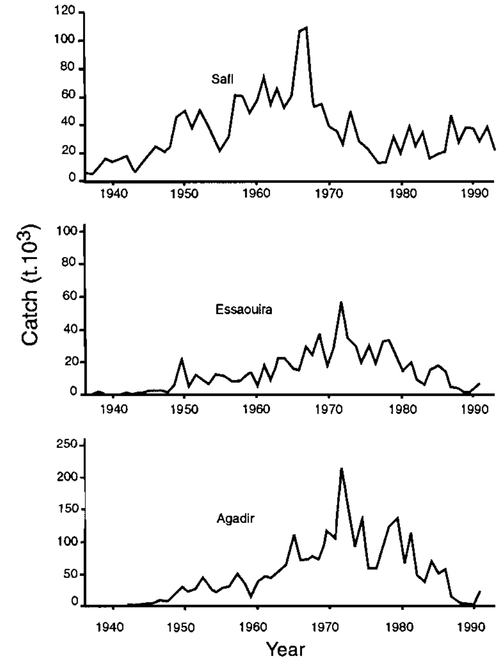


Fig. 7: Landings of sardine, central stock, area A, at Safi, Essaouira and Agadir showing southward range contraction.

1.2.4- Southern stock (Cape Bojador - Cape Blanc)

The southern boundary of the Saharan stock has widely fluctuated during the past decades. According to the surveys carried out by the Soviet Union since 1957 in northern CECAF region, southern limit of sardine along the Moroccan coast, before 1967, was approximately Cape Bojador. The Saharan stock outburst and its consecutive equatorward extent started toward 1967 and continued during the early 1970s. As sardine range expanded to the south, *Sardinella* distribution area regressed equatorward (Binet, 1988; Binet *et al.,* this vol.; Demarcq, this vol.). Some concentrations of sardine were even found off Senegal (Fréon and Stequert, 1979).

Sardine have progressively replaced the mackerel, horse mackerel and sardinellas that dominated the catch during the 1960s. Sardine catches underwent a rapid growth from 80 000 t in 1969 to 643 000 t in 1976 (Fig. 3c). Catches declined after the mid-1970s and remained at levels of 100 000 to 200 000 t till the end of 1980s. A further remarkable increase occurred in 1987, most likely consequent upon a strong year classes formed during the late 1980s.

With regard to the reverse trends presented by the central and Saharan stocks of sardine, which experienced a southward shift the question arises: what happened to sardine at the northern limits of its distribution area?

1.2.5- Sardine off European Atlantic coast

One feature of the eastern boundaries of the oceans is the extention of the temperate zone to low latitudes due to coastal upwelling and equatorward surface flow (Parrish *et al.*, 1983). As a result, the Atlantic sardine *(Sardina pilchardus*), a species of temperate region, extended between 10°C surface isotherm in the north and 20°C surface isotherm in the south (Fig. 8). The northern end its range overlaps with that of the distribution of herring; while its southern end overlaps with the distribution of sardinellas (Robles *et al.*, 1992).

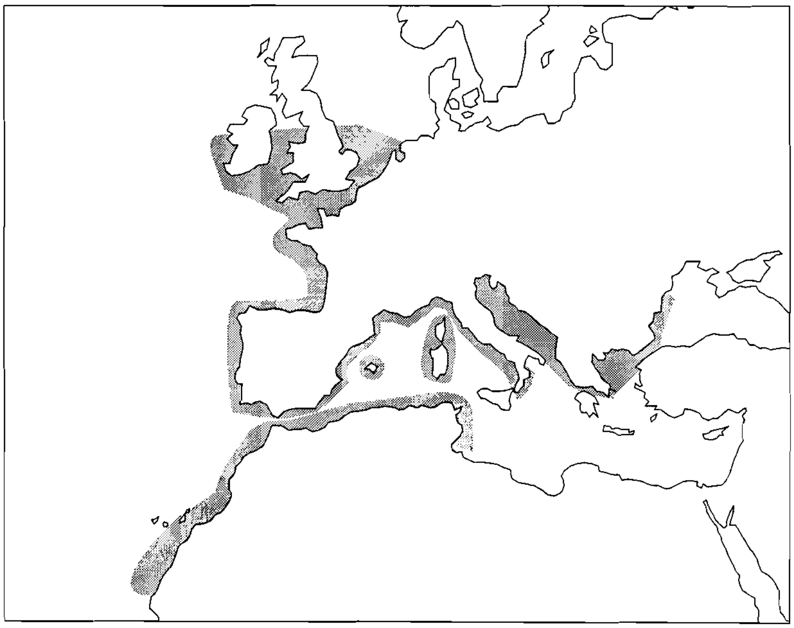


Fig. 8: Geographical distribution of *Sardina pilchardus* (from Belvèze, 1984).

Atlantic sardine form several stocks along the European and Northwest African coasts. The Atlantic sardine off Europe comprises two stocks: the Bay of Biscay / North Sea stock and the Iberian stock (from the Gibraltar Strait to the Cantabrian coast).

According to Cushing (1982), Southward and Boalch (1988) and Dickson *et al.* (1988) the sardine had also undergone some changes along the West European coast (Fig. 9). The Iberian sardine catch declined since the mid-1960s to the end of the 1970s, then increased again in the early 1980s. In the Eastern North Atlantic region, where long-term ecosystem variations are well documented, a sequence of modifications was noted from 1925-1935 onwards which was accompanied by a long-term fluctuations of *Sardina pilchardus* abundance in the English Channel (Southward and Boalch, 1988). From 1936 onwards, sardine eggs became abundant and this species replaced herring *Clupea harengus* as the dominant pelagic fish. Between 1965 and 1975, sardine spawning underwent a reduction in intensity and towards 1968 *Scomber scombrus* had begun to replace *Sardina pilchardus* as the dominant species till 1984 where sardine spawning peaked.

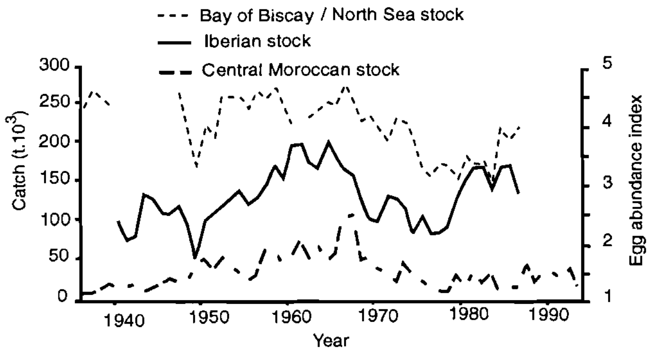


Fig. 9: Indices of *Sardina pilchardus* abundance in the English Channel (eggs survey data from Southward and Boalch, 1988) and catches off the Iberian Peninsula (P. Cury, pers. comm.) as compared with landings of sardine at Safi, Morocco.

We can note that while the sardine was expanding its range to the south in the late 1960s and early 1970s, its abundance was decreasing in the English Channel, Portugal and, simultaneously, on Moroccan fishing area A. If we take into account the broad distribution of *Sardina pilchardus* and the heterogeneity of its stocks and fishing areas, one could suspected a large scale climatic effect to have triggered sardine abundance and distribution changes. The outburst of *Sardina pilchardus* may be related to the strengthening of the upwelling off Sahara in the early 1970s (Sedykh, 1978; Domanevsky and Barkova, 1981; Belvèze and Erzini, 1983), while the intensification of the upwelling off Portugal during the same period has adversely affected the Iberian sardine (Dickson *et al.*, 1988).

2. ENVIRONMENTAL CHANGES

The principal hydrographic feature of the Moroccan Atlantic shelf is the upwelling of cold waters and its associated offshore Ekman transport, both driven by the trade winds (Wooster *et al.*, 1976; Parrish *et al.*, 1983). The general surface flow in this region is linked to the Canary Current.

Wind speed, offshore Ekman transport and sea surface temperature changes from 1946 to 1990 in three areas off the west coast of Morocco are presented in Figure 10. These data were provided by the National Center for Atmospheric Research (U.S.A) and extracted from the COADS file (Comprehensive Atmospheric Data Set, Roy and Mendelssohn, this vol.). Each of the three variables presents a similar trend. Wind speed and offshore Ekman transport intensity shows a sustained upward trend since the early 1950s which reversed toward the mid-1970s. At the same time sea surface temperature decreased progressively, then increased in the mid-1970s.

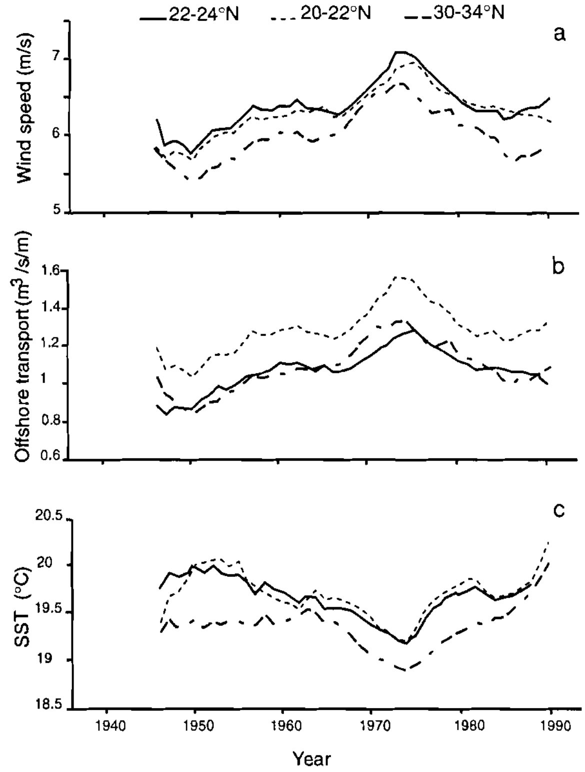


Fig. 10: Smoothed time series of (a) wind speed (m/s), (b) offshore Ekman transport (m^3/s/m) and (c) sea surface temperature (°C). (Data from COADS).

On the other hand, long-term observations of the air temperature at two Atlantic coastal stations, Casablanca and Essaouira, provided by the National Meteorology Office have shown a tendency towards cooling from the early 1960s, which became stronger during the 1970s, and then reversed itself towards the end of this decade (Fig. 11a,b). These observations are in accordance with those made by Le Goff (1985) on the evolution of the temperature in Morocco and are also in agreement with the temperature change in the whole North Atlantic region described by Cushing (1982) and Kelly (1983, 1984).

Lamb and Peppler (1987) have stressed the influence of the two main North Atlantic atmospheric centers (Azores High and Iceland Low) on the Moroccan climate. The variations of these atmospheric centers are also involved in large scale climatic changes in the North East Atlantic region (Kelly, 1984). Although the mechanisms involved are far from clear, it is likely that the long-term climatic evolution in Morocco is broadly linked to the large-scale climatic change in the North Atlantic region. As suggested by Dickson *et al.* (1988), the strengthening of northerly wind activity during the 1960s and 1970s have most probably affected all the West European and Northwest African coasts and resulted in an increase in coastal upwelling activity.

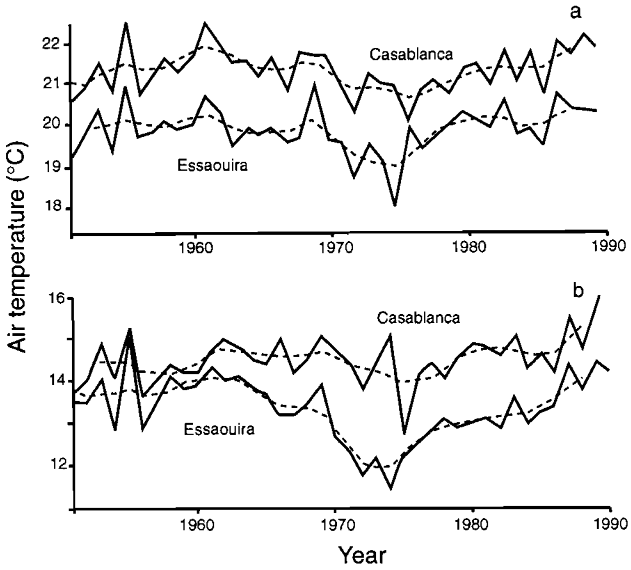


Fig. 11: Long-term changes of air temperature at two coastal stations: Casablanca and Essaouira, Morocco, (a) maxima; (b) minima.

3. DISCUSSION

Several long-term trends appear to be simultaneous in sardine abundance data and the environmental record. The widespread southward movement of sardine appears to be associated with the 1960s and 1970s strengthening of northerly winds. The question rises why do the same climatic factors affect the various stock differently?

According to Cushing (1982) the most probable way in which large scale climatic changes may influence fish stocks abundance over wide areas may be through primary and secondary production. Changes in these factors would result in marked differences in recruitment. From studies of phytoplankton blooms, it is evident that phytoplankton responds to changes in the intensity of wind (stress and mixing), which is associated with vertical stratification and determines the availability of nutrients in the upper layers of sea water (Radach, 1984).

In temperate regions, the production cycle may vary in amplitude, spread and time of the onset owing to differences in wind strength and direction (Cushing, 1982). Large scale effect of climate on phytoplankton and zooplankton biomass in the Eastern North Atlantic region have been studied by Dickson *et al.* (1988). Long-term increase in the northerly wind component over the Eastern North Atlantic and the North Sea between the 1950s and the 1970s was associated with a decline in phytoplankton and zooplankton biomass. Dickson *et al.* (1988) assume that the strengthening of the wind has induced a reduction and delayed the spring phytoplankton outburst and hence lead to a reduction of suitable food for zooplankton.

Strong winds off Moroccan coast generates a strong offshore advection and turbulence that alters phytoplankton production and induce a time-space lag between the phytoplankton and zooplankton. With an increase wind stress, the higher zooplankton biomass are advected to the shelf edge where the zooplankton makes good use of the phytoplankton that develops in the upwelled water drift (Binet, 1988, 1991). Strong upwelling favors large diatoms colony (e.g., *Thalassiosira parthenia*) that are not grazed by zooplankton (e.g., copepods). In contrast zooplankton species can feed very effectively on short food chains or single cells in older upwelled waters, where colonies disintegrate due to senescence (Elbrächter, 1982; Schnack, 1983).

The three areas of sardine production in Morocco are all characterized by a source of upwelling water and spawning ground which correspond to a region with wide continental shelf. Spawning seasons for the three stocks are out of phase with that of the upwelling maximum (Belvèze, 1984; Barkova and Domanevsky, 1985). From this point of view, the Moroccan sardine populations present the same reproduction pattern, the one difference being in the latitudinal position of the spawning grounds. The northern and the central population spawning grounds (respectively off Casablanca-Larache and off Sidi Ifni-Cape Juby) are downstream of the summer upwelling maxima, which occur between Larache and Tanger in the northern area and between Cape Sim and Cape Ghir. On the contrary, the Saharan spawning area overlaps with the Cape Bojador-Cape Garnett zone (Belvèze, 1984). This would suggest that the southern stock is more adapted to strong upwelling conditions. Inspecting somatic index of *Sardina pilchardus* from fifteen geographical areas, Andreu (1969) concluded that the sardine population with a high number of gill-rakers lives in areas with fluctuating environment. On the other hand, Furnestin (1950) and Furnestin and Furnestin (1970) found that the number of gill-rakers increase from the north to the south. This feature would allow the southern sardine to feed more efficiently on phytoplankton. Nieland (1980) found that the principal food item of sardine off Sahara was phytoplankton while in the central area, sardine fed mainly on zooplankton. Permanent upwelling and high primary production would explain this difference in diet, which results in a difference in growth rate that are in the southern area (Domanevsky and Barkova, 1981; Belvèze, 1984). Domanevsky and Barkova (1981) showed that the growth rates of southern sardine increase with upwelling intensity.

Having a phytoplanktivorous diet, and greater growth rates, the southern population may have been favoured by the strengthening of northerly winds along the European, and Northwest African Atlantic seaboards during the 1960s and the early 1970s, which have seemingly led to a rejuvenation of the ecosystems (Binet, 1988). Southward and Boalch (1988) found a good correlation between *Calanus* and *Sardina* egg numbers and they assumed that spawning depended on availability of copepods food. Referring to the CPR survey (Dickson *et al.*, 1992) noted a downward trend of copepods abundance between the 1950s and 1970s in the North East Atlantic region. Off Portugal, Dickson *et al.* (1988) offered an explanation for the inverse relationship between sardine and upwelling intensity: the fact that weak upwelling favors the development of a suitable initial food supply for the larvae and nauplii, which feed on small algae cells, and are thus better able to develop during weak upwelling episodes.

4. IMPLICATIONS FOR THE MOROCCAN SARDINE FISHERY

The reduction in the distribution range of the central stock of sardine, traditionally exploited by the Moroccan fishery, added to various political and economic factors, had a serious impact on the Moroccan fishing industry. Until the beginning of the 1980s, processing plants were located in the traditional fishing area (from Safi to Agadir) where the fishery activity was able to provide sufficient raw materiel. To help this industry to survive, Morocco expanded the exploitation in the 1980s to the southern area which harbors the bulk of the central stock. Hence processing plants were opened in the southern ports. If the fishery is now less subject to productivity constraints, it still remains under strong profitability constraints. The gain produced by increasing the catch in order to supply factories (mainly fish meal factories) is wasted, because of the increase of fishing costs. Under such conditions, the profitability of the Moroccan sardine fishery depend largely on the abundance of the central stock. Considering the alarming level attained by fishing mortality, this stock may place the fishery and downstream activities in a difficult position.

Thus, if the strategy presently adopted by Morocco for the management of the sardine stocks and fishery is to continue (namely a search for a profitability by increasing catches), the long-term perspective of the Moroccan sardine fishery should be to exploit the Southern stock. More studies are needed to establish a viable strategy for the exploitation of the southern stock by Moroccan fishers. In this respect, understanding the spatial and temporal dynamic of the sardine stocks and their links with climatic fluctuations is of paramount importance.

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REFERENCES CITED

Andreu B. 1969. Las branchispinas en la caracterizacion de las poblaciones de *Sardina pilchardus* (Walb). *Inv. Pesq.*, 33 (2): 425-607.

Barkova N.A. and L.N. Domanevsky. 1985. État des stocks de la sardine (*Sardina pilchardus* Walb.) dans la division 34.1.3. Rapport de la troisième réunion du groupe de travail ad hoc sur la sardine (*Sardina pilchardus* Walb.). *COPACE/PACE series*, 85/39: 80-96.

Belvèze H. 1984. *Biologie et dynamique des populations de sardine peuplant les côtes atlantiques marocaines et propositions pour un aménagement des pêcheries*. Thèse de doctorat d'Etat, Université de Bretagne Occidentale, 532p.

Belvèze H. and K. Erzini. 1983. Influence of hydroclimatic factors on the availability of sardine (*Sardina pilchardus* Walb.) in the Moroccan fisheries in the Atlantic. *In*: G.D. Sharp and J. Csirke (eds.). Proceedings of the Expert Consultation to Examine Changes in Abundance and Species Composition of Neritic fish Ressources. San José, Costa Rica, 18-29 April, 1983. *FAO Fish. Rep.*, 291 (2): 285-328.

Binet D. 1988. Rôle possible d'une intensification des alizés sur le changement de répartition des sardines et sardinelles le long de la côte ouest-africaine. *Aquat. Living Resour.*, 1: 115-132.

Binet D. 1991. Dynamique du plancton dans les eaux côtières ouest-africaines, écosystèmes équilibrés et déséquilibrés. *In*: P. Cury et C. Roy (eds.). *Pêcheries ouest-africaines: variabilité, instabilité et changement*. ORSTOM, Paris: 117-136.

Crawford R.J.M.and L.V. Shannon. 1988. Long-term changes in distribution of fish catches in the Benguela. *In*: T. Wyatt and M.G. Larrañeta (eds.). *Longterm changes in marine fish populations*. Symp. Vigo, 18-21 Nov. 1986.

CRUISE REPORTS "Dr FRIDTJOF NANSEN". 1989. An acoustic survey of the small pelagic fish resources of Morocco from Cape Safi to Cape Blanc. 27 aug.-18 sept. 1989. NORAD - *FAO/UNDP GLO*, 82/001. IMR Bergen.

CRUISE REPORTS "Dr FRIDTJOF NANSEN". 1992. *Survey of the pelagic fish resources off north west Africa*. Part 1. Morocco 16 January-10 february 1992. ISPM Casablanca/ IMR Bergen.

Cury P. et C. Roy (eds.). 1991. Pêcheries ouest-africaines: variabilité, instabilité et changement. ORSTOM, Paris, 525p.

Cushing D.H. 1982. *Climate and fisheries*. Academic Press, New York and London, 373p.

Dickson R. R., P. M. Kelly, J. M. Colebrook, W. S. Wooster and D. H. Cushing. 1988. North winds and production in the eastern North Atlantic. *J. Plankt. Res.*, 10 (1): 151-169.

Dickson R.R., P. Mälkki, G. Radach, R. Sætre, and M.P. Sissenwine. (eds.). 1992. Hydrobiological variability in the ICES area, 1980-1989. *ICES Marine Science Symposia. Mariebam*, 1991, 195 p.

Domanevsky L.N. and N.A Barkova. 1981. État du stock de *Sardina pilchardus* Walb., Clupeiformes *Clupeidae* dans la région de l'Afrique du nord-ouest. *COPACE/TECH.* 81/31 (Fr).

Elbrächter M. 1982. The distribution and ecological significance of the planktonic diatom *Thalassiosira partheneia*. *Rapp. P.-v. Réun. Cons. int. Explor. Mer*, 180: 244-245.

FAO. 1985. Rapport de la troisième réunion du groupe de travail ad hoc sur la sardine (*Sardina pilchardus* Walb.). *COPACE/PACE Series,* 85/39.

FAO. 1990. Rapport des groupes de travail ad hoc sur la sardine et sur les chinchards et les maquereaux dans la région nord du COPACE. *COPACE/PACE Series*, 90/50.

Fréon P. and B. Stéquert. 1979. Note sur la présence de *Sardina pilchardus* (Walb.) au Sénégal: étude de la biométrie et interprétation. *Cybium*, 3°sér., 6: 65-90.

Furnestin J. 1950. *Etude comparative de quelques caractères métistiques des sardines du golfe de Gascogne et du Maroc.* Mémoire n° 14 de l'Office des Pêches maritimes, Série spéciale: Biologie des clupeidés.

Furnestin J. et M.L. Furnestin. 1970. La sardine marocaine et sa pêche. Migrations trophique et génétique en relation avec l'hydrologie et le plancton. *Rapp. P.-v. Réun. Cons. int. Explor. Mer*, 159: 165-175.

Junkera S. 1986. Pêche de l'anchois (*Engraulis enchrasicolus*) dans le golfe de Gascogne et sur le littoral atlantique de Galice depuis 1920. Variations quantitatives. *Rev. Trav. Inst. Pêches marit.*, 48 (3 et 4): 133-142.

Kawasaki T. 1983. Why do some pelagic fishes have wide fluctuations in their number? Biological basis of fluctuation from the view point of evolutionary ecology. *In*: G.D. Sharp and J. Csirke (eds.). Proceedings of the Expert Consultation to Examine Changes in Abundance and Species Composition of Neritic Fish Ressources. San José, Costa Rica, 18-29 April, 1983. *FAO Fish. Rep.*, 291 (3): 1065-1080.

Kawasaki T. 1992. Mechanisms governing fluctuations in pelagic fish populations. *In*: A.I.L. Payne , K.H. Brink, K.H. Mann and R Hilborn (eds.). Benguela trophic functioning. *S.Afr. J. Mar. Sci.* 121: 873-879.

Kawasaki T., S. Tanaka, Y. Toba and A. Taniguchi. 1991. *Long-term variability of pelagic fish populations and their environment.* Pergamon Press, Oxford, 402p.

Kelly P.M. 1983. Climatic change: past and futur prospects. *In*: G.D. Sharp and J. Csirke (eds.). Proceedings of the Expert Consultation to Examine Changes in Abundance and Species Composition of Neritic Fish Ressources. San José, Costa Rica, 18-29 April, 1983. *FAO Fish. Rep.*, 291 (3): 595-605.

Kelly P.M. 1984. Recent climatic variations in the North Atlantic sector. *Rapp. P.-v. Réun. Cons. int. Explor. Mer*, 185: 226-233.

Kifani S. and F. Gohin. 1992. Dynamique de l'upwelling et variabilité spatio-temporelle de la répartition de la sardine marocaine *Sardina pilchardus* (Walbaum, 1792). *Oceanologica acta*, 15 (2): 173-186.

Lamb P.J. and R.A. Peppler. 1987. North Atlantic oscillation: concept and application. *Bull. Amer. Meteor. Soc.*, 68 (10): 1218-1225.

Le Goff Y. 1985. Études et échos climatologiques: Évolution contemporaine de la température au Maroc 1936-1980. *La météorologie*. 7° série, 6.

Lluch-Belda D.B., R.J.M. Crawford, T. Kawasaki, A.D. MacCall, R.H. Parrish, R.A. Schwartzlose et P.E. Smith. 1989. World-wide fluctuations of sardine and anchovy stocks: The regime problem. *S. Afr. J. Mar. Sci.*, 8: 195-205.

Lluch-Belda D., D.B. Lluch-Cota, S. Hernandez-Vaskez and C.A. Salinas-Zavala. 1992. Sardine population expansion in eastern boundary systems of the Pacific Ocean as related to sea surface temperature. *In*: A.I.L. Payne, K.H. Brink, K.H. Mann and R. Hilborn (eds.). Benguela trophic functioning. *S.Afr. J. Mar. Sci.*, 12: 147-155.

MacCall A. 1990. *Dynamic geography of marine fish populations.* Univ. Wash Sea Grant. Wash. Press, Seattle and London, 153p.

Nieland H. 1980. *Die Nahrung von Sardinen, Sardinellen und Maifischen vor der Westküste Afrikas.* Berichte aus dem Inst. für Meereskunde. Univ. Kiel, 75, 137 p.

Parrish R.H., A. Bakun, D.M. Husby and C.S. Nelson. 1983. Comparative climatology of selected environmental processes in relation to eastern boundary current pelagic fish reproduction. *In*: G.D. Sharp and J. Csirke (eds.). Proceedings of the Expert Consultation to Examine Changes in Abundance and Species Composition of Neritic Fish Ressources. San José, Costa Rica, 18-29 April, 1983. *FAO Fish. Rep.*, 291 (3): 731-777.

Pauly D. and I. Tsukayama (eds.). 1987. The Peruvian anchoveta and its upwelling ecosystem: three decades of change. *ICLARM Studies and Reviews*, 15, 351p.

Payne A.I.L., J.A. Gulland and K.H. Brink (eds.). 1987. The Benguela and comparable ecosystems. *S. Afr. J. Mar. Sci.*, 5.

Payne A.I.L., Brink K.H., Mann K.H. and R Hilborn (eds.). 1992. Benguela trophic functioning. *S.Afr. J. Mar. Sci.*, 12.

Radach G. 1984. Variations in the plankton in relation to climate. *Rapp. P.-v. Réun. Cons. int. Explor. Mer*, 185: 234-254.

Robles R., C. Porteiro and J.M. Cabanas. 1992. The stock of Atlantico-Iberian sardine: possible causes of variability. *ICES Mar. Sci. Symp.*, 195: 418-423.

Sedykh K.A. 1978. *The coastal upwelling of northwest Africa*. ICES CM/C 12 hydrographic Committee.

Sharp G.D and J. Csirke. (eds.). 1983. Proceedings of the Expert Consultation to Examine Changes in Abundance and Species Composition of Neritic Fish Ressources. San José, Costa Rica, 18-29 April, 1983. *FAO Fish. Rep.*, 291.

Soutar A. and J.D. Isaacs. 1974. Abundance of pelagic fish during the 19th and 20th centuries as recorded in anaerobic sediments of the Californias. *Fish. Bull.*, 72: 257-274.

Southward A.J. and G.T. Boalch. 1988. Aspects of long-term changes in the ecosystem of the western English Channel in relation to fish populations. *In*: T. Wyatt and M.G. Larrañeta (eds.). *Long-term changes in Marine fish populations*. Symp. Vigo, 18-21 Nov. 1986, 554p.

Schnack S. 1983. On the feeding of copepods on *Thalassiosira partheneia* from the nortwest African upwelling area. *Mar. Ecol. Prog. Ser.*, 11: 49-55.

Wooster W. S., A. Bakun and D.R. McLain. 1976. The seasonal upwelling cycle along the eastern boundary of the North Atlantic. *J. Mar. Res.*, 34: 131-141.

Wyatt T. and M.G. Larrañeta (eds.). 1988. *In*: T. Wyatt and M.G. Larrañeta (eds.). Long-term changes in marine fish populations. *Long-term changes in Marine fish populations.* Symp. Vigo, 1986, 554p.

Marine Environmental Conditions and Fishery Productivity in the Black Sea

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ABSTRACT

Some relationships between the marine environment and fishery productivity in the Black Sea are reviewed with emphasis on the coupling of oceanographic processes, plankton cycles and fish production in space and time. Reproductive niches of anchovy *Engraulis encrasicolus ponticus* and sprat *Sprattus sprattus*, the two most abundant fish species in the Black Sea, have been analyzed in relation to enrichment, concentration and retention processes. Non-linear statistical analyses (general additive models) were performed using time series of fish recruitment, adult biomass, sea surface temperature, wind speed, turbulence, river outflow and phosphorus discharge. Both species show clear relation between recruitment and adult stock. Conclusions can be drawn that sprat which is reproducing in the more severe winter conditions is generally more dependent on large scale environmental variability. The distribution and abundance of its progeny is associated with open sea divergence/ convergence process. Anchovy spawns, in summer, in coastal waters. Its recruitment shows a strong dependence on adult stock size, but is also related to river plume zones, and enrichment processes therein. The distribution of anchovy and sprat relative to SST corresponds to their known temperature preferenda.

RÉSUMÉ

Les relations entre l'environnement marin et la production halieutique en mer Noire sont étudiées. Les patterns d'association des processus océanographiques avec les cycles du plancton et la reproduction des poissons dans l'espace et le temps sont examinés et comparés. Les niches reproductives de l'anchois *Engraulis encrasicolus ponticus* Alex et du sprat *Sprattus sprattus* L., les deux espèces les plus abondantes en mer Noire, sont analysées en fonction de la biomasse des géniteurs et des processus d'enrichissement, de concentration et de rétention. Dans ce but, des analyses statistiques non linéaires (modèles additifs généralisés) ont été effectuées en utilisant des données chronologiques de recrutement, de biomasse d'adultes, de température de surface de la mer, de vitesse du vent, de turbulence, de ruissellement des rivières et d'apports en phosphore. Une nette relation entre le recrutement et le stock adulte est mise en évidence. On peut tirer la conclusion que le sprat se reproduit en hiver dans des conditions plus sévères qui sont dépendantes de la variabilité environnementale à grande échelle. La distribution et l'abondance de la progéniture sont associées aux processus de divergence/convergence au large. L'anchois se reproduit en été dans les eaux côtières. Une forte dépendance de son recrutement en fonction du stock d'adulte est démontrée et son abondance est apparemment liée aux zones de panaches des grandes fleuves et à l'enrichissement produit par eux. Les relations avec la température de la mer sont en accord avec les préférences thermiques pour l'anchois et le sprat.

INTRODUCTION

The peculiar oceanographic conditions and the high biological productivity of the Black Sea have already been pointed out by a great number of authors (Grese, 1979; Sorokin, 1982; Ivanov and Beverton, 1985; Vinogradov *et al.*, 1992). Yet the role and the mechanisms through which different marine environmental factors impact on the formation of biological production are still not fully clarified. The present paper is an attempt to review the relations between the physical conditions and the productivity in the Black Sea, based on hypotheses for the matching mechanisms of physical processes and production cycles of marine populations proposed by Cushing and Dickson (1976), Lasker (1985), Cury and Roy (1989) and Mann (1993).

1. THE PHYSICAL ENVIRONMENT AS A BASIS OF PRODUCTIVITY

The specific structure of Black Sea waters was noted at the very onset of oceanographic study. First of all is the existence of two layers, highly different with respect to hydrological parameters and divided by a permanent picnocline (halocline). The deep part (below 50-100 m), comprising 90% of the sea volume (Vinogradov *et al.*, 1992), remains relatively isolated from the surface layer, where the aerobic processes take place. Thus, below the basic picnocline layer, an anoxic zone is formed, preceded by an oxygen deficit zone where organic matter is oxidized to sulfates. Then, by anaerobic bacterial reduction, the sulfates are reduced to hydrogen sulfide. The latter is spread widely in the anoxic zone below 150-200 m (Sorokin, 1992). The geostrophic circulation in the surface layer of the basin is presented by the Main Black Sea Stream (MBS) which generates, in the central east and west regions, extensive cyclonic gyres and a multitude of smaller cyclone and anticyclonic gyres (Fig.1). At the external boundary of the MBS, due to its interaction with the continental slope, a ring of anticyclonic eddies is formed which generates a quasi homogenous Convergence Zone (CZ). Despite the persistence of the picnocline, recent studies show that the water column has an intense vertical dynamics, especially in Winter. Strong North and North-East winds elevate the main cyclonic gyre domes (20-30 m from the surface in some areas) which break the picnocline apart and leads to increase of the convective mixing with an average speed of 0.02 cm/s (Ovchinnikov and Popov, 1987). In this Divergence Zone (DZ), covering an area of about 40 000 km^2, 3-4 000 km^3 are upwelled, which exceed the volume of the river inflow by a factor of ten (Vinogradov *et al.*, 1992). The deep waters, lifted to the surface, mix with the cooled surface layer in a 1:5 ratio and generate the so called 'Cold Intermediate Layer' (CIL), typical of the three-layer summer hydrostructure. The CIL then downwells from the domes of the picnocline to the periphery of the cyclonic gyres until reaching the MBS which spreads them throughout the basin.

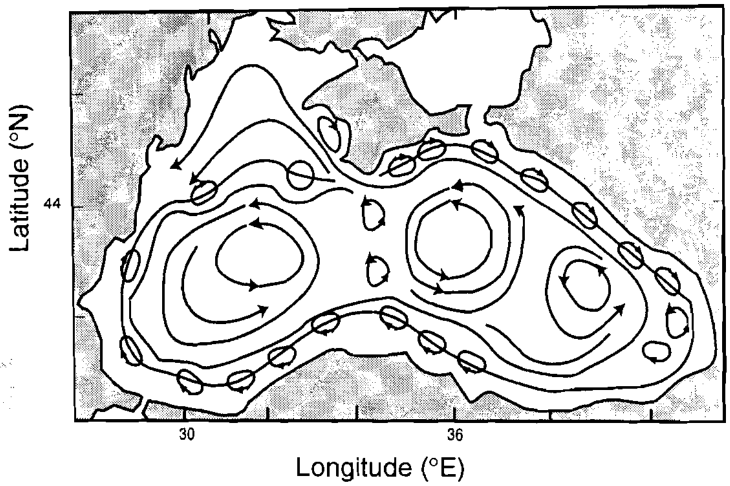

Fig. 1: Surface circulation in the Black Sea (Anon., 1990).

The upwelling of water in the DZ of the central basin is compensated by its downwelling in the CZ above the continental slope, which coincides with CIL downwelling to the periphery of the cyclonic gyres (Ovchinnikov *et al.*, 1991). Downwelling in CZ water is compensated by an intensification of the DZ upwelling as well as by the active upwelling of water on the shelf. Coastal upwelling occurs in some areas, due to geomorphologic particularities of the coast and bottom, and the local winds (e.g., Cape Kaliakra: Dimitrov *et al.*, 1987; Odessa Bay: Vinogradova and Vassileva, 1992; Peninsula of Crimea: Blatov and Ivanov, 1992).

In winter time, due to the impact of the low temperatures and the strong winds, the shelf zone is subjected to intense vertical mixing which covers the total water column from the surface to the bottom. In spring, the surface layer is heated and a seasonal thermocline occurs in the 25-30 m layer. Thus, the typical warm season three-layer structure is observed in the open sea, comprising an upper, quasi-homogeneous layer with the seasonal thermocline as its lower limit, 6-8°C cold intermediate layer between the seasonal thermocline and the permanent picnocline, and an anaerobic zone below the picnocline. Under this stratification, vertical mixing is negligible, ranging from 1 - 1.6 x 10^{-7} cm/s (Boguslavsky *et al.*, 1979). In the North Western Part (NWP) of the Black Sea, the summer vertical stratification is even stronger, due to river inflow. The Danube inflow forms an extensive river plume, which impacts the western coast all the way to the Bosphorus (Rozhdestvensky, 1954). The distribution of basic hydrochemical parameters, as well as that of organic matter and of living communities, depends on these structural peculiarities of the Black Sea waters.

2. PLANKTON PRODUCTIVITY CYCLES

The hydrophysical processes as well as the dynamics of the bio-production differ considerably in the central open sea and shelf zones, which will be considered separately. The latter includes the coastal ecosystems and the shallow NWP, impacted by the inflow of large rivers. The growth of phytoplankton in the open sea depends on the climate conditions, it begins in January-February and reaches its maximum as a winter bloom in February-March. The main prerequisite for it is the elevation of the constant picnocline above the critical depth of photosynthesis (Vinogradov *et al.*, 1992). Obviously, this period offers a combination of conditions (nutrient enrichment and stability) favorable for blooms and similar to those in upwelling zones (Mann, 1993). It can be assumed that, in the center of the cyclone gyres, there are 'pulses' of vertical mixing, followed by stable periods. Moreover, the cyclonic gyres and the picnocline form retention areas for plankton.

The more intensive blooms, caused mainly by *Nitzschia delicatissima*, *Risosolemia calcaravis* and other large diatoms, are noted, in the center of the cyclonic gyres, and, with equal, intensity on the surface to the picnocline, and average production reaches 0.5 - 0.7 gC.m^2.day^{-1} (Vinogradov *et al.*, 1992). At the end of March, the degradation of the bloom begins, wherein the microalgal cells sink and form a vertical distribution maximum on top of, and in the picnocline. The role of the heterotrophs and mixotrophs in the succession increases. In summer, with the establishment of the seasonal thermocline and with the exhaustion of the nutrients during the bloom, production decreases and the peridineans and euglenophytes start to dominate the plankton (Vinogradov *et al.*, 1992). Nazarov *et al.* (1991) distinguish three successions of the phytoplankton in NWP. The first begins in April, after the winter mixing and the increased river inflow. In April-May begins the spring phytoplankton bloom, reflecting the stabilization of the production layer above the thermocline. Summer, autumn and winter maxima are also observed every year. The summer (July-August) maximum is strongest. Mashtakova and Roukhiyaynen (1979) pointed out that, during the years with calm winters in NWP, the phytoplankton has a more pronounced seasonal maximum in April-May while, during the years with stormy winters, this maximum occurs in July-August. This relation is reciprocal in the eastern part: during the years with stormy winters, the biomass maximum occurs in February-March, while for calm winters, this maximum occurs in the summer period. These results lead to the conclusion that, in the deeper water eastern part, which resembles the central regions, the winter bloom is the key production cycle. The strong mixing and cooling of the NWP waters in stormy winters delays the optimum bloom conditions, which shifts the succession to the summer months. This, together with the increased influence of the river inflow, results in a seasonal maximum in July-August. Local upwelling events replacing periods of stability are also important for the initiation and the growth of the blooms in the shelf ecosystems. Zooplankton production is tuned at various spatial and time scales to the maxima of primary production. In the open sea, as well as in the shelf ecosystems, its minimal biomass and production occurs in winter. The thermophobic bathyplankton complex, with *Calanus helgolandicus* and *Pseudocalanus elongatus* as key species, is dominant in the open sea, at all seasons (Petipa, 1991). Its maximal biomass and production occur in spring while the minima occur in summer. Zooplankton growth on a mass scale begins in March in the 10-30 m layer and, after the establishment of the seasonal thermocline; the maximum biomass then spreads above and below this thermocline (Vinogradov *et al.*, 1992). Summer is the most productive season for all zooplankton, including eurythermic species such *Acartia clausi*, and the thermophilic species groups such as *Cladocera*. In summer, the pelagic larvae of zoobenthos species also occur in the plankton. Overall, the highest horizontal zooplankton densities are observed in CZ, on the periphery, between the main cyclonic gyres and in the river plume fronts.

3. FISH PRODUCTION PATTERNS IN RELATION WITH ENVIRONMENTAL CONDITIONS

Rass (1949) divides the Black Sea fish fauna into 4 main groups, based on their origins and ecology peculiarities:

1. Freshwater species;
2. Brakish Ponto-Caspian relicts;
3. Typical sea coldwater species with Boreal-Atlantic origin;
4. Typical sea warmwater species with Mediterranean origin.

The last two groups include the most widely spread and commercially important species in the Black Sea basin. Group 3 consists of: sprat (*Sprattus sprattus)* and whiting (*Merlangius merlangus euxinus*). Group 4 consists of: anchovy (*Engraulis encrasiclus ponticus*), horse mackerel (*Trachurus mediterraneus ponticus*), mackerel (*Scomber scombrus*), and bonito (*Sarda sarda*) (the last two species over winter in the Marmara Sea and feed in the Black Sea.). Reproduction of the coldwater species occurs mainly in winter (December-February) and is coupled with the dynamics of the thermophobic bathyplankton complex, while the warmwater species reproduce and feed in summer, in the warm surface layer, in relation to the dynamics of the summer epiplankton complex (Petipa, 1991). Consequently, it is appropriate to distinguish the main life patterns of the fish populations, related to the peculiarities of the annual production cycle presented below (Fig. 2).

Due to the intensive winter vertical mixing in DZ, the phytoplankton begins to bloom in the open sea in February-March. A maximum of sprat spawning is observed in December-February which may cover the entire basin (Arkhipov, 1993). Whiting spawns in the shelf zone, then the larvae are spread in the basin by horizontal streams. The thermophobic bathyplankton complex spawns during the whole year, with a maximum production in March-April, before the formation of the seasonal thermocline. Sprat and whiting larvae have maximum concentrations in April-May in the open sea as well as

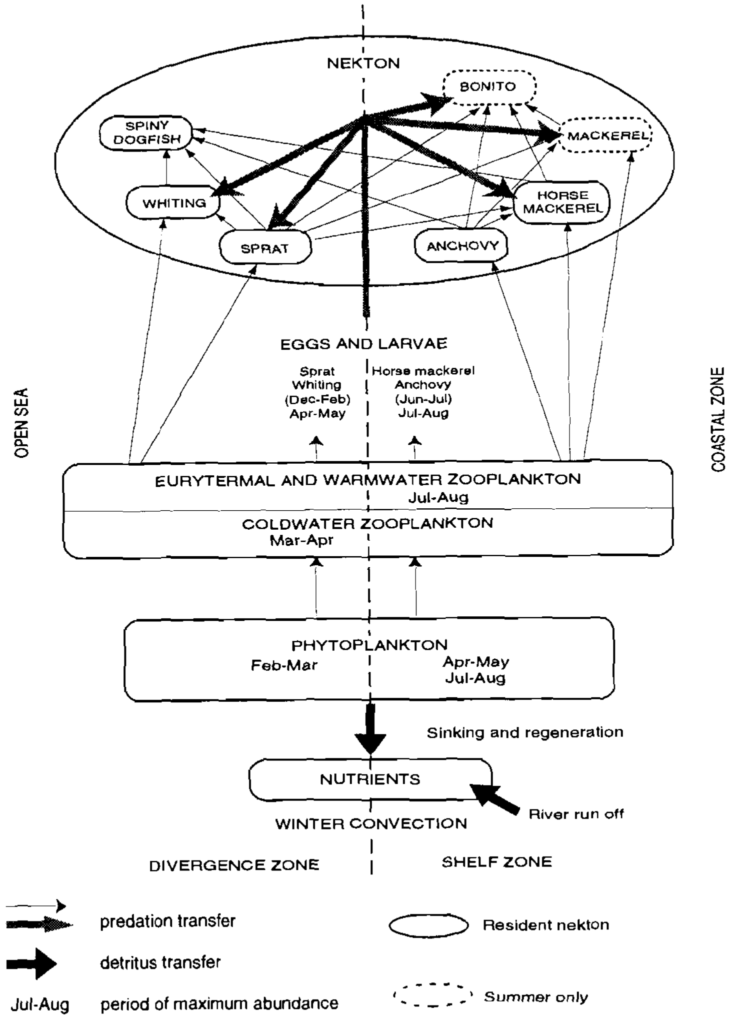

Fig. 2: Major trophic pathways in the Black Sea pelagic ecosystem.

in the shelf zone, in the 0-100 m layer, with maximal densities above the continental slope and on the edges of the main cyclonic gyres. Following the spring warm up of the waters, the larvae/juveniles withdraw below the seasonal thermocline, where they find favorable feeding conditions (zooplankton larvae) in the 10-50 m layer. Adult sprat and whiting undertake feeding migrations in the shelf zone during the spring period of homothermia. In summer they reside below the thermocline and, in some cases, when winds blow from the shore, they migrate to the coast together with the plankton complex, their main food.

In March-April the bloom begins in the shelf zone, using the nutrients from winter mixing and from river outflow. Maximum production in this zone occurs in the surface layer, in summer. At this time, the warm water fish migrate in NWP and in the coastal zones, for both feeding and spawning .

4. REPRODUCTIVE NICHES OF COLD WATER AND WARM WATER FISHES AS EXEMPLIFY BY SPRAT AND ANCHOVY

A comparative study of small pelagic clupeoid fishes should examine the three factors responsible for their reproductive success and thus for the high productivity of these species (Bakun, 1994):
- enrichment with nutrients;
- concentration of fish larvae and their food in a stable environment;
- retention of the concentrated patches favorable for fish growth and survival.

The components of Bakun's 'triad' are strongly dependent on the physical processes in the sea. Thus, enrichment is mainly caused by divergence, upwelling or river run-off, while concentration and retention (by convergence or stratification) are associated with active oceanographic structures such as currents, fronts, eddies or coastal upwelling. The niche concept (Hutchinson, 1978) is assumed as n-dimensional hyperspace occupied by the community, any point of which is defined by some value of environmental variables. We call a 'reproductive niche' the realized niche as a function of the reproductive population interacting with its environment. The reproductive population is characterized by both spawning stock and eggs, and larvae abundance and survival which account for the recruitment success sustaining the population. The niche space is determined by abiotic and biotic environment and, as well, by species preferences. On the basis of current knowledge in ecology and of statistical analyses we performed, we attempted to define elements of the reproductive niches of the two most abundant fish species in the Black Sea: anchovy and sprat, in relation with the above mentioned 'triad'. Coldwater and warm-water fishes differ by their seasonal pattern. In the Black Sea, the seasonal gradients of the hydrographic parameters are stronger than in the open ocean. As mentioned above, Black Sea fishes have different origins. Their specific preferences for environmental conditions predetermine their adaptation in the Black Sea. The clear seasonality of reproductive behavior in these species underlines that temperature is an important factor defining their niche.

In relation to the first factor from the 'triad', the enrichment, it was shown above that the spawning of sprat can be associated with the winter divergence and the winter/early spring plankton maxima. Winter presents rather adverse weather conditions so the reproductive niche of fish is situated such as to ensure optimal concentration and retention for eggs and larvae. Those are found mostly offshore in the 10-50m subsurface layer: a zone stabilized by the permanent picnocline. Horizontally, sprat eggs and larvae are concentrated in the CZ and on the edges of the main cyclonic gyres (Fig. 3). The most abundant Black Sea species is the anchovy, which spawns during summer when, intensive feeding and growth occurs as well. The enrichment processes underlying the summer production maxima in coastal waters and the NWP are more difficult to explain. Their complex patterns include temporal decay in plankton successions, due to intensified cooling of this zone in comparison with the open sea, river runoff with maxima in late spring, increasing importance of the regenerated production for food webs, local upwellings, intrusions through thermohaline fronts, internal waves, etc. The main feature characterizing the summer habitat is the strong stratification of the water, due to the seasonal thermocline, which is reinforced in coastal waters and the NWP by the plumes of the large rivers. Anchovy spawns mainly in the surface layer of these warm and stratified areas (Fig. 4). In this manner eggs and larvae are retained in the coastal layer, stabilized in depth by the thermocline and protected from offshore drift by thermohaline fronts. Trukhchev and Demin (1992) show that the NWP presents a local minimum of the surface wind driven velocity that is directed onshore.

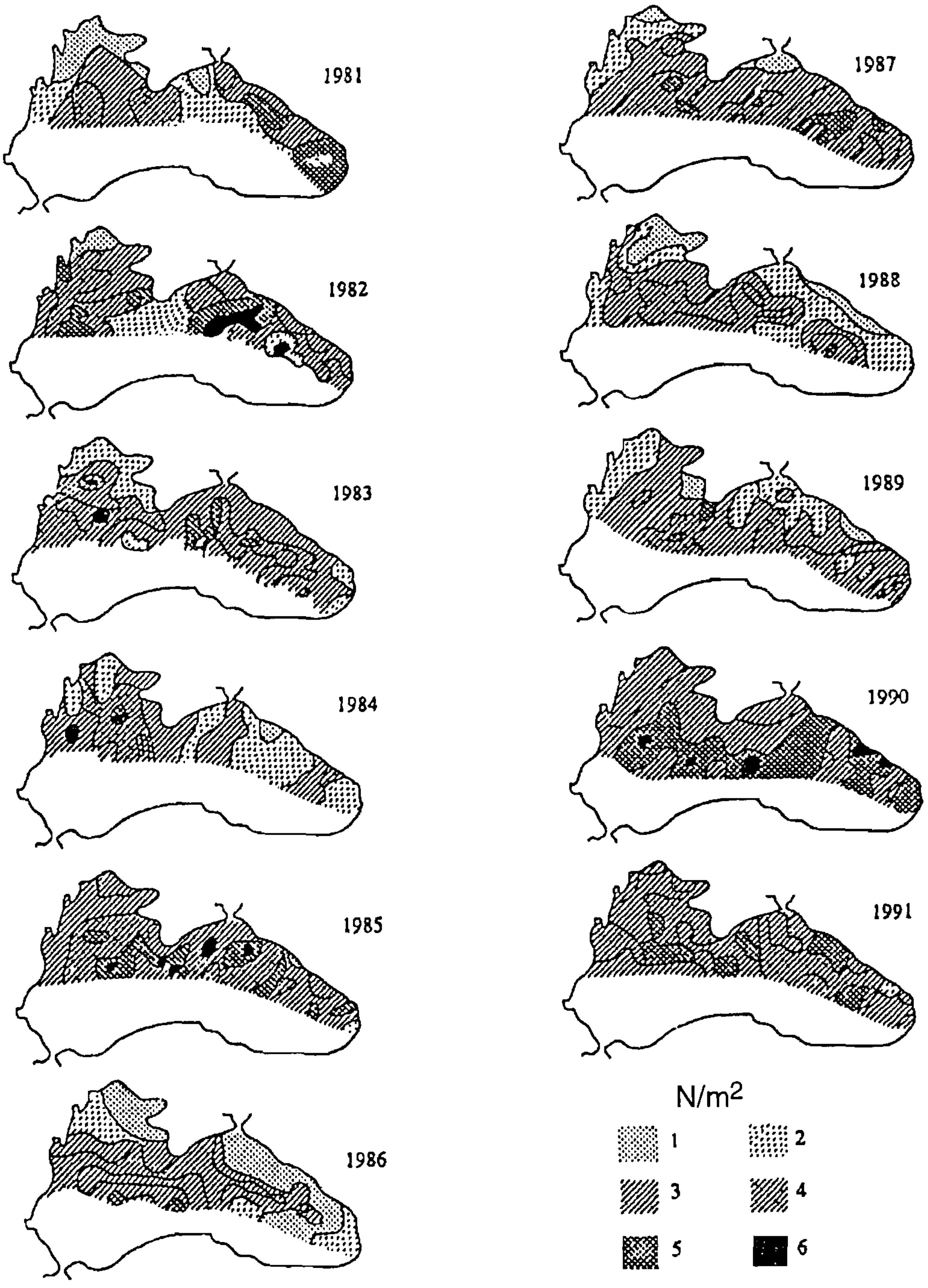

Fig. 3: Distribution of Black Sea sprat larvae and early juveniles in April-May 1981-1991 (after Arkhipov, 1993).

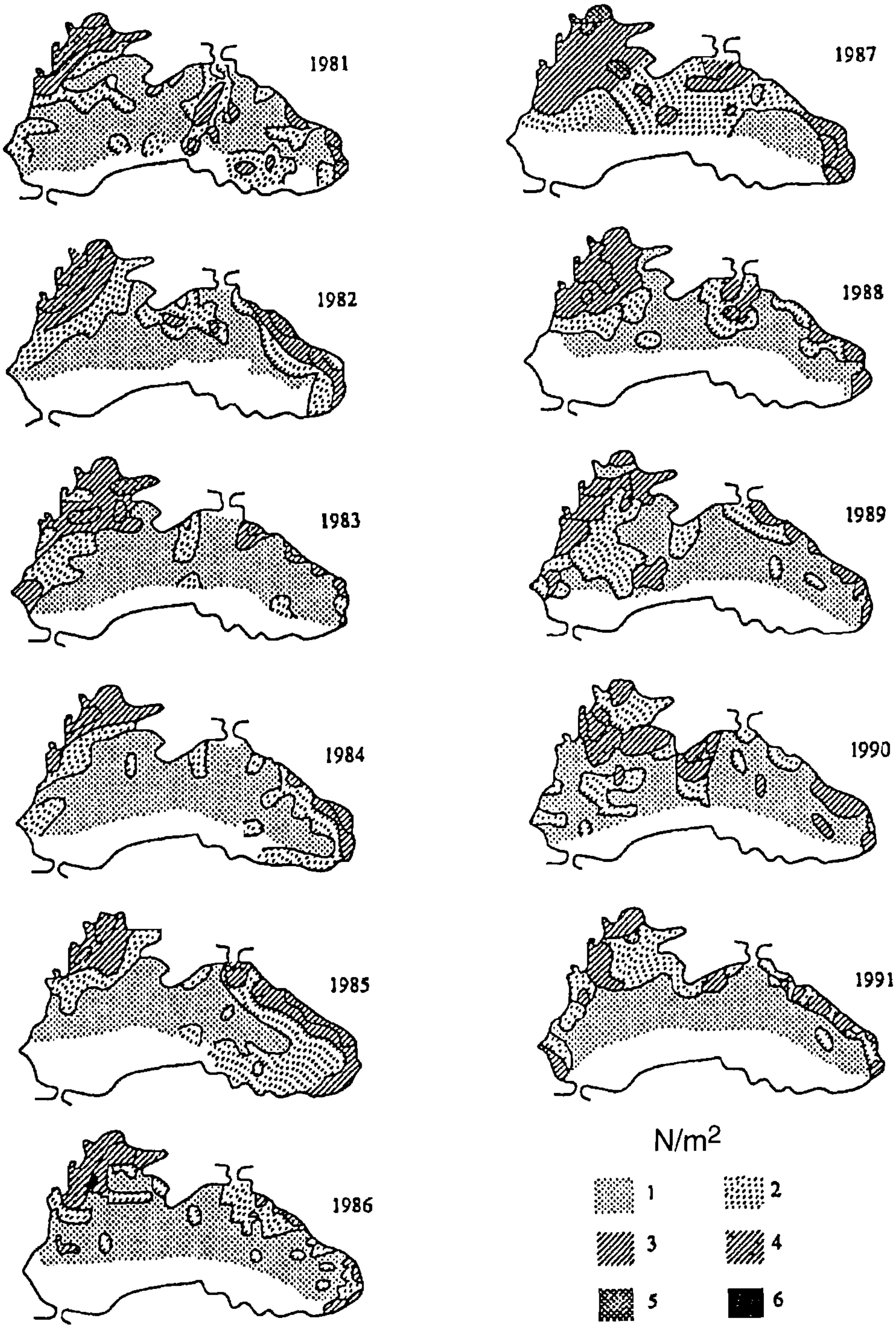

Fig. 4: Distribution of anchovy larvae and early juveniles in July-August 1981-1991 (after Arkhipov, 1993).

The sprat, as a cold water species of boreal origin, prefers the winter season when enrichment and plankton blooms occur offshore. It finds relative stability in the layer near the picnocline and in the CZ. During the summer sprat is then found in the cooler waters under the thermocline together with its preferred food, *Calanus* and *Pseudocalanus*.

In this manner the two most abundant fish populations anchovy and sprat 'share' their reproductive habitat in space and time. The overlapping between their adult trophic niches is also negligible (Petipa, 1991; Konsulov, 1975). Such a relative lack of competition allows these species to maintain large biomasses, while coupling them with the annual production cycle.

Statistical analyses can be used to study further the niche of anchovy and sprat. Relationships between recruitment, parental biomass and environmental factors are usually non-linear; so transformations of data should be performed to maximize the correlation among them. We have applied the generalized additive model of Hastie and Tibshirani (1990) to explore the appropriate forms of relationships between variables. The ACE algorithm (Alternating Conditional Expectations; Breiman and Friedman, 1985) has been used to estimate optimal transformations of the response variable and predictor variables for multiple regression. This method was used previously in recruitment studies by Cury and Roy (1989) and allowed them to define the 'optimal environmental window' concept. The use of the general additive model in fisheries science is discussed in details in Cury *et al.* (1995). Data used are shown in Tables 1 and 2. Recruitment and biomass series were estimated using VPA (Prodanov *et al.*, 1995). Monthly mean values of sea surface temperature (SST), wind speed and the wind speed cubed were extracted from COADS (Comprehensive Ocean-Atmosphere Data Set, CEOS Program, 1994) using the CODE program (Roy and Mendelssohn, this vol.), and averaged over the main spawning seasons: November- March for sprat and April-August for anchovy, for the area from 42°S-46°N and 28°W-34°E. The wind speed index is related to the wind-driven currents i.e., divergence/convergence and thus, with enrichment, concentration and retention on one hand, and instability and dispersion on the other hand. Wind cubed is a rough index of mixing in the upper layer (Bakun and Parrish, 1982). Data on river discharge and phytoplankton biomass are from Anon. (1992) and total phosphorus data in the Danube delta, from Juravleva and Grubrina (1993).

Both species anchovy and sprat show clear relation between recruitment and parental biomass. Transformations are close to logarithmic in shape, so density dependent regulation of recruitment can be assumed (similar to the Beverton and Holt stock-recruitment model). However, only 39% of sprat recruitment variance is explained by the model (Fig. 5a), while anchovy recruitment is highly determined by the stock size (R^2=0.87, Fig. 6a). On the other hand, if the analysis is restricted to a recent period (1966-1990), so that data are more reliable, the model, with a similar form of the functional relationship, explains 81% of sprat recruitment variance (R^2=0.81). From Figures 5b, c, d we can see that 67%, 66% and 77% respectively of sprat recruitment variance are explained by different combinations of hydroclimatic variables. The relationship with SST is negative and more pronounced above 10°C mean winter SST (November-March). The transformation of scalar wind speed, plotted against its original values, presents an optimum between 6.5 and 7 m/s and the transformation of the wind cubed, has an optimum near 600m^3/s^3 (Fig. 5b, c) These figures are similar to those originally documenting the 'optimal environmental window' concept of Cury and Roy (1989).

In his comparative study on three highly productive large marine ecosystems inhabited by clupeoid stocks, Bakun (1993) found that values of the wind mixing index <250 m^3/s^3 characterized sardine and anchovy spawning grounds. However, other reproductive sites mentioned in this paper as Agulhas Bank in the Benguela system and the Patagonia Shelf in south-eastern South America present much higher turbulence. In these regions the suitable reproductive habitat is assumed to occur in more stable subsurface layers. Similarly, the habitat of sprat is assumed to be in the 10-50m layer stabilized by the permanent picnocline and around eddies in the CZ, so the influence of surface turbulence would be reduced. In the last model presenting recruitment as a function of SST, wind and turbulence (Fig. 5d) the shape of the transformation for wind

	Sprat		Anchovy		River outflow	Total phosphorus
Year	Recruitment ($N.10^9$)	Parental biomass ($t.10^3$)	Recruitment ($N.10^9$)	Parental biomass ($t.10^3$)	($Km^2.year^{-1}$)	(t)
1955	28.43	25.4	—	—	—	—
1956	22.03	40.4	—	—	—	—
1957	63.35	40.3	—	—	—	—
1958	91.8	102.9	—	—	—	—
1959	79.66	164.4	—	—	—	—
1960	96.23	198.4	—	—	—	—
1961	76.21	231.5	—	—	—	—
1962	41.66	203.3	—	—	—	—
1963	27.47	142.2	—	—	—	—
1964	58.72	91.8	—	—	—	—
1965	24.36	101.5	—	—	384.9	—
1966	19.97	78.3	—	—	399.3	—
1967	13.67	57.9	75.1	294.8	371.7	—
1968	12.05	43.5	60	438.6	314.2	—
1969	29.03	33.2	64	484.2	352.7	—
1970	24.52	56.4	68.6	492.0	491.6	—
1971	110.01	65.8	54	509.2	306.6	21.6
1972	130.64	181.2	48.7	446.1	301.2	10.3
1973	170.5	287.4	63.2	367.4	287.5	15.7
1974	113	409.7	56.5	342.4	335.3	18.2
1975	85.13	553.5	81.2	325.2	369.7	27.6
1976	115	469.1	63.4	358.9	312.4	33.1
1977	84.37	485.9	87.3	355.9	359.7	30.7
1978	84.12	412.7	112	458.7	371.6	32.1
1979	97.68	370.1	144	708.1	395.2	75.5
1980	72.2	332.9	116	705.9	437.2	—
1981	43.05	280.9	93.4	667.2	416.7	93.2
1982	57.92	209.2	90.7	549.3	359.2	98.8
1983	76.09	184.6	101	515.3	280.6	56.9
1984	113	234.7	84.7	451.3	291.6	68.7
1985	169	313.2	107	512.1	321.2	52.2
1986	102	397.8	104	534.9	—	56.4
1987	117	398.7	62	501.6	—	51.8
1988	62.69	398.6	39.9	252.3	—	—
1990	47.61	115	26.7	137.5	—	—

Table 1: VPA estimates of recruitment and parental biomass of Black Sea sprat and anchovy (Prodanov *et al.*, 1995); river outflow into the Black Sea (Anon., 1992), and total phosphorus amount in the Danube River delta (Juravleva and Grubrina, 1993)

cubed shows a negative relation with recruitment. In such a model, however, one must be weary of the high degree of colinearity between the last two wind related variables, which can affect model reliability. Figure 6b presents the relation of the anchovy recruitment with SST and the wind variables. The model explains 52% of the variance, and the relation with wind speed is positive. The transformation of the wind mixing index has a negative slope. The relation with SST is positive, but the contribution of this variable to total explained variance (as shown by the range of the transformed values) is negligible. Figures 6c, and d show the dependence of anchovy recruitment on river discharge. The high coefficient of determination (R^2=0.73) of total phosphorus discharged by the Danube River identifies out river outflow as an important source of enrichment for summer production.

	Winter			Summer		
Year	SST	Wind speed	Turbulence	SST	Wind speed	Turbulence
1965	9.6	6.1	473.3	17.4	5.5	463.9
1966	10.8	6.9	647.9	19.3	5.5	340.3
1967	11.1	6.8	597.8	18.7	4.8	287.5
1968	10.3	7.3	764.4	18.8	5.2	332.7
1969	9.9	7.7	824.4	17.6	5.9	426.3
1970	10.9	7.5	615.2	17.9	4.0	238.4
1971	9.9	6.4	671.2	18.7	3.8	145.9
1972	9.7	5.4	758.1	19.7	4.2	278.8
1973	9.5	6.5	705.6	18.3	5.2	287.9
1974	8.6	7.2	687.0	16.8	4.3	196.8
1975	10.3	6.8	630.3	18.4	5.4	356.8
1976	9.1	7.3	833.5	17.5	4.7	260.1
1977	9.9	6.4	575.3	18.3	4.8	301.0
1978	9.2	6.4	579.6	17.7	4.1	202.0
1979	9.9	7.1	624.0	18.7	5.5	371.2
1980	9.5	7.0	693.0	17.9	4.2	180.9
1981	10.3	6.8	753.2	18.2	4.5	267.8
1982	9.4	7.5	811.6	17.6	6.0	382.3
1983	9.8	6.9	600.3	18.9	5.3	308.3
1984	9.5	7.0	600.5	17.6	5.9	368.0
1985	9.0	7.2	608.6	17.4	4.6	214.6
1986	10.0	6.0	370.9	18.9	4.7	279.0
1987	8.6	6.2	677.6	17.3	4.5	239.4
1988	9.1	7.2	735.7	18.8	4.2	344.2
1989	8.8	5.9	480.1	18.0	4.9	251.1
1990	8.8	7.3	892.3	18.1	3.9	193.4

Table 2: Sea surface temperature (°C), scalar wind speed (m/s) and turbulence index (wind speed cubed, m^3/s^3) from COADS (1994) averaged over November-March (winter) and April-August (summer).

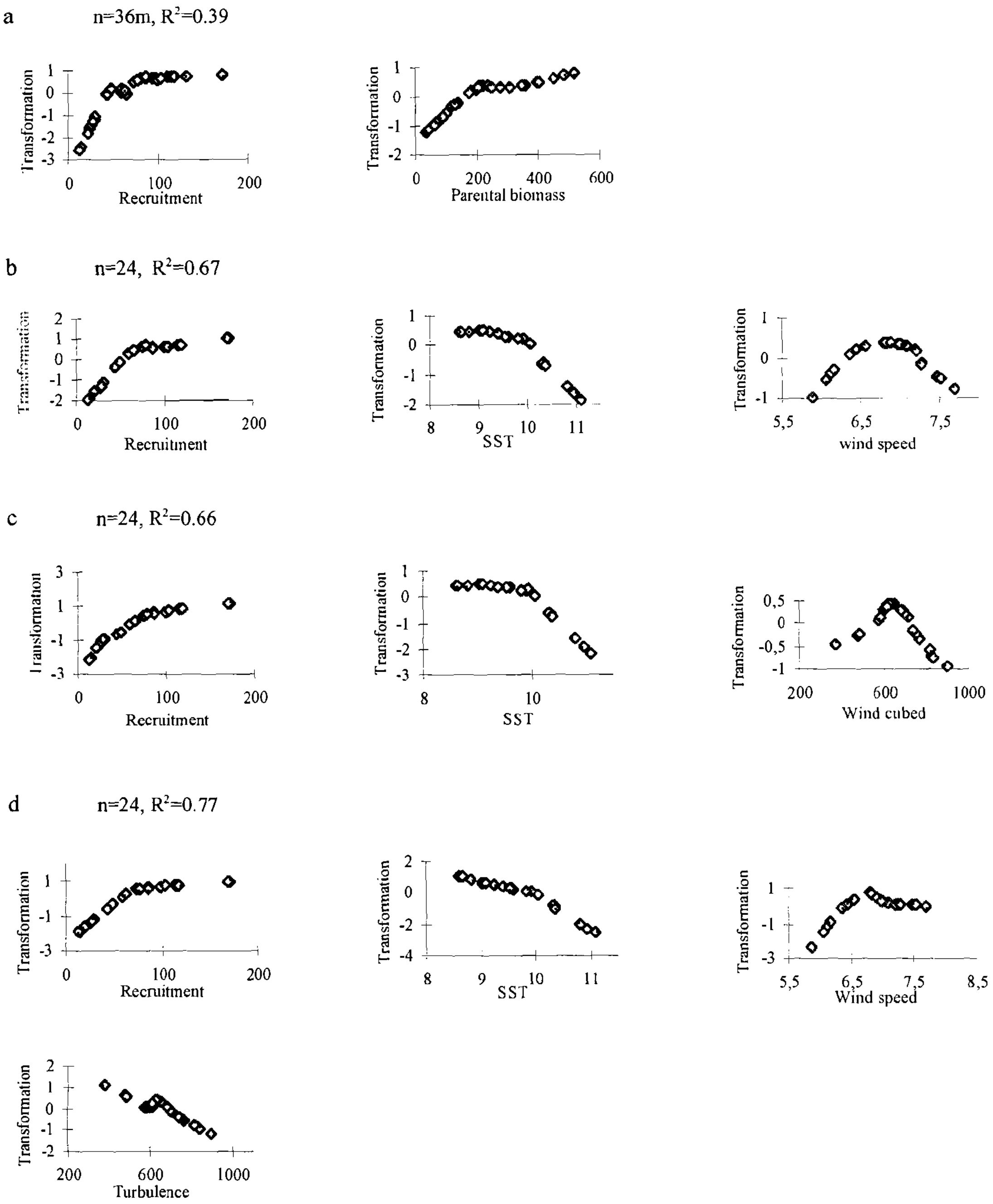

Fig. 5: Regressions of sprat recruitment as a dependent variable on parental stock biomass and different environmental factors (independent variables) using the ACE algorithm (data from Tables 1 and 2):

a) Recruitment vs. parental biomass;
b) Recruitment vs. SST and wind speed;
c) Recruitment vs. SST and turbulence index;
d) Recruitment vs. SST, wind speed and turbulence index.

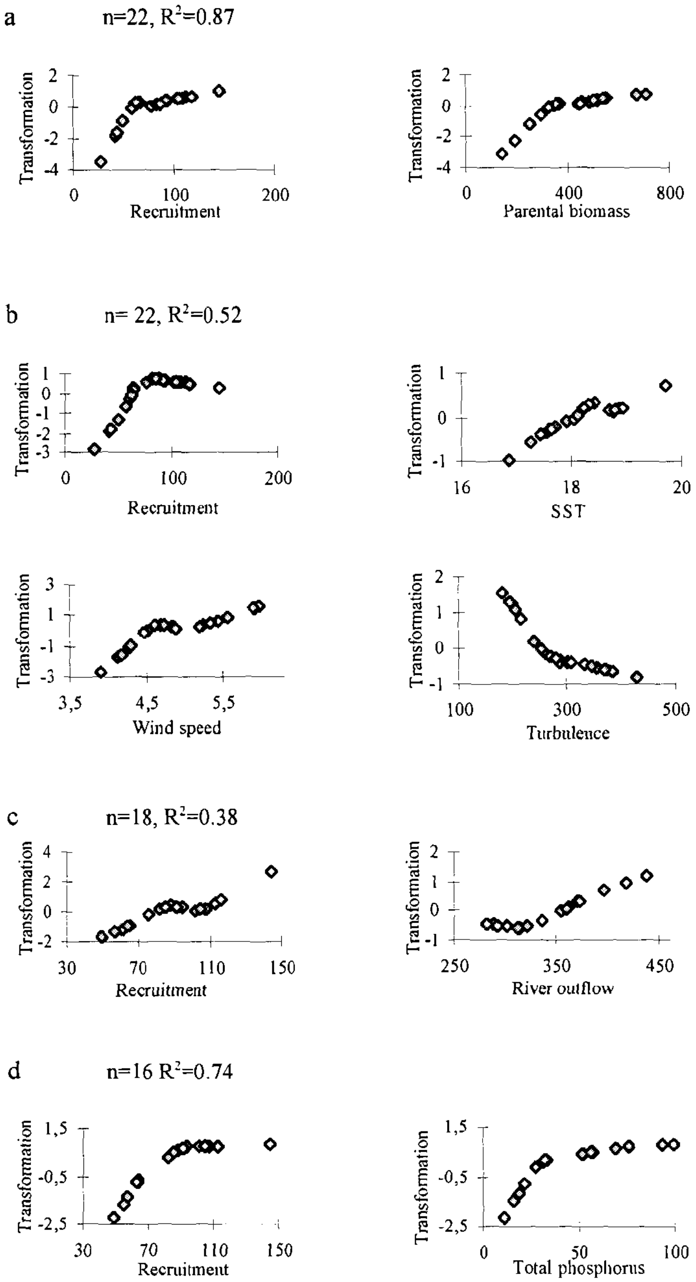

Fig. 6: Regressions of anchovy recruitment as a dependent variable on parental stock biomass and different environmental factors (independent variables) using the ACE algorithm (data from Tables 1 and 2):

a) Recruitment vs. parental biomass;
b) Recruitment vs. SST, wind speed and turbulence index;
c) Recruitment vs. total river outflow in the Black Sea;
d) Recruitment vs. total phosphrus in the Danube River delta.

5. CONCLUSIONS AND SUGGESTED OBJECTIVES FOR FUTURE INVESTIGATIONS

In the last 20 years, the Black Sea ecosystem suffered considerable changes due to the increased anthropogenic impact. The commercial fisheries, based mainly on pelagic species, peaked in the late 1970s. In the 1970s the eutrophication of the Black Sea became evident, characterized with increased rate of red tides, incidences of hypoxia in the bottom biocenoses, community alterations and advent of immigrants (Caddy and Griffiths, 1990). The sharp decrease of the top marine predators, together with the increased impact of the eutrophication led to increases of planktophageous species. The outburst of plankton not used in the food web itself led planktophageous megaloplankton which also feed on fish eggs and larvae. The negative human impact (overfishing, pollution) has led to destabilization of the ecosystem in the second half of the 1980s, and to a decrease of the biodiversity and the biological resources (Zaitsev, 1993). The increase impact of anthropogenic factors, relative to natural factors of the marine environment, is a subject of numerous debates in the scientific community. Expeditions conducted in the 1980s for the study of the open sea regions (Petipa, 1991) led to a realization of the importance of the winter circulation for the hydrological structure of the basin and for the annual production cycle (Ovchinnikov *et al.*, 1991). The concentration of the majority of the studies in the coastal zone and in the warm season, typical of the early period of the Black Sea marine science, led to overestimating the importance of the shelf systems in comparison with the open pelagic ecosystem, considered oligotrophic by some early investigators. The latest studies show sharp fluctuations of the fish stocks (Ivanov and Beverton, 1985; Daskalov and Prodanov, 1995a, 1995b.; Prodanov *et al.*, 1995). There is also a well-known variability of the primary and secondary production to consider, along with the hydrological and hydrochemical factors of the environment (Anon., 1992; Ovchinnikov and Osadchiy, 1991).

The high production and the peculiar dynamics of the system, its oceanography and biological studies dating for more than a century offer possibilities for long time series data analysis. Moreover, the unique features of the Black Sea — one of the cradles of European civilization — make this basin a very interesting object for comparative analysis. Bakun and Parrish (1982) developed this idea and pointed out the main criteria for comparative time series analysis of environment and fishery systems in upwelling regions. Caddy (1993), similarly, proposed a comparative evaluation of the fishery ecosystems of semi-enclosed seas. Since 1992 a group of fisheries scientists from the Black Sea region joined in a project 'Environmental management of fish resources', funded by The Central European University Foundation, devoted to the assessments of the main commercial fish stocks and diagnosis of their dynamics in relation to environmental changes and human impact (Prodanov *et al.*, 1995). The methods, the criteria and the general research framework are similar to those proposed by ICES, FAO Fisheries Department, ICLARM, and are based on the traditions of the Research Institutions for Black Sea. The objective is the preparation of a large operational data base on the status of fish resources and the conditions of the environment in order to identify regularities of their dynamics. This sould help model and manage the stocks in an ecological context.

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REFERENCES CITED

Anon. 1990. *Practical ecology of the sea: Black Sea*. Naukova Dumka, Kiev, 251p. In Russian.

Anon. 1992. *Hydrometeorology and hydrochemistry of USSR seas. Black Sea*, 4(1-2). Hydrometeoizdat, Sankt Petersbourg. In Russian.

Anon. 1994. *COADS on CD-Rom*, vol. 1: North Atlantic.CEOS (Climat and Eastern Ocean Systems) Program.

Arkhipov A.G. 1993. Estimation of abundance and peculiarities of distribution of the commercial fishes in the early ontogeny. *Vopr. Ihktiologii*, 33(4): 511-522. In Russian.

Bakun A. 1993. The California Current, Benguela Current, and southwestern Atlantic shelf ecosystems: a comparative approach to identifying factors regulating biomass yields. *In*: K. Sherman, L.M. Alexander and B.D. Gold (eds.). *Large marine ecosystems - Stress, mitigation, and sustainability*. AAAS. 376p.

Bakun A. 1994. Climate change and marine populations: interactions of physical and biological dynamics. Paper presented at the Greenpeace/University of Rhode Island "Workshop on the Scope, Significance and Policy Implications of Global Change and the Marine Environment", 14-17 May 1994.

Bakun A. and R.H. Parrish. 1982. Turbulence, transport, and pelagic fish in the California and Peru Current systems. *CalCOFI Rep.*, 23: 99-112.

Blatov A.S. and V.A. Ivanov. 1992. *Hydrology and hydrodynamics of the Black Sea coastal zone*. Naukova Dumka, Kiev. 242p. In Russian.

Boguslavsky S.G., M. Yu Belyakov and V.A. Gorov. 1979. Peculiarities of the hydrology of the Black Sea. *In*: V.N. Grese (ed.). *Productivity of the Black Sea*. Naukova Dumka, Kiev: 11-24. In Russian.

Breiman L. and J.H. Friedman. 1985. Estimating optimal transformations for multiple regression and correlation. *J.Am.Stat. Assoc.*,80 (391): 580-619.

Caddy J.F. 1993. Toward a comparative evaluation of human impacts on fishery ecosystems of enclosed and semi-enclosed seas. *Reviews in Fisheries Science*, FAO publ.

Caddy J.F. and R.C. Griffiths. 1990. A perspective on recent fishery. Related events in the Black Sea. *FAO Studies and reviews*, 63: 43-71.

Cury P. and C. Roy. 1989. Optimal environmental window and pelagic recruitment success in upwelling areas.*Can. J. Fish. Aquat. Sci.*, 46: 670-680.

Cury P., C. Roy, R. Mendelssohn, A. Bakun, D.M. Husby and R.H. Parrish. 1995. Moderate is better: exploring nonlinear climatic effect on Californian anchovy (*Engraulis mordax*). *In*: R.J. Beamish (ed.). Climate change and fish population. *Can. Spec. Publ. Fish. Aquat. Sci.*, 127: 417-424.

Cushing D.H. and R.R. Dickson. 1976. The biological response in the sea to climate change. *Advance in Marine Biology*, 14: 1-122.

Daskalov G. and K. Prodanov. 1995a. Stock assessment of sprat *Sprattus sprattus* L. off Bulgarian Black Sea coast using length cohort analysis. *Rap.comm.int. mer Médit.*, 34.

Daskalov G. and K. Prodanov. 1995b. Variability in growth of sprat *Sprattus sprattus* L. off Bulgarian Black Sea coast with reference to the environmental changes in the sea. *Black Sea' 94: Proceedings of the international conference with a Workshop on Regional Cooperation Project for Integrated Research and Monitoring of the Black Sea, 12-17 Sept. 1994, Varna*: 81-85.

Dimitrov P.S., A.S. Stoyanov, E.K. Demirov and D.P. Solakov. 1987. On the phenomenon of upwelling in the western part of the Black Sea and its connection with the bloom of the plankton. *Comptes- rendus de l'Académie bulgare des Sciences*, 40(10): 127-130.

Grese V.N. (ed.). 1979. *Productivity of the Black Sea*. Naukova Dumka, Kiev, 388p. In Russian.

Hastie T. and R. Tibshirani. 1990. *Generalized additive models*. Chapman and Hall, London.

Hutchinson G.E. 1978. *An introduction to population ecology*.Yale University Press Ltd:, London, 274p.

Ivanov L. and R.J.H. Beverton. 1985. The fisheries resources of the Mediterranean, Part II: Black Sea. *FAO Studies and Reviews*, 60, 135p.

Juravleva L.A and N.A. Grubrina. 1993. Phosphorus regime in low stream of the Danube River and its discharge in the Black Sea.*Gidrobiol. J.*, 29 (6): 81-88.

Konsulov A. 1975. Trophic dependence of sprat *Sprattus sprattus sulinus*, Antiba distribution.*Proc. Inst. of Fisheries - Varna*, 14: 71-83.

Lasker R. 1985. What limits clupeoid production? *Can. J. Fish. Aquat. Sci.*, 42 (suppl. 1): 31-38.

Mann K.H. 1993. Physical oceanology, food chains, and fish stocks: a review. *ICES J.Mar.Sci.*, 50: 105-119.

Mashtakova G.P.and M.I. Roukhiyaynen. 1979. Seasonal dynamics of phytoplankton. *In*: V.N. Grese (ed.). *Productivity of the Black Sea*. Naukova Dumka, Kiev, 85-88. In Russian.

Nazarov N.A., A.A. Nesterov and V.T. Soldat. 1991. The state of fish stocks and pelagic fisheries in the Southeast Pacific. Sb.-Nauchn.- Tr.- Atlantino.: 92-102. In russian.

Ovchinnikov I.M. and Yu.I. Popov. 1987. Cold intermediate layer formation in the Black Sea. *Oceanology*, Acad. Sci. URSS, 27(5): 739-748. In Russian.

Ovchinnikov I.M., L.V. Moskalenko, Yu.I. Popov, O.I. Prokopov and V.V. Serditenko.1991. Some pecularities of hydrological conditions in the Black Sea in the winter period. *In*: M.E. Vinogradov (ed.). *Variability of the Black Sea ecosystem: natural and anthropogenic factors*. M. Nauka. 345p. In Russian.

Ovchinnikov I.M., Osadchiy, 1991. Secular variability of winter climatic conditions influencing peculiarities of hydrological conditions in the Black Sea. *In*: M.E. Vinogradov (ed.). *The variability of the Black Sea ecosystem: natural and anthropogenic factors*. M. Nauka: 85-89. In Russian.

Petipa T.S. 1991. Problems and development of the studies on pelagic ecosystems of the Black Sea. *In*: M.E. Vinogradov (ed.). *The variability of the Black Sea ecosystem: natural and anthropogenic factors*. M. Nauka: 336-345. In Russian.

Prodanov K., G. Daskalov, K. Mikhaylov., K. Maxim, E. Ozdamar, V. Shlyakhov, A. Chashchin and A. Arkhipov. 1995. *Environmental management of fish resources in the Black Sea and their rational exploitation*. Final Report CEU (Central European University)/RSS - Project, Praha.

Rass T.S. 1949. Black Sea ichthyofauna and its exploitation. *Proc.Inst. Oceanology*, Acad. Sci. URSS, 4. In Russian

Rozhdestvensky A.V. 1954. The role of Danube for formation of the Black Sea salinity. *Tr.Morsk.Biol.Stanc.*, Varna, 18: 1-20. In Bulgarian.

Sorokin Yu.I. 1982. *The Black Sea: nature and resources*. M. Nauka, 216p.

Trukhchev D.I. and Yu.L. Demin. 1992. The Black Sea general circulation and climatic temperature and salinity fields.*Woods Hole Oceanog. Inst. Tech. Rep.*, WHOI-92-34, CRC-92-02, 130p.

Vinogradov M.E., V.V. Sapozhnikov and E.A. Shushkina. 1992. *The Black Sea ecosystem*. 110p. In Russian.

Vinogradova L.A. and V.N. Vassileva. 1992. *The dynamics of the long standing and modelling of the Black Sea N.-W. part coastal waters ecosystem state*. Hydrometeoizdat, Sankt Petersburg. In Russian.

Zaitzev Yu.P. 1993. Impacts of eutrophication on the Black Sea fauna. *In*: Fisheries and environmental studies in the Black Sea system. *FAO Studies and Reviews*, 64:63-85.

The Recruitment of the Chilean Sardine (*Sardinops sagax*) and the "Optimal Environmental Window"

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ABSTRACT

The relationships between the recruitment of Chilean and Peruvian sardine and environmental factors from 1974 to 1990 are analyzed. Recruitment indices (numbers at age 2) as well as parental biomasses are calculated using sequential population analysis. Sea surface temperature, wind mixing, and upwelling indices are used to characterize the variability of the environment in the spawning area. The analysis is performed using generalized additive models. No apparent relationship exists between recruitment and temperature. The relationship between recruitment and upwelling or wind mixing appears to be dome shaped. Switches between a sardine and an anchovy dominated ecosystem, appears also as an important contributor to recruitment variability.

RÉSUMÉ

Les relations entre le recrutement de la sardine au Chili et au Pérou et des facteurs environnementaux sont analysées de 1974 et 1990. Les indices de recrutement (nombre de poissons à l'âge de deux ans) ainsi que la biomasse parentale sont calculés en utilisant des analyses séquentielles des populations. La température de surface, le mélange dû au vent et des indices d'upwelling sont utilisés pour caractériser la variabilité de l'environnement dans la zone de ponte. L'analyse est faite en utilisant des modèles additifs généralisés. Il n'y a pas de relation apparente entre le recrutement et la température. La relation entre le recrutement et l'upwelling ou le mélange par les vents apparaît en forme de dôme. Les changements de dominance par la sardine ou l'anchois au sein de l'écosystème apparaissent importants pour expliquer les fluctuations du recrutement.

INTRODUCTION

Chilean sardine, *Sardinops sagax*, increased significantly its abundance in the Southeast Pacific since the late 1960s, becoming the most important fisheries resource in Chile in the 1980s (Serra, 1983). After 1985, sardine landings started to decline and anchovy catches increased again, suggesting a change in the dominant species within the ecosystem (Serra, 1989; Lluch-Belda *et al.*, 1992). It is well known that the most productive regions are associated with upwelling systems, such as the Benguela, the Canary, the California or the Humboldt current systems. Clupeoids are the most abundant resources in these ecosystems, suggesting a strong connection between pelagic fish population dynamics and upwelling processes.

Observed decadal changes in abundance of the sardine and of the anchovy have been related to global warming (Kawasaki, 1993; Lluch-Belda *et al.*, 1989 and 1992; Sharp, 1993). Bakun (1990) suggests that global warming results in an increase of the equatorward wind leading to an intensification of the upwelling process in eastern boundary current ecosystems. Sardine has been associated with warmer conditions in the ocean (subtropical or oceanic conditions) and anchovy with cooler conditions (coastal or upwelling conditions) (Loeb and Rojas, 1988; Serra, 1989).

The eastern margin of the Southeast Pacific is a typical upwelling system. Equatorward trade winds induce offshore Ekman transport which brings cold and nutrient-rich subsurface water to the euphotic layer, enhancing primary production. The strength of upwellings is closely related to the wind: an increase of the alongshore wind results in an intensification of the offshore transport which favors an increase of the upwelling process. Wind also generates mixing in the surface layers. Cury and Roy (1989) studied the links between recruitment variability and upwelling intensity in the major eastern boundary current ecosystems. They showed that there is a dome-shaped relationship between recruitment and upwelling intensity. There are two factors that explain the non-linearity of the curve: on the left side, the wind is weak and the limiting factor is the production of food due to low intensity of the upwelling; on the right side of the curve, the upwelling is strong and wind mixing or offshore transport are the limiting factors. Thus, there is an 'optimal environmental window' at moderate levels of upwelling, where the effects of the limiting factors are minimized.

This paper explores the links between environmental indices such as sea surface temperature, wind mixing and upwelling index, with recruitment variability of the sardine stock off southern Peru and northern Chile, i.e., which represents the 'central sardine stock' (Parrish *et al.*, 1989), located from 15°S to 25°S. This stock has sustained the main pelagic fisheries in northern Chile since the early 1970s to the late 1980s, and a smaller fishery in southern Peru.

1. MATERIALS AND METHODS

The data on sardine spawning stock and recruitment were produced by the working group GTE-93 of IFOP/IMARPE. They derived this information through sequential population analysis (i.e., VPA) from 1974 to 1990 (17 years). The spawning stock was expressed in tons and the recruitment in numbers at age 2.

The environmental data considered are the sea surface temperature (SST), the wind mixing (WM) and the coastal upwelling indices (CUI). Mean annual SST was calculated from data collected at the Arica coastal station located in northern Chile. Wind data from the Comprehensive Ocean-Atmosphere Data Set (Roy and Mendelssohn, this vol.) were used to estimate WM and CUI in southern Peru (14°S-18°S). Since the shared sardine stock between Peru and Chile is distributed from about 15°S to 24°S and that approximately 20% of the total spawning area is located in southern Peru (17°S-18°S), we made the

Year	Recruitment Nr.10^6	Spawning biomass (t.10^3)	Sea Surface Temperature(°C)	Coastal Upwelling Index ($m^3/s/m$)	Wind mixing (m^3/s^3)	Ecosystem Factor
1972	–	–	17.4	1.41	422	–
1973	–	–	15.3	0.97	263	–
1974	14782	2119	15.5	1.15	323	1
1975	21183	2907	15.4	1.25	372	1
1976	38782	3759	16.3	1.30	429	1
1977	40266	5593	16.8	1.19	359	1
1978	39166	6769	15.9	1.11	302	1
1979	36700	7953	17.5	1.14	310	1
1980	35520	9305	18.8	0.89	235	1
1981	25427	8924	17.1	1.11	340	1
1982	17350	8457	19.9	1.41	418	1
1983	48143	6787	17.5	1.37	394	2
1984	35346	5682	16.9	1.15	316	2
1985	19374	5883	16.1	0.98	242	2
1986	20004	4695	16.3	1.03	282	2
1987	20875	4246	17.1	1.31	384	2
1988	13299	3603	15.3	1.50	499	2
1989	9451	3094	15.8	1.24	355	2
1990	6451	2472	15.4	1.22	366	2
1991	3247	2072	16.2	–	–	2

Table 1: Sardine and environmental data used in the analysis (see text).

assumption that the environmental data are representative for northern Chile; this is also suggested by a similar general trend of both SST and CUI. The data used in the analysis are shown in Table 1.

The statistical method used in this study, is a generalized additive model (Hastie and Tibshirani, 1990), an extension of multiple linear regression, first applied to fishery science by Mendelssohn and Cury (1987). The ACE algorithm (Alternating Conditional Expectation, Breiman and Friedman, 1985) allowed Cury and Roy (1989) to explore the form of the relationship between recruitment success and environmental indices in several upwelling ecosystems. In the analysis of the relation between recruitment and environmental factors, linear statistical methods are commonly used. Because present knowledge is not sufficient to know a priori the correct form of the relationship, it is desirable to use methods which estimate the appropriate functional form. With ACE, the form of the variables is obtained by plotting the transformed values versus the original values. This approach allowed Cury and Roy (1989) to test the hypothesize that the relationship between recruitment and upwelling intensity is dome-shaped in Ekman-type upwelling, and linear in non Ekman-type upwellings. The statistical method are documented by Cury *et al.* (1995), and thus not described further in this paper.

2. RESULTS

The relationships between SST, WM (or CUI) and recruitment are shown in Figure 1. Large variations of recruitment occur without any apparent link with these environmental parameters. Using the ACE algorithm to analyze the relationship between the environmental parameters and recruitment, only a small proportion of the observed variance in recruitment can be explained. Using SST, WM and CUI for the 1972 to 1991 time period, the explained variance is: 16%, 15% and 23% respectively. When spawning biomass is added to the regression for the period 1974 to 1990, the variance explained becomes 53% with CUI. While the transformation of recruitment is linear, the shape of the transformations for WM and

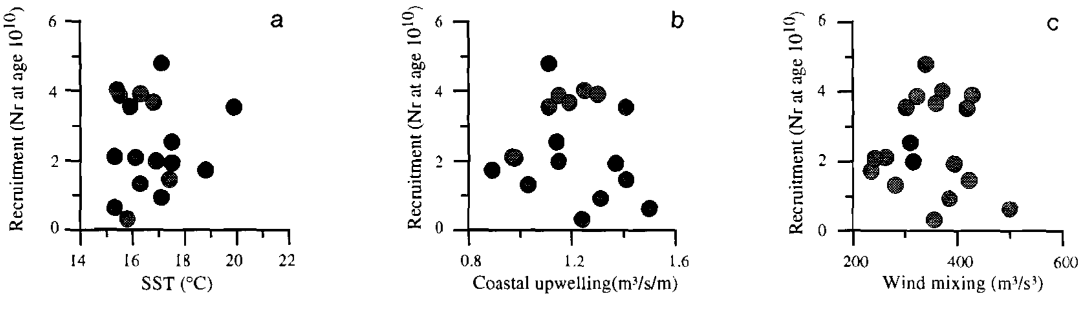

Fig. 1: Recruitment of Chilean sardine at age 2 from 1974 to 1990 vs (a) SST; (b) coastal upwelling index; and (c) wind mixing.

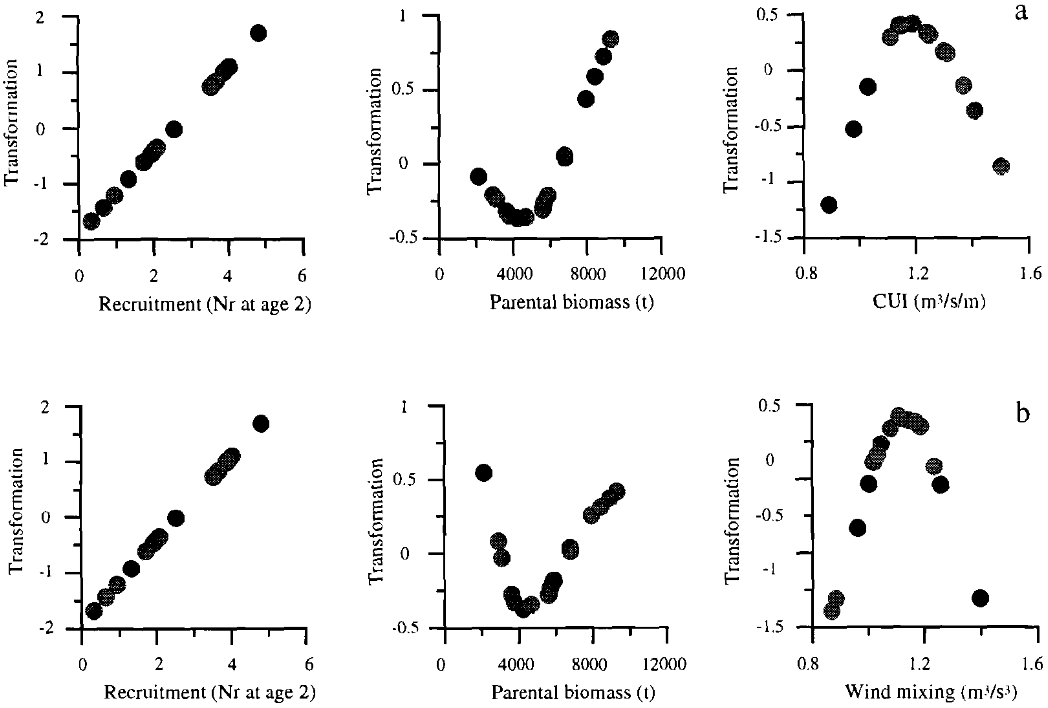

Fig. 2: Transformation from the ACE algorithm considering :
a) sardine recruitment in numbers x 10^{10} at age 2, parental biomass and coastal upwelling index (R^2=0.23);
b) sardine recruitment in numbers, parental biomass and wind mixing (R^2=0.15).

CUI is dome-shaped (Fig. 2), with a maximum of 360 m^3/s^3 for WM and 1.1 $m^3/s/m$ for CUI. There is a V-shaped transformation for parental biomass.

The dominance from anchovy to sardine changed in the late 1960s (Serra, 1983 and 1989; Loeb and Rojas, 1988), and changed again after 1983 when anchovy again became the dominant component in the ecosystem. This last switch can be seen in the spawning stock/recruitment plot (Fig. 3) where a change in the form of the relationships suggests a change in the pelagic ecosystem, which became favorable for anchovy and unfavorable for sardine. A similar dynamics is well documented for the Californian sardine and anchovy (Skud, 1982). In order to evaluate a possible impact of fish dominance on the population, an Ecosystem Factor (EF) was introduced into the analysis; the 'sardine dominated ecosystem' is coded as 1 and the 'anchovy dominated ecosystem' as 2 (Table 1). The results given by the ACE algorithm using EF with WM or CUI, improved the percentage of explained variance to 75% and 71% respectively. The dome-shaped transformations for both WM and CUI remain unchanged (Fig. 4).

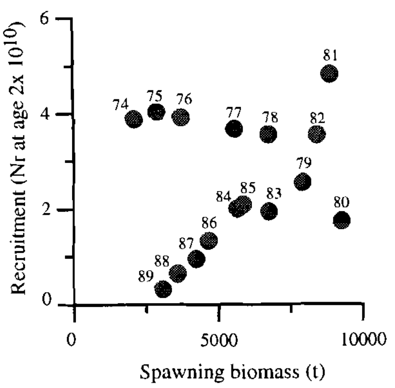

Fig. 3: Sardine spawning stock-recruitment plot. The numbers above the data points correspond to the years at recruitment of age-group 2 fish.

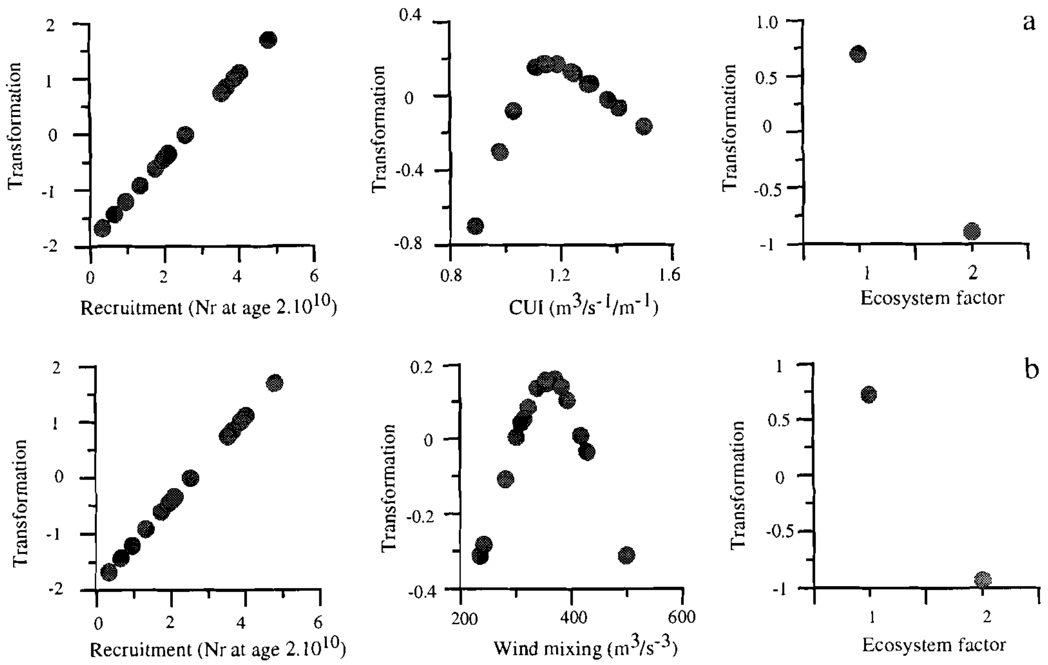

Fig. 4: Transformation from the ACE algorithm considering:
a) recruitment in numbers, Coastal Upwelling Index and the Ecosystem Factor (R^2=0.71)
b) recruitment in numbers, Wind Mixing and the Ecosystem Factor (R^2=0.75).

DISCUSSION

The dome-shaped pattern between recruitment and CUI or WM is consistent with Cury and Roy's (1989) findings and other results obtained in different upwelling systems (Roy *et al.*, 1992; Cury *et al.*, 1995). Following Cury and Roy (op. cit.), the dome-shaped relationship between recruitment and the environment results from the positive effect of upwelling on larval food and the counteracting effect of wind mixing or offshore transport on larval mortality (Lasker, 1975; Peterman and Bradford, 1987, Parrish *et al.*, 1981). However, in this study, CUI and WM are both derived from wind speed observations collected by ships of opportunity. CUI and WM are positively correlated and they give almost identical results. Using these variables, it remains impossible to separate the effect of the upwelling process from the effect of wind mixing on recruitment.

The results obtained with SST are against the general belief that 'warm' environmental conditions favor the abundance of sardines. Recruitment variability appears to be related to the upwelling process, but in a non-linear fashion. The environment is an important contributor to recruitment variability but it is not the only such factor. The switch from a sardine to an anchovy-dominated ecosystem, as it occurred after 1983, appears to be an important contributor to recruitment variability. A consequence of the changes within the biological components of the ecosystem is that different levels of abundance can be reached for a given value of the upwelling intensity depending on the dominant species within the ecosystem, so it does not explain the long term change in abundance of the sardine (Skud, 1982).

REFERENCES CITED

Bakun A. 1990. Global climatic change and intensification of coastal ocean upwelling. *Science*, 247: 198-201.

Breiman L. and J.H. Friedman. 1985. Estimating optimal transformations for multiple regression and correlation. *J. Am. Stat. Assoc.*, 80(391): 580-619.

Cury P. and C. Roy. 1989. Optimal environmental window and pelagic fish recruitment success in upwelling areas. *Can. J. Fish. Aquat. Sci.*, 46: 670-680.

Cury P., C. Roy, R. Mendelssohn, A. Bakun, D.M. Husby and R.H. Parrish. 1995. Moderate is better: exploring nonlinear climatic effect on Californian anchovy. *In*: R.J. Beamish (ed.). Climate and northern fish populations. *Can. Spe. Pub. Fish. Aquat. Sci.*, 121: p 417-424.

Hastie T. and R. Tibshirani. 1990. *Generalized additive models*. Chapman and Hall, London.

Kawasaki, T. 1993. Recovery and collapse of the far eastern sardine. *Fish. Oceanogr.*, 2(3/4): 244-253.

Lasker R. 1975. Field criteria for survival of anchovy larvae: the relation between onshore chlorophyll maximum layers and successful first feeding. *Fish. Bull.*, 73: 453-462.

Lluch-Belda, D., R.J.M. Crawford, T. Kawasaki, A.D. MacCall, R. H. Parrish, R. A. Schwartzlose and P. E. Smith. 1989. Worldwide fluctuations of sardine and anchovy stocks: the regime problem. *S. Afr. J. Mar. Sci.*, 8:195-205.

Lluch-Belda D., R.A. Schwartzlose, R. Serra, R. Parrish, T. Kawasaki, D. Hedgecock and R.J.M. Crawford. 1992. Sardine and anchovy regime fluctuations of abundance in four regions of the world oceans: a workshop report. *Fish. Oceanogr.*, 1(4): 339-347.

Loeb V. and O. Rojas. 1988. Interannual variation of ichthyoplankton composition and abundance off northern Chile, 1963-83. *Fish. Bull.*, 88(1): 1-24.

Mendelssohn R. and P. Cury. 1987. Fluctuations of a fortnightly abundance index of the Ivoirian coastal pelagic species and associated environmental conditions. *Can. J. Fish. Aquat. Sci.*, 44: 408-428.

Parrish R.H., C.S. Nelson and A. Bakun. 1981. Transport mechanism and reproductive success of fishes in the California Current. *Biol. Oceanogr.*, 1(2): 175-203.

Parrish R.H., R. Serra and S. Grant. 1989. The monotypic sardines, *Sardina* and *Sardinops*: their taxonomy, distribution, stock structure and zoogeography. *Can. J. Fish. Aquat. Sci.*, 46: 2019-2036.

Peterman M.R. and M.J. Bradford. 1987. Wind speed and mortality rate of a marine fish, the northern anchovy (*Engraulis mordax*). *Science*, 235: 354-356.

Roy C., P. Cury and S. Kifani. 1992. Pelagic fish recruitment success and reproductive strategy in upwelling areas: environmental compromises. *S. Afr. J. Mar. Sci.*, 12: 135-146.

Serra R. 1983. Changes in the abundance of pelagic resources along the Chilean coast. *FAO Fish. Rep.*, 291 (2): 255-284.

Serra R. 1989. Long-term variability of the Chilean sardine. *In*: T. Kawasaki, S. Tanaka, Y. Toba and A. Taniguchi (eds.). *Long-term variability of pelagic fish populations and their environment*. Pergamon Press, Oxford, 165-172.

Sharp, G. 1993. Fisheries, El Niño-southern oscillation index and upper-ocean temperature records: an eastern Pacific example. *Oceanography*, 6(1):13-22.

Skud, B. 1982. Dominance in fishes: the relation between environment and abundance. *Science*, 216 (9): 144-149.

Pelagic Fish Stocks and Environmental Changes in the South-East Pacific

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ABSTRACT

Anchovy (*Engraulis ringens*) and sardine (*Sardinops sagax*) landings in the north of Chile and in Peru between 1950 and 1993 are analyzed. Abundance variations of both species are expressed as catch per unit effort (CPUE), and compared with VPA (Virtual Population Analysis) estimates. Environmental fluctuations are analyzed through historical series of the Southern Oscillation Index (SOI), sea surface temperatures (SST), and the upwelling and turbulence indices. A global production model is fitted to data from the anchovy fishery of the north of Chile and in Peru from 1957 to 1977. The model explains variations of CPUE as a function of fishing effort and of SST, included as a linear subfunction of carrying capacity (B_∞). A similar model for the sardine fishery is fitted to data from the north of Chile from 1975 to 1992. The latter includes CPUE, fishing effort, and SST as a quadratic subfunction of B_∞ as explanatory variables. It is concluded that both resources were intensively exploited and affected by environmental changes that impacted surplus production. Anchovy develops better in a relatively cold environment; meanwhile sardine shows a clear preference for warm periods, but not as extreme as the El Niño 1982-83.

RÉSUMÉ

Les évolutions des captures d'anchois (*Engraulis ringens*) et de sardine (*Sardinops sagax*) au nord du Chili et au Pérou sont analysées entre 1950 et 1993. Les variations d'abondance des deux espèces sont estimées en utilisant les captures par unité d'effort (CPUE) et comparées avec les estimations des VPA (Analyses Virtuelles des Populations). Les fluctuations environnementales sont analysées à partir des séries historiques de l'indice d'oscillation Sud, de la température de surface (SST), et des indices d'upwelling et de turbulence. Un modèle global est ajusté pour la pêcherie d'anchois au nord du Chili et au Pérou entre 1957 et 1977. Ce modèle explique les variations de CPUE en fonction de l'effort de pêche et de la SST introduite comme une fonction de la capacité biotique (B_∞). Un modèle similaire est appliqué pour la sardine pour le nord du Chili entre 1975 et 1992. Ce dernier inclut la CPUE, l'effort de pêche et la SST en tant que fonction quadratique de B_∞. Il est conclu que ces deux ressources furent intensivement exploitées et affectées par les changements environnementaux qui ont des effets négatifs sur la production. L'anchois se développe mieux dans un environnement relativement froid, tandis que la sardine montre une nette préférence pour des périodes chaudes, cependant qui ne soient pas aussi extrêmes que le El Niño 1982-83.

INTRODUCTION

In the Pacific Ocean, south of the equator and in close relationship with the center of high atmospheric pressures located between 20°-35°S and 90°-110°W, lies the south-east Pacific anticyclonic gyre. The eastern sector of this gyre is the Chile-Peru Current System, a northern extension of the West Wind Drift reaching the south American coast at around 40°S (Bernal and Ahumada, 1985).

Thus, the oceanographic regime of the region is determined by the combined action of: 1) the Humboldt current, carrying cold waters and low salinities from the subantartic region towards the north; 2) coastal upwellings generated by the predominantly south-southwest winds along the coast of Chile (with maxima in the spring-summer season), and south southeast winds in Peru (with maxima in winter); 3) the intrusion of subtropical waters of high temperature and salinity from the north towards the coast; and 4) below the surface, a southward flux of equatorial subsurface water of high salinity and low oxygen content, which plays an important role in the distribution of marine pelagic resources (Robles *et al.*, 1976; Guillén, 1983; Bernal *et al.*, 1983; Parrish *et al.*, 1983; Bernal, 1990).

The region is also affected by the El Niño events, which produces an anomalous warming of surface waters. These events occur at irregular intervals in conjunction with the Southern Oscillation, a large fluctuation of atmospheric pressure between the tropical southeast Pacific and the West Pacific (Wyrtki, 1975; Guillén, 1983; Ramage, 1986; Philander, 1990). The region is also affected by environmental changes associated with cold periods and longer warm periods (Cañon, 1986; Yáñez and Barbieri, 1988; Sharp and McLain, 1993).

This dynamic and variable system is however one of the most productive regions of the world ocean, though with a low diversity of pelagic species. These species however are very abundant and thus support important fisheries: which is particularily the case of anchovy (*Engraulis ringens*) and sardine (*Sardinops sagax*), exploited in Peru (Fig. 1a) and the north of Chile (Fig. 1b).

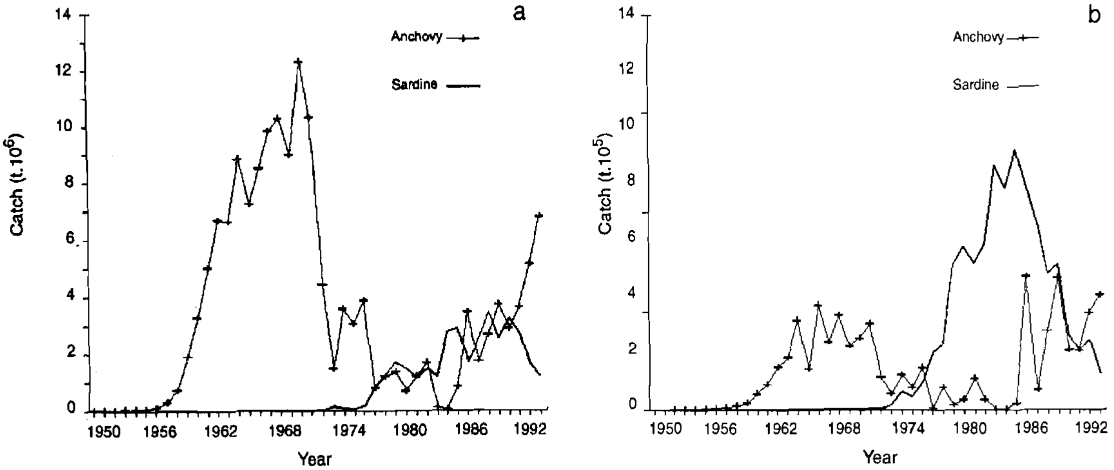


Fig. 1: Catch of major pelagic species in: a) Peru (IMARPE, 1950-94), and b) northern Chile (SAG, 1950-77; SERNAP, 1978-94).

Variability is an inherent feature of these resources. This variability is generally associated with both the intensity of exploitation and changes in environmental conditions (Csirke and Sharp, 1983; Cañon, 1986; Yáñez, 1989). This variability, well analyzed may become a source of information for a better understanding of the dynamics of the above mentioned species (Bernal, 1990).

Quinn *et al.* (1978) estimated that certain features of the Southern Oscillation can be used as precursors of El Niño events. Michelchen (1985) suggested that the interannual variations of coastal upwellings in West Africa are related to the variability of the Southern Oscillation. Binet (1988) discussed the possible role of an intensification of the westerly winds in the distribution changes of pelagic fishes of West Africa. Bakun (1992) suggested that an intensification of the winds causing upwelling may be due to greenhouse effects.

Parrish and MacCall (1978) analyzed the horse mackerel fishery off California, and incorporated oceanographic variables into the stock-recruitment models, thus explaining 75% of total variance. Mendelssohn and Cury (1987) analyzed the catch per unit effort (CPUE) of small pelagic fishes Côte-d'Ivoire (1966-82), as a function of the sea surface temperature (SST) collected by merchant ships, which explained 43% of the variance. Cury and Roy (1989) indicated that there exists an 'optimum environmental window' for the success of the pelagic resources recruitment in upwelling areas. Patterson *et al.* (1993) analyzed the collapse of the horse mackerel in the Eastern Central Pacific. They found that catchability varied with environmental conditions and stock size. Fréon (1988), analyzing the small pelagic fisheries of West Africa, proposed the incorporation of environmental variables in global production models. Later, an interactive software was developed for this purpose (Fréon *et al.*, 1993).

Mendelssohn (1989) fitted an additive non-linear model using the parental biomass and Trujillo's transport in Peru, thus explaining 75% of the variance of recruitment of anchovy in Peru. Muck (1989) analyzed biomass changes, individual growth, dominance of species, feeding strategies and oceanographic parameters off Peru. He concluded that overfishing and high temperatures affected the anchovy which led to increases of sardine, jack mackerel and horse mackerel, among other species. Muck *et al.* (1989) showed that the anchovy's area of distribution is biomass and SST related. Yáñez (1991) showed that the decrease of anchovy CPUE from 1957 to 77 could be explained by fishing effort and SST; whereas the change in the CPUE of sardine from 1973 to 88 was explained by fishing effort and Bakun's upwelling index (1973). Yáñez *et al.* (1994) showed that the distribution of anchovy and sardine in time and space in the north of Chile varied along with intra and interannual changes of SST as measured by NOAA satellites.

This brief review establishes — if needed be — the need to consider environmental variables when assessing the pelagic fish stocks of upwelling systems. Thus, we move on to describe these environmental variables.

1. ENVIRONMENTAL FLUCTUATIONS

Time series of environmental changes are analyzed, these include sea surface temperatures (SST) from 1950 to 1990 off Peru (4°-18°S), from the COADS dataset (Mendelssohn and Roy, this vol.); SST of tidal gauges of Arica (18°28'S) (1951-93), and Antofagasta (23°40'S) (1950-93); magnitude and direction of the wind from the meteorological station of Antofagasta (1950-93), used to obtain an upwelling index (Bakun, 1973) and a turbulence index (Elsberry and Garwood, 1978); and atmospheric pressures of Darwin (12°26'S-130°52'E) and Tahiti (17°33'S-149°20'W) (1950-93), used to estimate the Southern Oscillation index (SOI) (Ropelewski and Jones, 1987). Monthly anomalies were computed for each of the series and smoothed by 13 month centered moving average procedures. The monthly anomalies were also integrated to generate a series of accumulated values, taking into account their monthly signs.

The relationship of the Chile-Peru environmental system with changes of the ocean-atmosphere system is of a global nature. In fact, the SOI shows aperiodical decreasing trends associated to the occurrence of the El Niño events (Fig. 2a); since 1976 negative anomalies prevailed, due to a long term weakening of the South-East Pacific anticyclone (Fig. 2b). It should be noticed that after the 1987 El Niño event, the SOI recovered its positive values, then diminished again when the El Niño of 1992-93 developed.

Associated with such SOI variations, the monthly mean SST off Peru showed positive anomalies during the El Niño events (Fig. 3a); after the 1950-75 period, a clear dominance of positive anomalies settled in at least until 1990 (Fig. 3b). Along the coast of the north of Chile, monthly mean SST also shows the effects of El Niño events: there is a predominance of negative anomalies from 1950 to 1975, followed by a warm period, and a cooling trend in the last period under study (Fig. 4, 5).

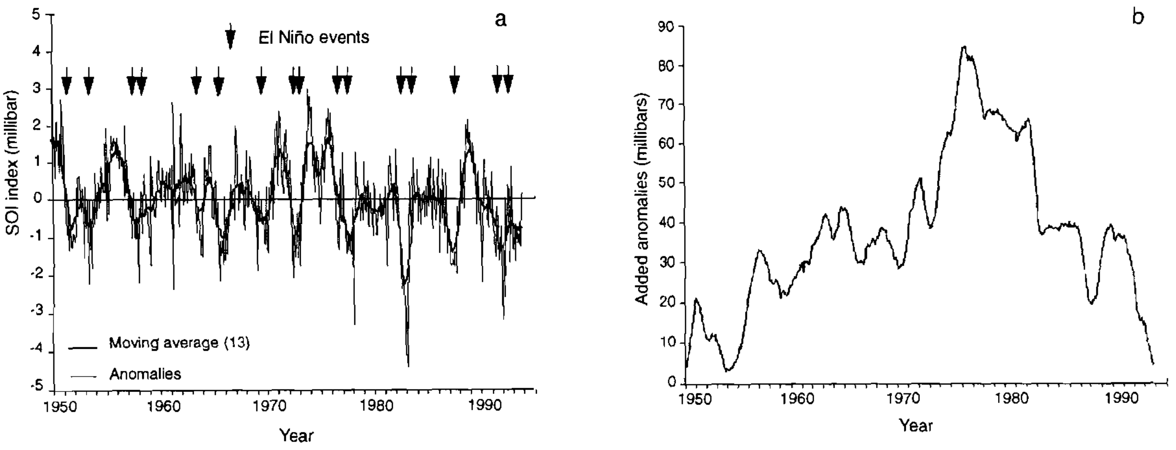


Fig. 2: Monthly mean Southern Oscillation Index (SOI) from 1950 to 1993: a) anomalies, and b) added anomalies.

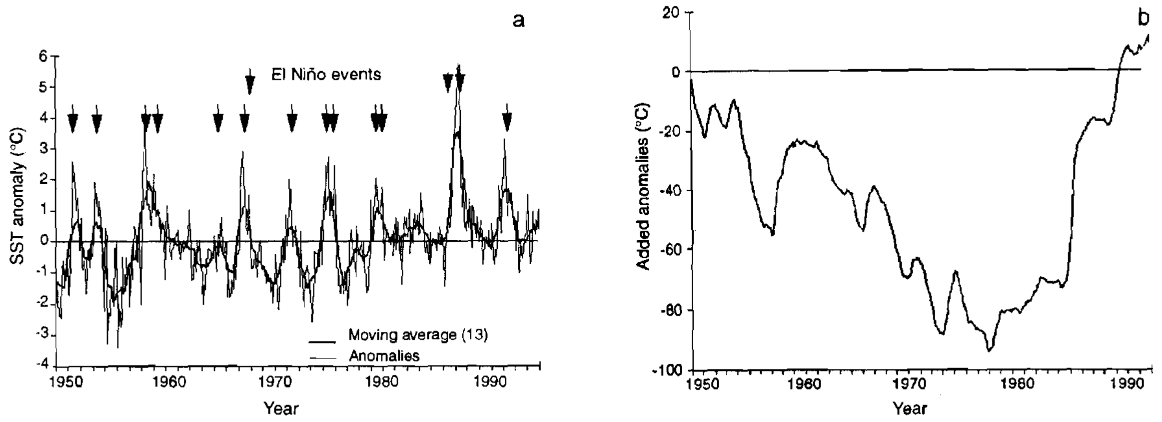


Fig. 3: Monthly mean sea surface temperature off Peru (1950-90): a) anomalies, and b) added anomalies.

The monthly anomalies of the upwelling index at the meteorological station of Antofagasta showed a predominance of negative values from 1950 to 1975; later on, the anomalies became mainly positive, with a tendency to decrease from the mid 1980s (Fig. 6a). The anomalies of the turbulence index follows the same trend, as an effect of the S-SW predominant winds (Fig. 6b). Bakun (1990) showed similar trends for wind stress along the coast of California, the Iberian Peninsula, Morocco and Peru, from 1950 to 86. This author suggests the existence of a mechanism through which the greenhouse effect would strengthen the upwellings by intensifying wind strength along the coast.

Thus, there appear to be a positive relationship between SST trends and the wind indexes. It is likely that the observed warming trend starting in 1976, may have been caused by an invasion of subtropical waters from the north and coastward, associated with the long term weakening of the Pacific anticyclone. The intrusion of these waters would have caused a

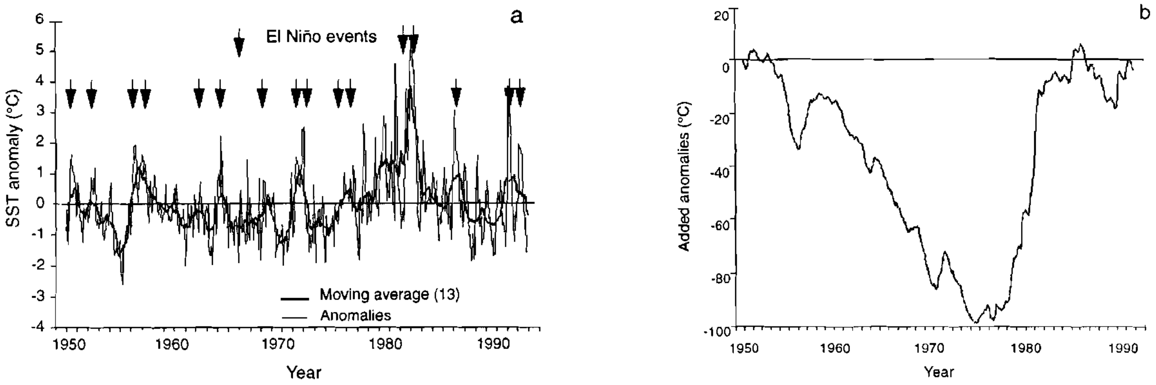


Fig. 4: Monthly mean sea surface temperature at Arica coastal station (1951-93): a) anomalies, and b) added anomalies.

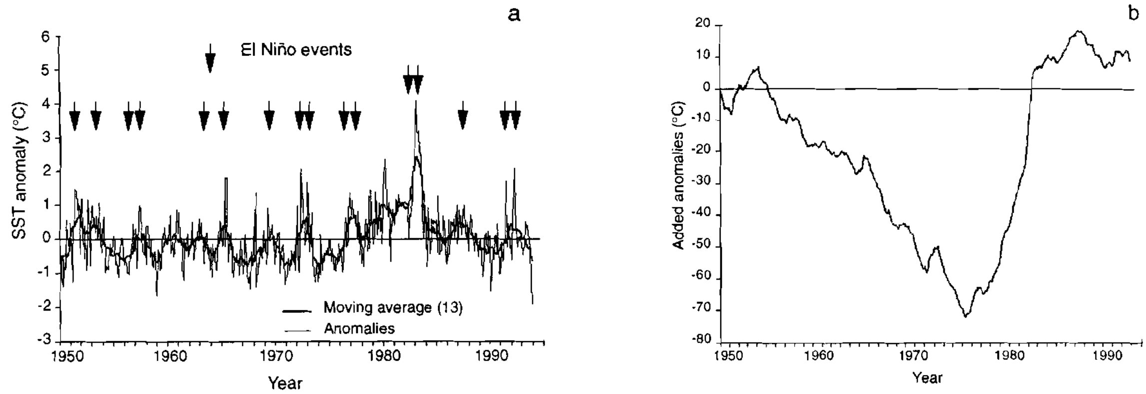


Fig. 5: Monthly mean sea surface temperature at Antofagasta coastal station (1950-93): a) anomalies, and b) added anomalies.

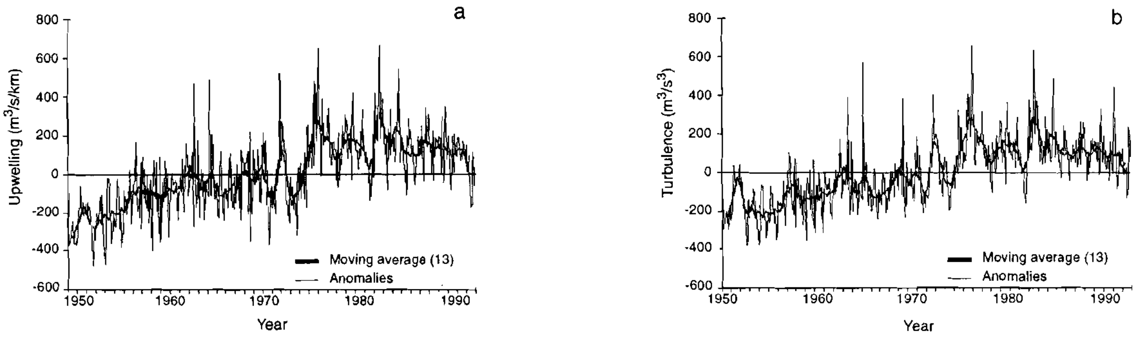


Fig. 6: Monthly mean anomalies at Antofagasta coastal station (1950-93) of: a) upwelling index; b) turbulence index.

deepening of the thermocline; thus, the upwelling would not bring cold waters to the surface, but warm and nutrient-poor waters (Guillén, 1983; Ramage, 1986).

Cañón (1986) indicated that this effect become strongest during the extraordinary strong El Niño event of 1982-83: the subtropical layer of water reached a thickness of 150-200 m, over a large and extensive region.

The seasonal variations of the Pacific convergence zones are influenced by variations in intensity and position of the subtropical anticyclones (Rutllant, 1985). In general, during the Southern Hemisphere winter the Pacific anticyclone is well developed, and the south Pacific convergence reaches its most westerly position, crossing 20°S at 175°W. In summer, it crosses the 20°S at 145°W, and is located to the equator. The interannual variations of the SOI show a behaviour similar to that of the seasonal variation.

It is therefore deduced that the predominance of SOI negative anomalies since 1976 may be associated with a long term eastward displacement of the climatic action centers, in particular areas of pressures. This would explain the increase of winds favourable to upwellings in the north of Chile and in Peru. On the contrary, in the area of Talcahuano (37°S), decrease of SOI is observed after 1975, which may be associated with a period of anticyclonal weakness (Yáñez *et al.*, 1992).

2. PELAGIC FISHERIES AND ENVIRONMENTAL CHANGES

2.1. The anchovy fishery

IMARPE (1970) indicated that the anchovy fishery extends almost along the entire Peruvian coast, and penetrates waters of the northernmost extreme of Chile, without any clear discontinuity to suggest the presence of isolated and independent populations. Thus, for the analysis of the relationships between the catch, the CPUE and the fishing effort (f), a single anchovy population was assumed.

Still, the possibility that several unit stocks existed was not dismissed (Serra, 1983; Pauly and Tsukayama, 1987), including the hypothesis of a great number of local subpopulations (Mathisen, 1989).

In any case, anchovy catches off Peru and in the north of Chile have the same trend (Fig. 1a, b), with fluctuations associated with El Niño events and the environmental changes previously mentioned (Fig. 2 and 6). The largest landing of the northern zone of Chile in the latest years, compared to historical levels, is due to the technological development of the fleet (Caballero *et al.*, 1992). The CPUE estimated here, combining the CPUE of the north of Chile (1957-77) (Yáñez and Barbieri, 1988) and that of Peru (1961-70) (IMARPE, 1972), follows the same trend as the Peruvian anchovy biomass (Fig. 7) estimated by Pauly *et al.* (1987) by means of a length-structured version of VPA, the same method is also used in Mendoza *et al.* (this vol.).

The anchovy catch series used by Yáñez (1991), were here reanalyzed with the CLIMPROD program of Fréon *et al.* (1993). The linear relationship between $CPUE_i$ and the f_i, i.e., contemporary effort (f_i) had a coefficient of determination of R^2 = 79%, increasing to 82% when a weighted fishing effort (fr_i) is recalculated to account for the two age classes which contribute to the catches (Fox, 1975), thus explaining the strong relationship between the decreasing index of abundance and fishing effort which increased from 1957 to 1977.

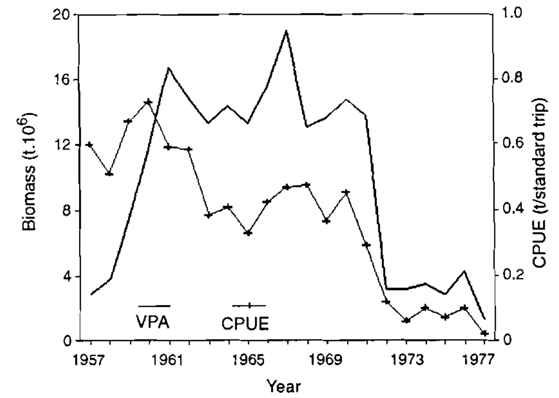


Fig. 7: Anchovy CPUE off southern Peru-northern Chile region, and biomass off northern-Central Peru, estimated by length-structured VPA.

A second explanatory variable was then considered: SST of Arica, in form of the mean of the second semester of year i-1 and the first semester of year i ($SSTA_i$). The fitted model much reduced the differences between the estimated and the observed values (R^2=91%):

$$CPUE_i = 3{,}5727 - 0{,}1609 \,.\, SSTA_i - 1{,}69 \,.\, 10\text{-}8 * fr_i \qquad \text{(see Fig. 8a)}$$

$$C_i = CPUEi \,.\, fr_i \qquad \text{(see Fig. 8b)}$$

This model, similar to the one fitted with $SSTA_i$ data off Peru, does not suffer from multicolinearity problems between the explanatory variables, nor shows trends in its residuals; it was validated by the jackknife method (R^2=87%). The partial correlation coefficients are: -0,95 between the $CPUE_i$ and fr_i; -0,61 between the $CPUE_i$ and $SSTA_i$; and -0,65 between fr_i and $SSTA_i$. The simple linear regression between fr_i and $SSTA_i$ has a R^2=9%.

The anchovy is typically a neritic species (60-80 n. miles off the coast; 50 m depth); it spawns very near the coast, is recruited at 6-9 months and participates significantly in the catches until it reaches 2 years (IMARPE, 1970 and 1972; Serra *et al.*, 1979; Serra, 1983; Santander and Flores, 1983). Bernal *et al.* (1983), and Santander and Flores (1983) showed that anchovy spawning declines during warm years. During warm periods, the upwelling continues but the upwelled waters are warm and low in nutrients, thus resulting in a decreasing abundance of phyto- and zooplankton (Guillén, 1983; Chávez *et al.*, 1989).

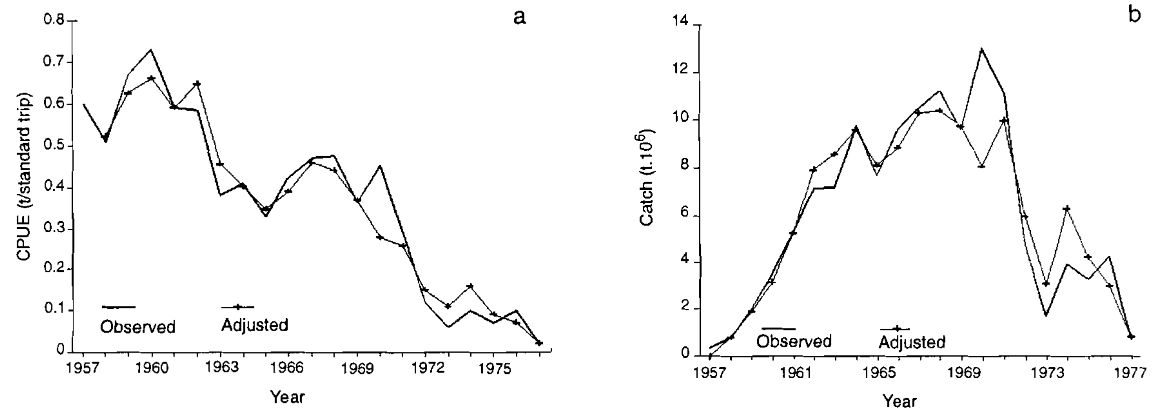


Fig. 8 : Observed and predicted values for anchovy off Peru-northern Chile region of: a) CPUE; b) catches.

Since during El Niño events, the winds that generate the upwelling do not decrease, but intensifies (Romero and Garrido, 1985; Bakun, 1987), the increased turbulence thus generated disperses eggs and larvae, disrupts the spatial distribution of food in patches, and thus affects recruitment (Bakun, 1984). Mendelssohn (1989) showed that a large parental biomass and a moderate level of transport produces the best recruitment. Chavez *et al.* (1989) indicated that, in warm periods, primary production decreases and that changes of plankton composition occur, which affect the survival of anchovy larvae and their recruitment levels. Loeb and Rojas (1988) indicated that starting with the 1972-73 El Niño, there was a succession of years of poor anchovy larval survival off Peru and Chile.

It can therefore be suggested that during the period analyzed (1957-77), the anchovy, while intensively exploited, was also affected by warm periods that modified the production system itselft (Fig. 9). The fitted model considers that the environmental influence impacts the abundance of the resource,notwistanding changes in catchability. Csirke (1989) found that the catchability coefficient (g) is inversely related with the size of the population. He also showed that, after 1972, Peruvian anchovy fluctuations appeared to be constained by a much reduced carrying capacity. Yáñez *et al.* (1994) showed that during warm years, a high degree of concentration of the resource occurs near the coast, also affecting its latitudinal distribution; Santander and Flores (1983) indicated that the same happens to the spawning areas. The long warm period visible since 1976 is thus associated with the increasing abundance of sardines, a predator of anchovy eggs (Santander and Flores, 1983).

It is likely that the noticeable abundance of eggs and larvae observed since 1985 (Loeb and Rojas, 1988; Castillo *et al.*, 1994), as well as the extraordinary increase of catches in recent years (Fig. 1), are related to cooling trend, visible in spite of the El Niño events of 1987 and 1991-92 (Fig. 4 and 5).

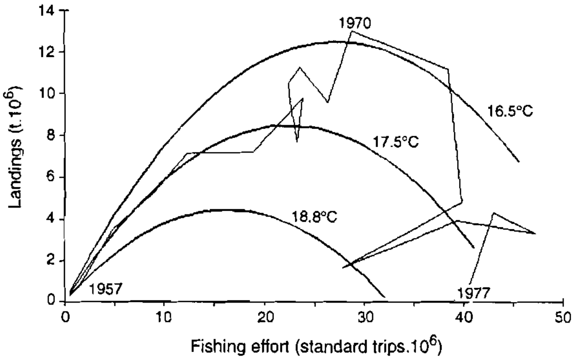


Fig. 9: Relationships between anchovy catches, fishing effort and three levels of SST along the Peru-northern Chile coast.

2.2. The sardine fishery

In the late 1960s the sardine experienced an increase in abundance and expended geographical distribution in the south-east Pacific (Serra and Tsukayama, 1988). This became obvious in the northern zone of Chile after the El Niño event of 1972-73, and even more clearly from 1976 on, (Drago, 1984; Yáñez, 1989; Cubillos and Fuenzalida, 1990).

De Buen (1960) considers that it is the subspecies *Sardinops sagax musica* which inhabits coasts of Chile while *S. sagax sagax* occurs off Peru and around the Galapagos islands. Chirichigno *et al.* (1982) indicated that the latter is limited to the FAO fishing areas 77C (1°39'N and 5°S), 87A (5°-6°S), 87B (6°-18°S) and 87C (18°-37°S); the former occurs only in fishing area 87C (18°-37°S). There is a need to identify with greater precision the distribution limits of both subspecies. There is also the possibility of the existence of two subpopulations, apparent when abundance levels were low. Now, due to their high abundance the two subgroups become mixed over their distribution area (Serra and Tsukayama, 1988).

During the 1964-73 period, the anchovy in Chile had two very well-defined spawning areas, one in the northern zone (18°21'-24°S), the other off Talcahuano (35°-38°S); meanwhile the sardine spawning area was restricted to the first one of these, with a mean density of eggs equal to about 16% of the estimated egg density of anchovy (Serra, 1983; Bernal *et al.*, 1983). Contrary to what happened to the anchovy, during the warm years associated with the El Niño events of 1965, 1969 and 1972-73, sardine showed positive anomalies in its spawning intensity, independently of anchovy's egg abundance (Bernal *et al.*, 1983).

From the standpoint of population dynamics and population genetics, an interesting working hypothesis is to assume that when anchovy dominated the pelagic ecosystem of Chile and Peru, the sardine populations were restricted within two separate refuge zones, one to the north of Chile and the other to the north of Peru, thus effectively limiting genetic drift among the two subpopulations (Bernal *et al.*, 1983).

After the decrease of anchovy (Fig. 7), sardine in Chile increased their area of distribution even establishing a spawning center in the area of Talcahuano (Serra, 1983). This expansion of sardine occurred after the El Niño of 1972-73, reflecting a replacement of the epipelagic dominant filtering fish in the ecosystem (Bernal *et al.*, 1983).

With the El Niño of 1972-73, a large increase in the spawning and larvae distribution of the sardine was observed in Peru, spreading out to the whole coast and concentrating outside 35 n. miles, apparently avoiding the coastal spawning area of the anchovy (Santander and Flores, 1983). From this year until 1982, sardine spawning area expended with until 1979. Moreover, the higher concentrations are getting closer to the coast (10-20 n. miles), close to those of anchovies. Sardine decreased since 1980/82, with slight increases when there is a warming such as that of 1982-83.

Present ichthyoplankton abundance levels of pelagic species in the north of Chile, confirms the persistence of the change in the specific composition detected since 1985, characterized by the strong dominance of the anchovy over the sardine and jack mackerel (Castillo *et al.*, 1994).

In the northern zone of Chile the increase of sardine abundance until 1980-82 (Serra, 1991), and of its catches until 1985 (Fig. 1b), are associated with a long term warm trend (Fig. 4 and 5). This trend period should have favoured the increase of spawning intensity and recruitment levels produced three years later, thus yielding a Ricker (1954) type stock-recruitment relationship and a dome-shaped relationship between recruitment and SST (Yáñez, 1989). An increment of the abundance of 5-8 year old individuals would have then been produced, which are most represented in the catches of the expansion phase of the fisheries (Serra and Tsukayama, 1988; Martinez *et al.*, 1986).

It is also likely that, up to a certain limit, fishing activity would have not affected the growth of stock abundance, due to exploitation rate remaining below the natural rate of increase of the resource (Yáñez, 1991). However, sardine abundances tend to diminish after the El Niño of 1982-83 (Fig. 10), when the environment begins to show a cooling trend (Fig. 4 and 5).

The sardine fishery of the north of Chile for the years was analyzed using the CLIMPROD program. The following variables were considered: annual catches (C_i; t) (Fig. 1b), annual fishing effort (f_i) estimated as standard trips with catch (vcpst) (Yáñez, 1991; Yáñez *et al.*, 1993), and annual mean SST, recorded at the tidal gauge station of Antofagasta (SST_i).

The calculated $CPUE_i$ (t/vcpst), follows almost the same trend as the sardine stock biomass (B_i 3+) estimated by Barría and Serra (1993) by means of VPA (Fig. 10; R^2=91%). A weighted fishing effort (fr_i) was recalculated by considering the significant participation of the 3-4 years classes in the catches. The close relationship between $CPUE_i$ and $SSTP_i$ ((R^2=80%) is established, viz. $CPUE_i = - 5469 + 598\ SSTP_i - 16.22\ (SSTP_i)^2$, where $SSTP_i$ is the mean SST from spawning to recruitment at 3-4 years of age.

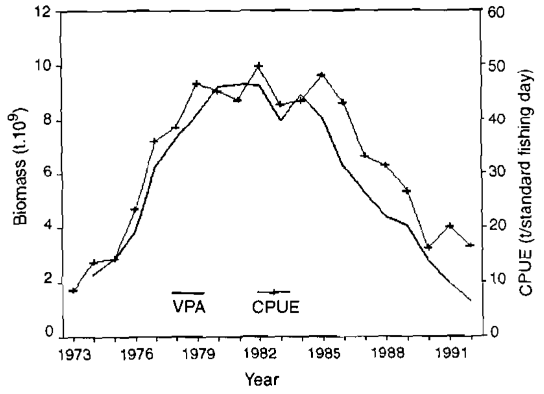


Fig.10: Sardine CPUE and biomass (estimated by VPA) off northern Chile.

By additionally considering the weighted effort (fr_i), the following quadratic lineal model is adjusted (R^2=92%):

$CPUE_i = - 5282 + 570\ SSTP_i - 15.15\ (SSTP_i)^2 - 8.03 \cdot 10^{-4}\ fr_i$ (see Fig. 11a)

$C_i = CPUE_i \cdot fr_i$ (see Fig. 11b)

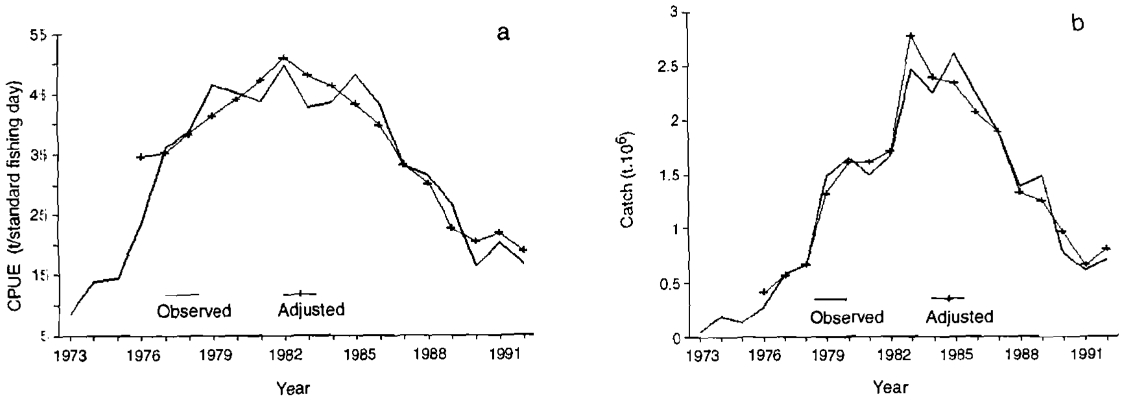


Fig 11: Observed and predicted values for sardine off northern Chile: a) CPUE; b) catch.

It can be thus deduced that environmental changes modify conditions for surplus production by the sardine stock off northern Chile (Fig. 12). Warm conditions would be favourable (as long as they are not as extreme as those observed during the El Niño event of 1982-83), while cold conditions would be unfavourable.

From 1974 to 1983, the 5+ year groups represented on the average 89% of the annual catch (Serra and Tsukayama, 1988). Since 1985, a sustained decrease of the older age groups begins, while individuals of 7 years or more disappeared; at the same time a strong increase in the catches of 2 and 3 year old individuals was observed (Martínez *et al.*, 1993). Thus, the mean age at first capture now roughly corresponds to the first maturity, of 4.2 years (Martínez *et al.*, 1986; Yáñez, 1989).

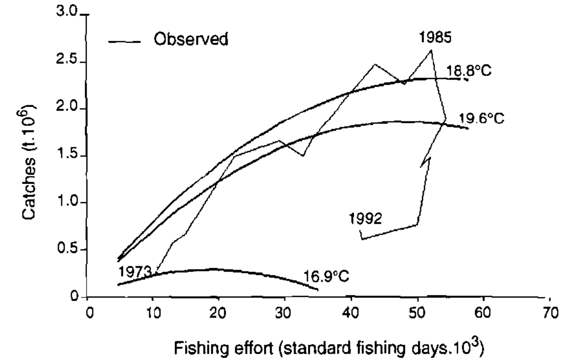


Fig. 12: Relationships between catches, fishing effort and three values of sea surface temperature for sardine off northern Chile.

The parental stock increase led to a density-dependent relationship such as in Ricker (1954). Surprisingly after the successful recruitment of 1984, associated with the maximum parental biomass observed in 1981, recruitment linearly diminishes with the adult stock (Fig. 13). This decrease coincides with the occurrence of the strong El Niño event of 1982-83 and the sub sequent cooling trend of the environment (Fig. 4 and 5). This implies a temperature-dependent relationship, which can be seen observed by relating recruitment to mean SST of years i, i-1 and i-2 (Fig. 14). In this case, the environment affects natural mortality and individual growth during the previous period to recruitment (Fréon, 1988).

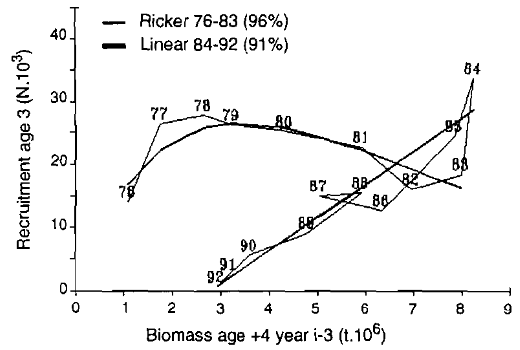


Fig. 13: Stock-recruitment relationships for sardine off northern Chile (%= variance explained by plot).

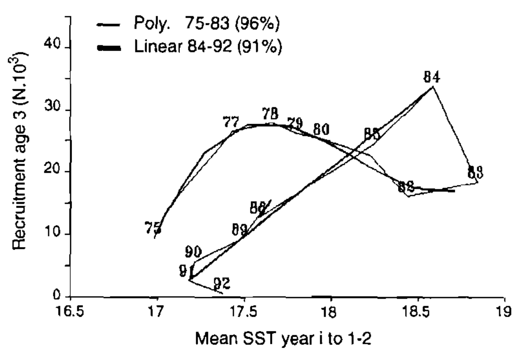


Fig. 14: SST-recruitment relationships for sardine off northern Chile (%= variance explained by plot).

Changes of the thermal structure as observed with the NOAA satellites also affect the sardine distribution in the north of Chile (Yáñez *et al.*, 1993 and 1994). The sardine concentrated near the coast during the warm periods, as happened in 1987-92. During periods such as the 1988-91, with cooler characteristics, sardine spread out in the zone, even over the 200 n. miles off the coast, particularly between 18°-19°S.

CONCLUSION

Anchovy was intensively exploited during the period 1957-77, and also affected by El Niño events, which diminishes its competitor's abundance and catches. Thereafter the fishery did not recover due to a long term warm period and to the increase of predator species such as the jack mackerel, horse-mackerel and of sardine.

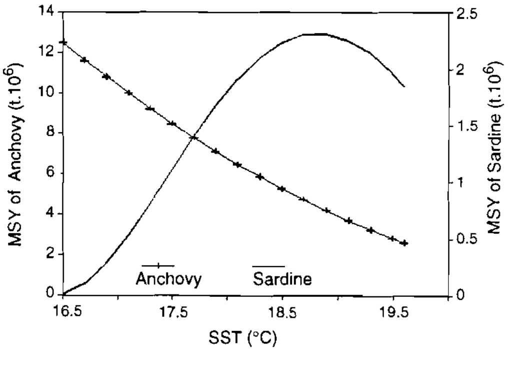
In effect, with a very reduced abundance of anchovy during a significant period of time (1973-85) and favoured by the environmental change observed from the mid 1970s, sardine increased its distribution and abundance, becoming the dominant species in the system. At the same time an intensive exploitation developed which, together with the strong El Niño of 1982-83 and the cooling trend observed later, induced a decrease of sardine abundance. This led to the collapse of the fishery in northern Chile, which decreased from 2.6 million t in 1985 to 0.2 million t in 1994.

Nevertheless, after 1985, anchovy catches increased noticeably, well beyond the historical levels in Chile (1 million t in 1966; 2.7 million t in 1994) (SERNAP, 1994), and approaching such levels in Peru (12 million t in 1970; 10 million t in 1994) (IMARPE, 1994).

For both fisheries, models were fitted considering fishing effort and an environmental variable (SST) as affecting the abundance of these resources. In the case of anchovy, SST appears as additional variable in the adjusted model while for sardine it is a key parameter. However the fits indicated that environmental variations modified the production models of both species (Fig. 9 and 12). Anchovy favours cooler environmental conditions, while the sardine prefer warmer conditions.

Contrary to conventional models, these models generate different MSY level for different environmental settings (Fig. 15).

Fig. 15: MSY as a function of SST for anchovy in Peru and northern Chile, and for sardine in northern Chile.



In spite of their limitations, applications of this type allows a better understanding, and sometimes forecast of the fisheries trends (Fréon and Yáñez, 1995). According to Csirke (1984), fisheries management should be prescriptive and preventive instead of being only reactive. Models including parameters such as SST — whose changes can be predicted — may thus help for fisheries management.

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REFERENCES CITED

Bakun A. 1973. Coastal upwelling indices, west coast of North America, 1946-1971. *U.S. Dept. Commer., NOAA Tech. Rep. NMFS SSRF*, 671, 103 p.

Bakun A. 1984. Report of the working group on Environmental Studies and Monitoring. *FAO Fish. Rep.*, 291 (1): 41-54.

Bakun A. 1987. Monthly variability in the ocean habitat off Perú as deduced from maritime observations, 1953 to 1984. *In*: D. Pauly and I. Tsukayama (eds.). *The Peruvian anchoveta and its upwelling ecosystem: three decades of change*. IMARPE-GTZ-ICLARM: 46-74.

Bakun A. 1990. Global climate change and intensification of coastal ocean upwelling. *Science*, 247: 198-201.

Bakun A. 1992. Global greenhouse effects, multi-decadal wind trends, and potential impacts on coastal pelagic fish populations. *ICES Mar. Sci. Symp.*, 195: 316-325.

Barría P. and R. Serra. 1993. *Estado de situación de la sardina y estimación de la captura total permisible para 1993*. IFOP-Subpesca, Santiago, Chile, 34 p.

Bernal P. 1990. La oceanografía del sistema de corrientes de Chile-Perú en relación a las pesquerías pelágicas: una revisión. *In*: M.A. Barbieri (ed.). *Perspectivas de la actividad pesquera en Chile*. Escuela de Ciencias del Mar, UCV. Valparaíso: 35-48.

Bernal P. and R. Ahumada. 1985. Ambiente oceánico. *In*: F. Soler (ed.). *Medio ambiente en Chile*. E. Universidad Católica de Chile. 57-105.

Bernal P., F. Robles and O. Rojas. 1983. Variabilidad física y biológica en la región meridional del sistema de corrientes Chile-Perú. *FAO Fish. Rep.*, 291 (3): 683-711.

Binet D. 1988. Rôle possible d'une intensification des alizés sur le changement de répartition des sardines et sardinelles le long de la côte ouest-africaine. *Aquat. Living Resour.*, 1: 115-132.

Caballero L., L. Santillán and G. Rosson. 1992. Investigación del esfuerzo pesquero en las pesquerías pelágicas de sardina española (zona norte) y jurel (Talcahuano). *SGI-IFOP/CORFO*, Santiago, Chile, 92/16, 51 p.

Cañón J.R. 1986. Variabilidad ambiental en relación con la pesquería nerítica de la zona norte de Chile. *In*: P. Arana (ed.). *La pesca en Chile*. Escuela de Ciencias del Mar, UCV, Valparaíso. 195-205.

Castillo J., J.L. Blanco, M. Braun, H. Reyes and H. Robotham. 1994. *Evaluación directa del stock de sardina, anchoveta y jurel (regiones I a IV)*. FIP-IFOP, Valparaíso, Chile, 228 p.

Chávez F.P., R.T. Barber and M.P. Sanderson. 1989. The potential primary production of the Peruvian upwelling ecosystem, 1953-1984. *In*: D. Pauly, P. Muck, J. Mendo and I. Tsukayama (eds.). *The Peruvian upwelling ecosystem: dynamics and interactions*. IMARPE-GTZ-ICLARM. 50-63.

Chirichigno N., W. Fisher and C.E. Nauen. 1982. Catálogo de especies marinas de interés económico actual o potencial para America Latina. Parte 2. Pacífico Centro y Suroriental. *FAO/PNUD, Infopesca. SIC*. 82 (2), 588 p.

Csirke J. 1984. Report of the working group on Fisheries Management, Implications and Interactions. *FAO Fish. Rep.*, 291 (1): 67-90.

Csirke J. 1989. Changes in the catchability coefficient in the Peruvian anchoveta *(Engraulis ringens)* fishery. *In*: D. Pauly, P. Muck, J. Mendo and I Tsukayama (eds.). *The Peruvian upwelling ecosystem: dynamics and interactions*. IMARPE-GTZ-ICLARM: 207-219.

Csirke J. and G. Sharp. (eds.) 1983. Reports of the Expert Consultation to Examine Changes in Abundance and Species Composition of Neritic Resources. *FAO Fish. Rep.*, 291 (1): 1-101.

Cubillos L. and R. Fuenzalida. 1990. El período cálido de 1976-1984 y sus efectos en los desembarques de algunos peces de importancia comercial de la zona norte de Chile. *Cienc. y Tec. del Mar*, CONA. 14: 3-19.

Cury P. and C. Roy. 1989. Optimal environmental window and pelagic fish recruitment success in upwelling areas. *Can. J. Fish. Aquat. Sci.*, 46: 670-680.

De Buen F. 1960. La sardina y sardina española (*Sardinops sagax*) en la costa sur de América del Océano Pacífico (Chile, Perú e Islas Galápagos). *FAO Fish. Biol. Synop.*, 13: 265-286.

Drago G. 1984. *Dinámica de los principales stocks pelágicos (Engraulis ringens y Sardinops sagax) explotados en la zona norte de Chile (18°20'-24°S) (1959-82)*. Tesis, Escuela de Ciencias del Mar, UCV, Valparaíso, 81 p.

Elsberry R.L. and R.W. Garwood (Jr.). 1978. Sea-surface temperature anomaly generation in relation to atmospheric storms. *Bull. Amer. Meteorol. Soc.*, 59: 786-789.

Fox W.W. (Jr.). 1975. Fitting the generalized stock production model by least-squares and equilibrium aproximation. *Fish. Bull.*, 73 (1): 23-36.

Fréon P. 1988. Introduction of environmental variables into global production models. *In*: T. Wyatt and M.G. Larrañeta (eds.). *Long-term changes in marine fish populations*. Symp., Vigo, España, 18-21 Nov. 1986: 481-528.

Fréon P., C. Mullon and G. Pichon. 1993. CLIMPROD: Experimental interactive software for choosing and fitting surplus production models including environmental variables. *FAO Comp. Infor. Series (Fisheries)*, 5: 1-76.

Fréon P. and E. Yáñez. 1995. Influencia del medio ambiente en evaluación de stock: una aproximación con modelos de producción. *Invest. Mar.*, Valparaíso, 23: 25-47.

Guillén O. 1983. Condiciones oceanográficas y sus fluctuaciones en el Pacífico Sur oriental. *FAO Fish. Rep.* 291 (3): 607-658.

IMARPE. 1970. Informe del cuadro de expertos sobre dinámica de la población de la anchoveta peruana. *Bol. Inst. Mar Perú*, 2 (6): 324-372.

IMARPE. 1972. Informe de la segunda reunión del panel de expertos en dinámica de la anchoveta peruana. *Bol. Inst. Mar Perú*, 2 (7): 373-458.

IMARPE. 1950-94. *Estadísticas de desembarque de las principales pesquerías nacionales registradas entre 1950 y 1994*. Instituto del Mar del Perú, Oficina de Estadística y Estudios Económicos Pesqueros.

Loeb V.J. and O. Rojas. 1988. Interannual variation of ichthyoplankton composition and abundance relations off northern Chile, 1964-83. *Fish. Bull.*, 86 (1): 1-24.

Martínez C., C. Salazar, J. Mendieta and A. Aranis. 1986. Desarrollo y perspectivas de la pesquería pelágica en el norte de Chile (Arica-Coquimbo). *In*: P. Arana (ed.). *La pesca en Chile*. Escuela de Ciencias del Mar, UCV, Valparaíso: 165-182.

Martínez C., L. Caballero, U. Parker, G. Böhm, J. Oliva, V. Fernández, S. Peña, R. Gili, H. Hidalgo, P. Barría, R. Serra and M. Nilo. 1993. Diagnóstico de las principales pesquerías nacionales: pesquerías pelágicas zona norte (I-IV Región). *SGI-IFOP-CORFO*, 94 (5), 74p.

Mathisen O.A. 1989. Adaptation of the anchoveta (*Engraulis ringens*) to the Peruvian upwelling system. *In*: D. Pauly, P. Muck, J. Mendo and I. Tsukayama (eds.). *The Peruvian upwelling ecosystem: dynamics and interactions*. ICLARM Conf. Proc., 220-234.

Mendelssohn R. 1989. Reanalysis of recruitment estimates of the Peruvian anchoveta in relationship to other population parameters and the surrounding environment. *In*: D. Pauly, P. Muck, J. Mendo and I Tsukayama (eds.). *The Peruvian upwelling ecosystem: dynamics and interactions*. ICLARM Conf. Proc., 364-385.

Mendelssohn R. and P. Cury. 1987. Fluctuations of a fortnightly abundance index of the Ivoirian coastal pelagic species and associated environmental conditions. *Can. J. Fish. Aquat. Sci.*, 44: 408-421.

Michelchen N. 1985. About inter-annual coastal upwelling variations off NW-Africa with reference to changes of Southern Oscillation. In: C. Bass, R. Margalef and P. Rubies (eds.). *Int. Symp. on the most important upwelling areas off western Africa (Cape Blanco and Benguela), Barcelona*. I: 93-100.

Muck P. 1989. Major trends in the pelagic ecosystem off Perú and their implications for management. *In*: D. Pauly, P. Muck, J. Mendo and I Tsukayama (eds.). *The Peruvian upwelling ecosystem: dynamics and interactions*. ICLARM Conf. Proc., 386-403.

Muck P., A. Zafra de Moreno and C. Aranda. 1989. The seasonal dynamics of sea surface temperature and its impact on anchoveta distribution off Perú. *In*: D. Pauly, P. Muck, J. Mendo and I. Tsukayama (eds.). *The Peruvian upwelling ecosystem: dynamics and interactions*. ICLARM Conf. Proc., 31-44.

Parrish R.A. and A.D. MacCall. 1978. Climate variations and exploitation in the Pacific mackerel fishery. *Fish. Bull.*, 167: 1-110.

Parrish R.A., A. Bakun, D.M. Husby and C.S. Nelson. 1983. Comparative climatology of selected environmental processes in relation to eastern boundary current pelagic fish reproduction. *FAO Fish. Rep.*, 291 (3): 731-777.

Patterson K.R., T.J. Pitcher and T.K. Stokes. 1993. A stock collapse in a fluctuating environment: the chub mackerel *Scomber japonicus* (Houttuyn) in the eastern central Pacific. *Fisheries Research*, 18: 199-218.

Pauly D., M.L. Palomares and F.C. Gayanilo. 1987. VPA estimates of monthly population length composition, recruitment, mortality, biomass and related statistic of Peruvian anchoveta, 1953 to 1981. *In*: D. Pauly and I. Tsukayama (eds.). *The Peruvian anchoveta and its upwelling ecosystem: three decades of change*. ICLARM Conf. Proc., 142-166.

Pauly D. and I. Tsukayama. 1987. On the implementation of management-oriented fishery research: the case of the Peruvian anchoveta. *In*: D. Pauly and I. Tsukayama (eds.). *The Peruvian anchoveta and its upwelling ecosystem: three decades of change*. ICLARM Conf. Proc., 1-13.

Philander S.G. 1990. El Niño, La Niña, and the Southern Oscillation. *Inter. Geophysics Ser.*, Academic Press Inc., 46: 1-293.

Quinn W.H., D.O. Zopf, K.S. Short and R.T.W. Kuo Yang. 1978. Historical trends and statistics of the Southern Oscillation, El Niño, and Indonesian droughts. *Fish. Bull.*, 76 (3): 663-678.

Ramage C. 1986. El Niño. *Investigación y Ciencia*, 119: 40-48.

Ricker W.E. 1954. Stock and recruitment. *J. Fish. Res. Bd. Can.*, 11 (5): 559-623.

Robles F., E. Alarcón and A. Ulloa. 1976. Las masas de agua en la región norte de Chile y sus variaciones en un período frío (1967) y en períodos cálidos (1969, 1971-73). *FAO Inf. Pesca*, 185: 94-196.

Romero H. and A.M. Garrido. 1985. Influencias genéticas del fenómeno El Niño sobre los patrones climáticos de Chile. *Invest. Pesq. (Chile)*, 32: 19-35.

Ropelewski C.F. and P.D. Jones. 1987. An extension of the Tahiti-Darwin Southern Oscillation index. *Mon. Weath. Rev.*, 115: 2161-2165.

Rutlland J. 1985. Algunos aspectos de la influencia climática, a nivel mundial y regional, del fenómeno El Niño. *Invest. Pesq. (Chile)*, 32: 9-17.

SAG. 1950-1977. *Anuarios estadísticos de pesca*. División de Pesca y Caza, Servicio Agrícola y Ganadero, Chile.

Santander H. and R. Flores. 1983. Los desoves y distribución larval de cuatro especies pelágicas y sus relaciones con las variaciones del medio ambiente marino frente al Perú. *FAO Inf. Pesca*, 291 (3): 835-867.

Sharp G.D. and D.R. McLain. 1993. Fisheries, El Niño-Southern Oscillation and upper-ocean temperature records: an eastern Pacific example. *Oceanography*, 6 (1): 13-22.

SERNAP. 1978-1994. *Anuarios estadísticos de pesca*. Servicio Nacional de Pesca, Chile.

Serra R. 1983. Changes in the abundance of pelagic resources along the Chilean coast. *FAO Fish. Rep.*, 291 (2): 255-284.

Serra R. 1991. Long-term variability of the Chilean sardine. *In*: T. Kawasaki, S. Tanaka, Y. Toba and A. Taniguchi (eds.). *Long-term variability of pelagic fish populations and their environment*. Pergamon Press: 165-172.

Serra R., M. Aguayo, O. Rojas, F. Inostroza and J.R. Cañón. 1979. Sardina española *Sardinops sagax* musica (De Buen), Teleostomi Clupeiformes Clupeidae. *In*: Estado actual de las principales pesquerías nacionales. Bases para el desarrollo pesquero. Peces. *CORFO-IFOP*. AP, 79 (18), 37p.

Serra R. and I. Tsukayama. 1988. Sinopsis de datos biológicos y pesqueros de sardina *Sardinops sagax* (Jenyns, 1842) en el Pacífico suroriental. *FAO Sinop. Pesca*, 13 (1), 60 p.

Wyrtki K.G. 1975. El Niño: the dynamic response of the equatorial Pacific Ocean atmospheric forcing. *J. Phys. Oceanogr.*, 5 (4), 572 p.

Yáñez E. 1989. Fluctuaciones de los principales recursos pelágicos explotados en la zona norte de Chile y variaciones ambientales asociados. *In*: *Memorias del simposio internacional de los Recursos vivos y las Pesquerias en el Pacifico Sudeste.* Virna del Mar, 9-13 mayo, 1988. Rev. Pacifico Sur (N° Spec.): 509-520.

Yáñez E. 1991. Relationships between environmental changes and fluctuating major pelagic resources exploited in Chile (1950-1988). *In*: T. Kawasaki, S. Tanaka, Y. Toba and A. Taniguchi (eds.). *Long-term variability of pelagic fish populations and their environment.* Pergamon Press: 301-309.

Yáñez E. and M. A. Barbieri. 1988. Principal pelagic resources exploited in northern Chile and their relationship to environmental variations. *In*: T. Wyatt and M.G. Larrañeta (eds.). *Long-term marine fish populations.* Symp., Vigo, España, 18-21 Nov. 1986: 197-219.

Yáñez E., M. A. Barbieri and L. Santillán. 1992. Long-term environmental variability and pelagic fisheries in Talcahuano, Chile. *In*: A.I.L. Payne, K.H. Brink, K.H. Mann and R. Hilborn (eds.). Benguela tropic functioning, *S. Afr. J. Mar. Sci.*, 12: 175-188.

Yáñez E., C. Canales, M.A. Barbieri, A. González and V. Catasti. 1993. Estandarización del esfuerzo de pesca y distribución espacial e interanual de la CPUE de anchoveta y de sardina en la zona norte de Chile entre 1987-1992. *Invest. Mar., Valparaíso*, 21: 111-132.

Yáñez E., M.A. Barbieri, A. González, O. Pizarro, M. Bravo, C. Canales and S. Salinas. 1994. Sea surface thermal structure associated to the pelagic fish resources distribution in northern Chile. *In*: *Remote sensing for marine and coastal environments.* ERIM, Michigan (USA). II: 149-162.

Sardinella aurita Population Dynamics Related to Environmental Parameters in the Southern Caribbean (Venezuela)[1]

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ABSTRACT

In this study the population dynamics of *Sardinella aurita* in eastern Venezuela and its relation to upwelling is analyzed using a surplus-production approach and a length-based, analytical approach, implemented with the CLIMPROD and ELEFAN software, respectively. Due to underexploitation of the stock, the model retained by CLIMPROD was not validated by the jackknife method. Nonetheless, a multiple regression of catch as a function of effort and upwelling index permitted to establish the statistical significance of upwelling. In the later years of the study period, there is an increasing trend in recruitment and exploited biomass, and a decreasing trend in exploited parental biomass. Finally, relationships between catch-effort data, population parameter estimates and upwelling indices are explored by standard statistical techniques and the ACE algorithm.

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RÉSUMÉ

Dans cette étude, la dynamique de population de *Sardinella aurita* dans la partie est du Venezuela et sa relation avec l'upwelling est analysée à partir d'un modèle global de production (utilisant le logiciel CLIMPROD) et une approche analytique utilisant les longueurs (logiciel ELEFAN). A cause de la sous-exploitation du stock, le modèle retenu par CLIMPROD n'est pas validé par le méthode du « jackknife ». Cependant une régression mutiple des captures en fonction de l'effort et d'un indice d'upwelling permet d'établir la signification statistique de l'upwelling. Durant les dernières années de l'étude, il existe une tendance positive dans le recrutement et la biomasse exploitée ainsi qu'une tendance négative dans la biomasse parentale exploitée. Enfin, les relations entre les données de captures et d'efforts de pêche, les estimations des paramètres de population et les indices d'upwelling sont explorées par les analyses statistiques classiques et l'algorithme ACE.

INTRODUCTION

The regional climate in the southeastern Caribbean is determined by the seasonal migrations of the Inter-Tropical Convergence Zone (ITCZ). The dry season, from November to May, occurs when the ITCZ migrates towards the Equator, reaching its southernmost position during February and March. The rainy season is determined by the northwards migration of the ITCZ, which reaches its northernmost position during the months of July through September. Correspondingly, in a yearly cycle, the temporal variations in wind speed provide a well defined seasonal signal. During the dry season, from January through May, the northeast trade winds are dominant. During this season, average wind speed is above 4 $m.s^{-1}$ and attains maximum average values of about 5 $m.s^{-1}$ in March. From June through December, average monthly values are below 4 $m.s^{-1}$ and minima under 3 $m.s^{-1}$ are observed in September (Aparicio, 1986).

The Northeastern Venezuela shelf is the site of the most important fishing grounds in the Caribbean Sea. This shelf is oriented East-West along the southeastern boundary of the Caribbean Sea (Fig. 1). The study area covers approximately 240 miles in the East-West axis and reaches a maximum of 60 miles in the North-South axis. Shelf topography is rather complex with numerous islands (Margarita, Coche, Cubagua, Los Testigos, La Tortuga, etc.), embayments (the Gulf of Cariaco and Gulf of Santa Fe, among others), capes (Tres Puntas, Chacopata, Puerto Santo, etc.), submarine valleys (Araya and Carupano), offshore banks (Cumberland) and, especially, the largely anoxic Cariaco Basin, located within the shelf and reaching depths of around 1 400m. The trade wind regime, shelf topography and coastline orientation favor the occurrence of upwelling events during the dry season (Herrera and Febres, 1975).

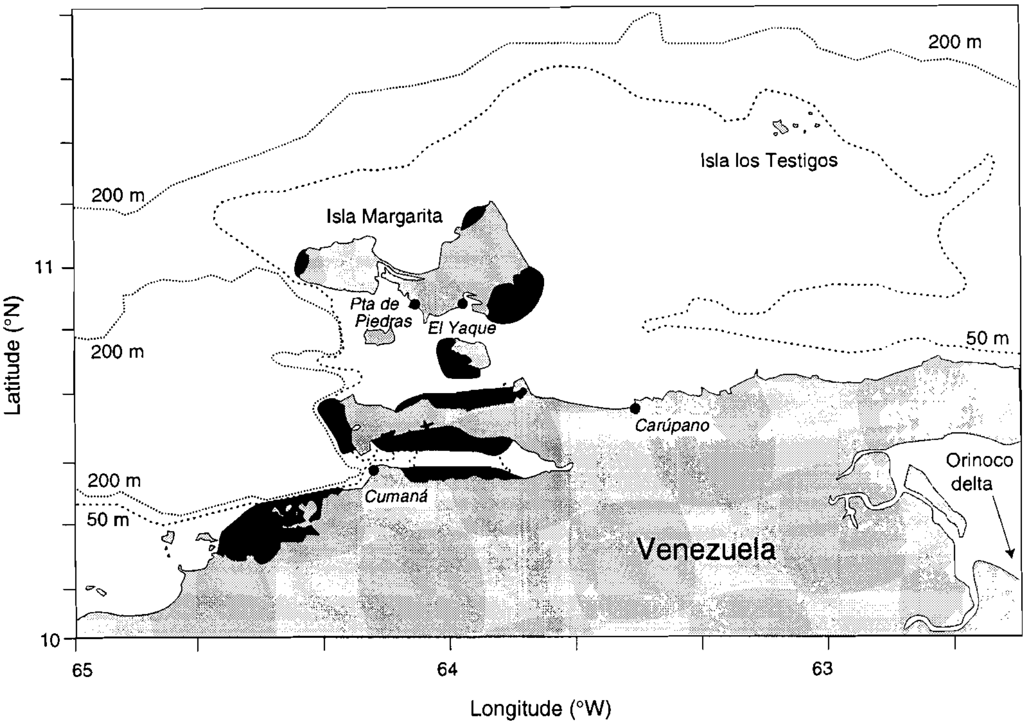


Fig. 1: The northeastern Venezuela shelf.

Another important feature of the study area is the relatively high input of low salinity water from river discharge. The Orinoco River has an estimated annual discharge of 36 000 $m^3.s^{-1}$ (Monente, 1990) with maximum output during August and September. Recent analysis of satellite data (Muller-Karger *et al.*, 1989) indicates that, during the rainy season, the influence of Amazon River water in the Caribbean is less important than that of the Orinoco.

The combined effect of wind-induced coastal upwelling in the dry season and river runoff in the rainy season generate relatively high levels of biological productivity. Primary production estimates are highly variable in space and time. Maximum values over 3 $gC.m^2.day^{-1}$ have been recorded in coastal upwelling areas and minimum values around 200 $mgC.m^2.day^{-1}$ have been measured offshore of main upwelling sources (Varela *et al.*, in prep.). Mendoza (1993) estimated that total annual primary production on the northeastern Venezuela shelf averaged 3 300 t km^{-2} (wet weight).

Sardinella aurita represents the most important finfish biomass on the northeastern Venezuela shelf. The main area occupied by this population is apparently limited to the east by the low salinity Orinoco waters and to the west by reduced upwelling and the narrow shelf west of Tortuga Island.

The fishery for *S. aurita* in this region started in the 1930s and is still strictly artisanal and labor-intensive, using small boats and seines known locally as 'peñeros' and 'chinchorros', respectively. The nature of the fishery limits fishing operations to a narrow band which rarely exceeds 5 nautical miles, covering a small area relative to known stock distribution. Most of the catch is canned; however small amounts are iced for direct human consumption and as bait for pelagic and demersal fisheries. After a period of increase, total estimated catch (Fig. 2) remained relatively stable around 40 000 t between 1964 and 1974, followed by a period of strong fluctuations up to 1983. Total catch has increased significantly in recent years to a level of around 60 000 t (Anon., 1990).

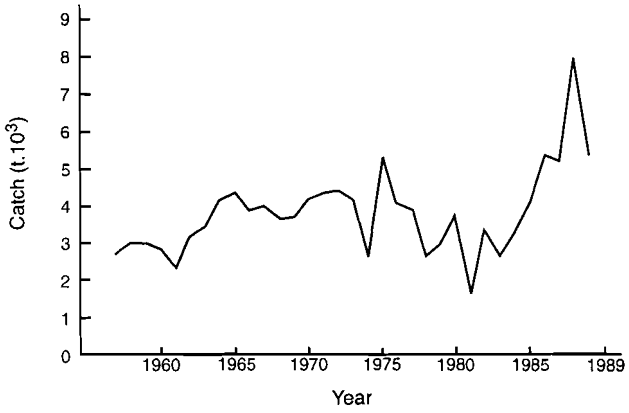


Fig. 2: Total catch of *Sardinella aurita* in eastern Venezuela, 1957-1989.

In this paper we analyze existing data on catch, effort, CPUE, length frequencies and environmental variables in order to study exploitation, population parameters and interactions between the resource and its environment.

1. MATERIAL AND METHODS

1.1. Environmental series

Sea surface temperature recorded at tidal gauges along the northeastern Venezuela coast lack adequate spatial and temporal coverage. The same situation occurs for wind data obtained at sea from ships of opportunity. Therefore, monthly mean values of wind speed and direction from coastal meteorological stations in the area are used as basic data for generating upwelling indices.

Four coastal meteorological stations are located within the study area: Cumaná (time series: 1969-1990) and Carúpano (1979-1989) on the mainland, and El Yaque (1976-1989) and Punta de Piedras (1973-1989 for wind speed and 1975-1989 for wind direction) in Margarita Island. However, considering the short series recorded at Carúpano, this station was not used for further analyses.

Two upwelling indexes were calculated using the above data :

1) A coastal upwelling index (CUE1) computed from wind stress (Bakun, 1973) and expressed as offshore Ekman transport in $m^3.s^{-1}$ per 100 m of coastline; and
2) An upwelling index (CUE2) based on mean yearly integrated wind speed values above 3.5 $m.s^{-1}$ at Cumaná and 4.8 $m.s^{-1}$ at Punta de Piedras (data from the nearby station of El Yaque were not available at the time of the study). Due to seasonality in the data series, each year i extended from November in the year i-1 to October of year i. This index was calculated to account for the complex topography of the area, which may generate upwelling events even when wind direction is not oriented along the East-West axis (Senior, in prep.).

1.2. Catch and effort analysis

Catch and effort data were obtained from industry reports to the Ministry of Agriculture and Husbandry (MAC). The only available fishing effort unit is the number of successful sets. Therefore CPUE is expressed in t per successful set.

These data and the environmental series were analyzed using the CLIMPROD expert system (Fréon *et al.*, 1993) and the ACE (Alternating Conditional Expectation) algorithm (Breiman and Friedman, 1985) in its latest version, which allows to force a monotonic transformation of the dependent variable. The contribution of each independent variable to total explained variance is estimated according to the range of its transformed values. As far as possible, the limitations of the algorithm for a short data series were taken into account by applying a jackknife-like approach (Fréon *et al.*, 1992).

The CLIMPROD expert system permits to select a surplus production model including the effect of an environmental variable. Due to the low number of annual observations (17) and the absence of independence between CPUE and effort or between catch and effort, the coefficient of determination is always high (between 78% and 95%) and hence its absolute value was not taken into account.

1.3. Analysis of length-frequency data

The data base consists of monthly catch and length frequency data extending for the period 1967-1989, which have been collected by personnel of MAC. However, due to variability in data, quality estimates of fishing mortality are based essentially on information for the period 1976-1989 and growth, recruitment and biomass estimates on data for the period 1967-1989. The Compleat ELEFAN software package (Gayanilo *et al.*, 1989) was used for parameter estimates:

- Growth parameters from the von Bertalanffy equation were obtained through modal progression analysis. Length frequency distribution decomposition was carried out using Battacharya's (1967) method. Estimates of L_∞ and K were initially obtained using the Gulland and Holt (1959) plot. Finally, the ELEFAN I method was used in order to improve these preliminary estimates;
- Pauly's (1980) empirical relation allowed to obtain an approximate value of natural mortality (M). Following Pauly's (op. cit.) suggestion concerning schooling pelagic fish, the estimates were corrected using a factor of 0.8;
- Biomass and fishing mortality were obtained from a virtual population analysis (VPA) for unequal time intervals as developed by J.G. Pope (see Pauly and Tsukayama, 1983), and implemented in the Compleat ELEFAN.

Monthly length-frequency and catch data were used in this application of the model. 'Cohorts' are obtained from monthly growth curves which 'cut' through the length frequency distributions. In this analysis, a unique non-seasonal growth curve obtained from the average values for the period 1976-1989 was used. In all cases a moderate level of terminal fishing mortality (Exploitation rate, $E = F/(F+M)=0.33$, with $F = 0.7$ and $M = 1.4$ year^{-1}) was assumed, based on auxiliary information (acoustic and associated trawling surveys). The transformation of length data into weight was based on the relationship established by González (1985). The estimates of parental biomass were obtained assuming knife-edge maturation at L_m=19.5 cm (Fréon *et al.*, in press).

Finally, bivariate and multiple relationships between exploitation, population parameters and environmental series were explored by standard statistical methods and the ACE algorithm.

2. RESULTS

2.1. Environmental series

Figs. 3a and 3b show the time series of monthly anomalies of CUE1 for the coastal meteorological stations of Cumaná and El Yaque, respectively. Both series reflect the strong seasonal component of trade wind intensity with maxima during March-April and minima during September-October. In the series generated from the Cumaná meteorological station, a strong negative anomaly is observed during a 16 month period from April 1971 to July 1972. A long term trend of decreasing CUE1 can also be seen in the Cumaná series. The series generated from the El Yaque meteorological station shows a protracted negative anomaly from mid 1980 to the end of 1982. The long-term decreasing trend is also present, but is not as evident as in the Cumaná series.

The yearly CUE2 series (Fig. 4) presents a decreasing trend during the study period, which mainly reflects the trend observed in the Cumaná CUE1 series. A marked negative anomaly is observed in the year 1981, corresponding to the observed anomaly in the CUE1 series for the El Yaque meteorological station. The 1971-1972 anomalies observed in CUE1 from Cumaná is not reflected in CUE2 because its is only due to a change in wind direction.

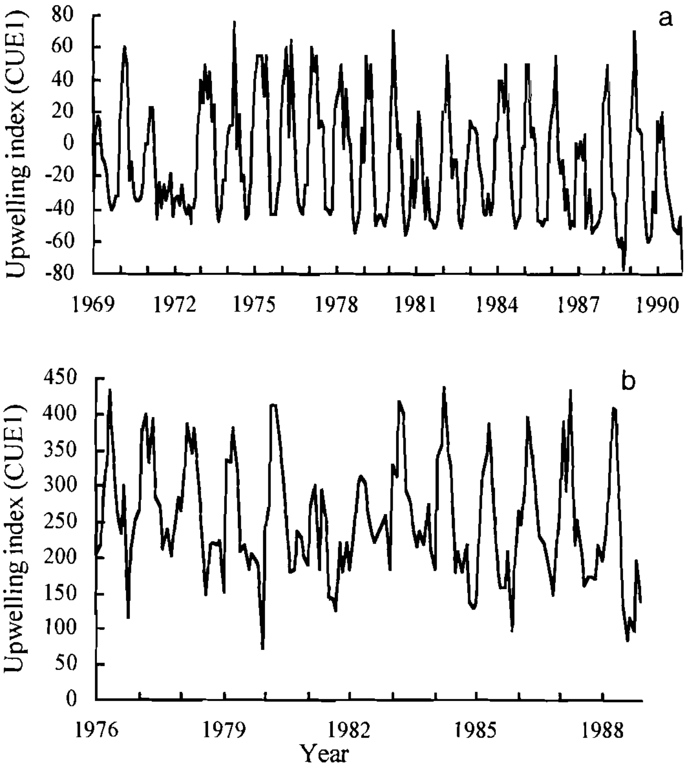


Fig. 3: Upwelling indices
(a) CUE1 time series (Ekman transport in m^3 per 100 m of coastline) estimated from Cumaná meteorological station data;
(b) CUE1 time series estimated from El Yaque meteorological station data.

Fig. 4: CUE2 time yearly time series (average integrated wind speed above 3.5 $m.s^{-1}$ at Cumaná meteorological station and 4.8 $m.s^{-1}$ at El Yaque meteorological station).

2.2. Surplus production approach

In the application of the CLIMPROD expert system, we have used catch per set as an index of abundance, and assumed that the number of exploited age classes as three, that recruitment occurs before the end of the first year and that upwelling influences the stock over a 4-year period (from maturity at year 0 and on to the exploited classes the three following years). We also considered that its influence acts simultaneously on catchability and abundance.

The four variables used in model adjustments (catch, effort, CPUE or CUE2) show a distribution that is not far from normal, except for CPUE, which presents an asymmetrical distribution (Fig. 5). The relationship between CPUE and effort appears linear or at least monotone (Fig. 6a). The model selected by CLIMPROD combined a conventional exponential surplus production model with an exponential effect of the environment:

$$CPUE = aV^b \exp (c V^b E)$$

where V represents the upwelling index averaged over four years and E represents fishing effort weighted over three fishing years. Fits were made both with CUE1 and CUE2, providing slightly better results for the first index. This was mainly due to the lack of response of the stock to the 1971-1972 Ekman transport anomaly. Moreover, the CUE2 series is longer. Therefore, in the rest of the paper we only present results obtained with the latter index, especially since we determined that differences were negligible compared to those obtained with CUE1. The R^2 coefficient was equal to 65% but was not validated by the jackknife method. The non-biased R^2 estimate was equal to 43%, and all regression coefficients, except c, were significantly different from zero, which suggests that fishing effort has no major effect on CPUE as opposed to the upwelling index (Fig. 6b).

The ACE algorithm applied to the variables Log $CPUE_i$ (dependent variable year i), E_i and V_i (independent variables year i) shows positive linear transformations for $CPUE_i$ and V_i and negative non-linear for E_i, which approaches a function of the type $1/E_i$ (Fig. 7). The form $1/E_i$ may imply a total independence between catch and effort ($C/E = f(1/E)$) or that the relation is not parabolic, but linear with an origin different from zero. To verify this, the algorithm was applied to the dependent variable C_i (catches year i) and E_i and V_i as independent variables (Fig. 8). In this case, all transformations are positive and linear, with an R^2 value of 95% and a strong contribution of E_i. Finally, an exploratory analysis of the relation between C_i and lagged values of E and V (results not presented) shows that the major effects of environmental variables on catch occurs without lags.

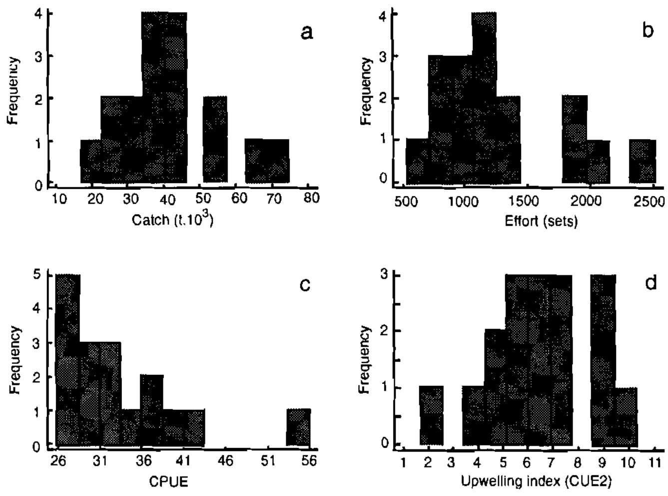


Fig. 5: Univariate distributions of a) Catch; b) Effort; c) CPUE; and d) CUE2.

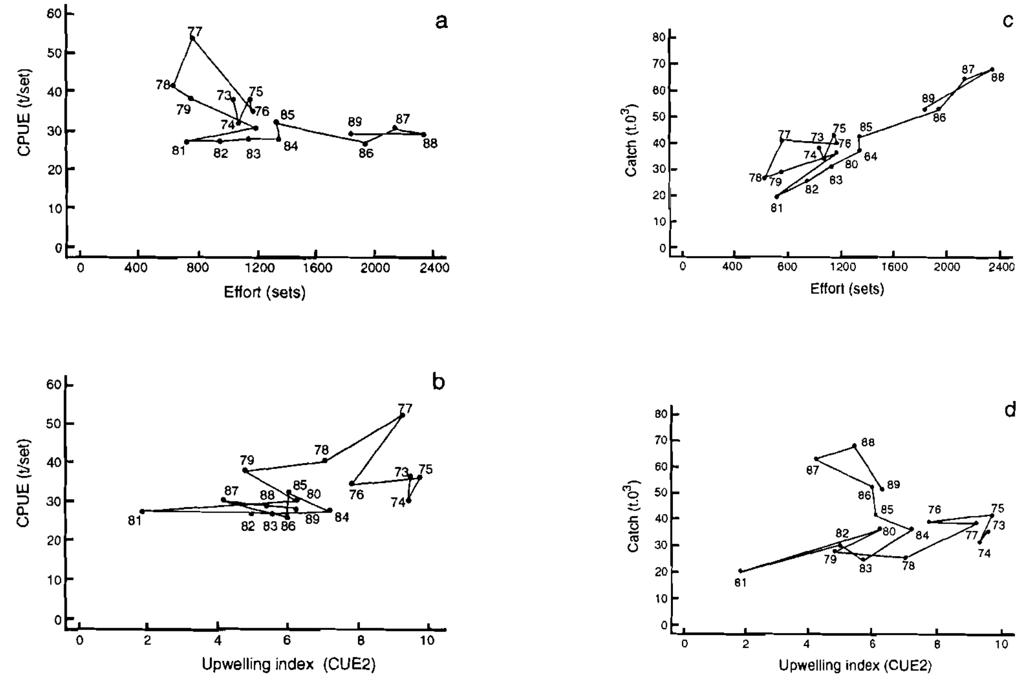


Fig. 6: Bivariate relations between: a) CPUE and effort; b) CPUE and CUE2; c) Catch and effort; and d) Catch and CUE2.

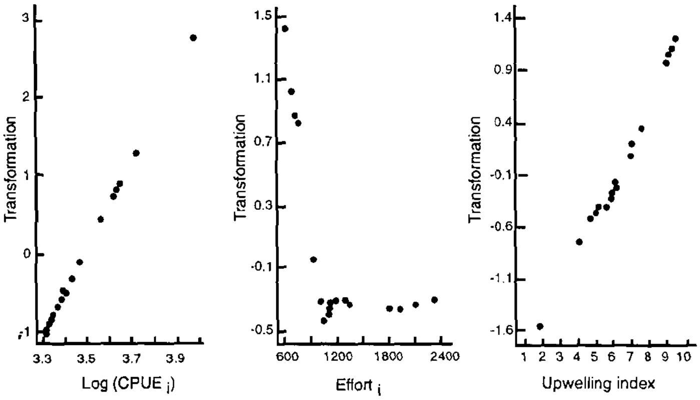


Fig. 7: Optimal unlagged transformations obtained by ACE for Log CPUE (dependent variable), fishing effort and CUE2 (independent variables).

In view of these results, instead of a surplus production model, we estimated a multiple linear regression of the form:

$$C_i = a + bE_i + cV_i$$

The coefficient of determination of this regression was 90% and all regression coefficients were significantly different from zero ($P<0.05$). Several statistical tests indicate that the regression is valid (ANOVA, residual analysis; see Fig. 9). However, this regression is not a model and it cannot be used for stock assessment, nor for predictions outside the observed range of E and V.

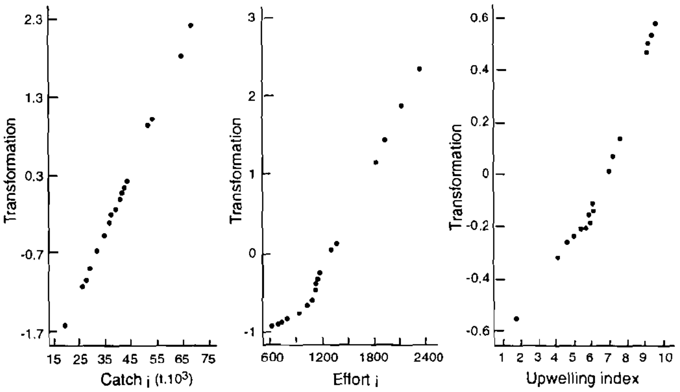


Fig. 8: Optimal unlagged transformations obtained by ACE for catch (dependent variable), fishing effort and CUE2 (independent variables).

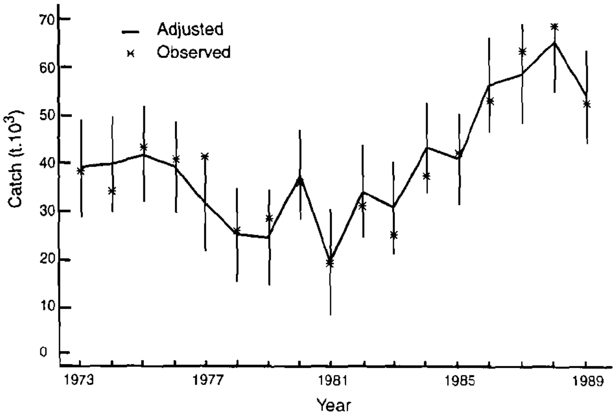


Fig. 9: Temporal series of catch observed and adjusted by a multiple regression using fishing effort and CUE2 as independent variables; vertical bars represent 95% confidence intervals of predicted values.

2.3. Analytical approach

Table 1 shows the growth parameter estimates (L_∞, K and Ø') for the study period. The yearly values correspond to average growth observed for the different cohorts present in any year. The average values for the study period were L_∞ = 266 mm total length and K = 1.26 year^{-1}. This average growth curve is depicted in Figure 10.

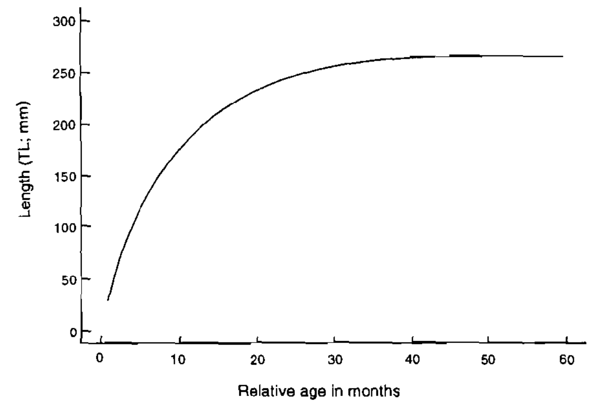


Fig. 10: Average *Sardinella aurita* growth curve for 1967 to 1989, based on L_∞ = 266 mm (TL) and K = 1.26 year^{-1}.

Year	1967	1968	1971	1972	1973	1975	1976	1977	1978	1979	1981	1982	1983	1984	1985	1986	1987	1988	1989	Mean
L_∞ (TL;mm)	240	243	275	273	266	285	262	274	240	278	238	290	252	285	288	266	260	272	260	266
K (year^{-1})	1.05	1.29	1.20	1.50	1.40	1.75	1.45	1.02	1.40	1.04	1.04	1.25	1.20	1.10	1.10	1.35	1.40	1.68	1.10	1.26
Ø*	4.78	4.88	4.96	5.05	5.00	5.15	5.00	4.88	4.91	4.90	4.77	5.02	4.88	4.95	4.96	4.98	4.98	5.09	4.87	4.94

* Values of Ø' were calculated from Ø' = log K + 2 * log L_∞ (Munro and Pauly, 1983).

Table 1: Growth parameter estimates for *Sardinella aurita* from eastern Venezuela (1967-1989).

Figure 11 presents the time series of number of 100 mm recruits into the fishing area during the period 1976-1988. In a general way, we may observe relatively low values, between 40 million and less than 200 million individuals (which correspond to 400 and 2000 t respectively) with a decreasing tendency between 1976 and 1982. This trend is reversed in the following years, until maximum values (around 700 million individuals) are observed at the end of the series. The analysis of the seasonal signal (results not presented) shows that between 1976 and 1983, higher recruitments occur from October to February and between 1984 and 1988 maximum values are observed from June to October.

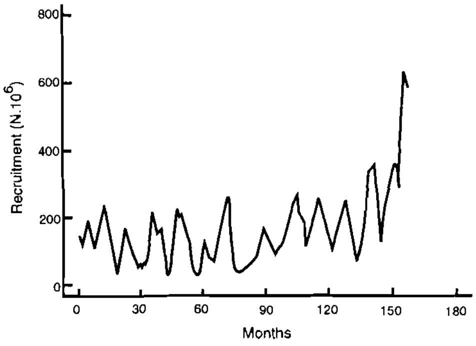


Fig. 11: Time series (1976-1988) of recruitment estimates of *Sardinella aurita* in eastern Venezuela, in millions of 100 mm individuals.

Figure 12 presents the time series of total exploited biomass, parental exploited biomass and catches for the period 1976-1988. As may be expected, the trend in biomass is similar to that of recruitment (Fig. 11). Exploited biomass maximum values (around 60 000 t) are observed at the end of the study period. Parental biomass estimates present minimum values during the period 1978-1980 and a marked decreasing trend in the years following the peak period (about 34 000 t in 1985). The catch series permits to infer that the exploitation ratio was relatively high during the years 1976-1980. However the increase in total biomass, which after 1986 was composed mainly of juveniles, has reduced the impact of exploitation. This effect may be observed in Figure 13, which shows the general decreasing trend of fishing mortality maxima over time.

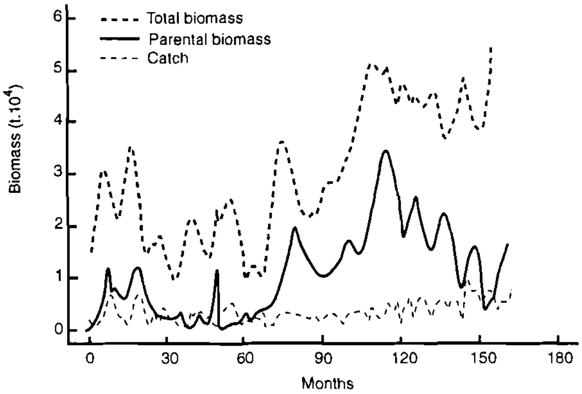


Fig. 12: Time series (1976-1988) of exploited biomass, exploited parental biomass and total catch.

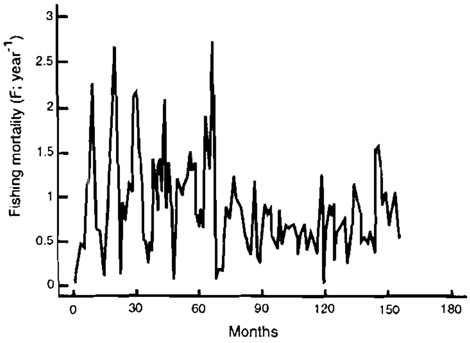


Fig. 13: Time series (1976-1988) of fishing mortality (F) estimates for *Sardinella aurita* in eastern Venezuela.

2.4. Exploratory data analysis of interactions between resource and environment

As a first approach, we attempted to establish relationships between variables used in the surplus production approach and estimates obtained through the analytical approach (i.e., VPA). There was no apparent relationship between average annual CPUE and yearly exploited biomass estimates or between fishing mortality estimates and fishing effort in number of sets. As might be expected, given the structure of VPA, there is a positive relationship between catches and exploited biomass. However, the relationship between exploited biomass and fishing effort is much closer (Fig. 14). A stepwise multiple regression of catch as a function of biomass and effort did not retain biomass as a significant explanatory variable ($F=0.23$; $df=12$) due to colinearity between effort and exploited biomass. Furthermore, there is a clear negative exponential relation, as expected on theoretical grounds, between catchability ($q = F/f$) and exploited biomass ($R^2=0.34$, $P<0.001$, $n=156$ months; Fig. 15).

As a second approach we searched for relationships between population estimates obtained from length frequency analysis and environmental variables. The growth performance index (Ø') is positively correlated with catch (Fig. 16), effort and, to a lesser degree, CUE2. A multiple regression of catch as a function of effort and growth index explains 79% of sample variance and both independent variables are highly significant ($P<0.01$). However, a stepwise multiple regression

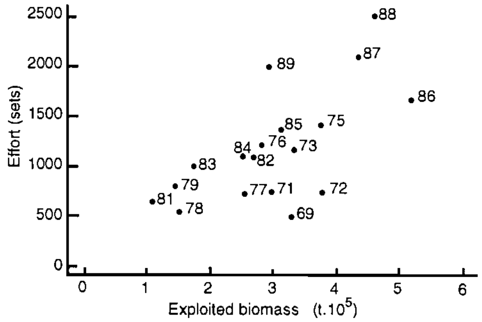


Fig. 14: Relation between fishing effort and exploited biomass of *Sardinella aurita* off eastern Venezuela.

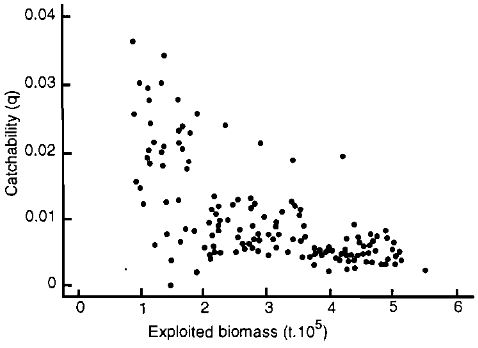
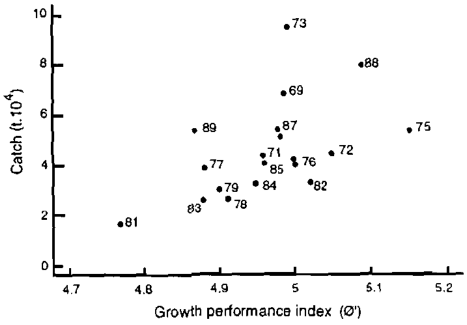


Fig. 15: Relation between catchability and exploited biomass of *Sardinella aurita* off eastern Venezuela.

in which catch is explained by the three above mentioned variables (effort, CUE2 and Ø') fails to incorporate the growth coefficient as a significant component (F= 0.024). This effect is probably due to colinearity between effort and growth performance index.

Fig. 16: Relationship between growth performance index and catch.



The ACE algorithm (Breiman and Friedman, 1985) and multiple regression were used to further explore relationships between recruitment in year i, parental biomass (years i and i-1) and environmental conditions during years i and i-1 (i.e., $CUE2_i$ and $CUE2_{i-1}$). This first pass permitted to establish that most of the explained variance of recruitment in year i (R^2= 0.78) was associated with the year i for parental biomass (PB_i) and $CUE2_{i-1}$ and weakly with $CUE2_i$. We therefore eliminated $CUE2_i$ and obtained similar transforms for the remaining variables, with the same amount of explained variance (Fig. 17). However, the transformation for parental biomass is non-monotone and difficult to interpret from a biological perspective. In order to introduce linearity or at least monotonicity into our data set, we used separately Ricker's (Log R/PB) and Beverton and Holt's (PB/R) transformations for establishing stock-recruitment relationships. In both cases, linear or monotone transformations were obtained between recruitment and PB/R and Log (R/PB): also a dome-shaped relationship between recruitment and $CUE2_{i-1}$ was obtained (Fig. 18). That is low, yearly integrated wind speed in year i-1 may have a positive effect on recruitment, at least until a threshold is reached beyond which accumulated wind effects become negative. However, considering the possible influence of the single outlier associated with the low accumulated wind speed anomaly in 1981, we tested the robustness of the transformations by eliminating this data point. The results

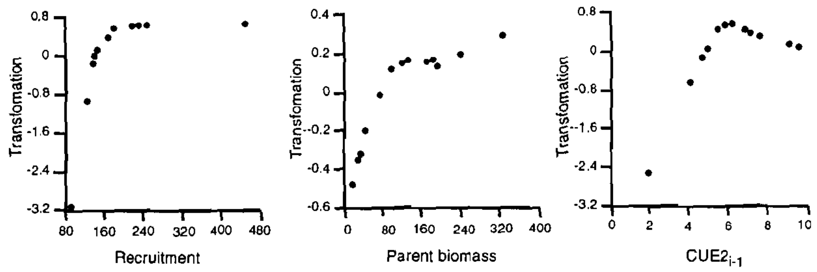


Fig. 17: Optimal transformations estimated by the ACE algorithm: PB/R (dependent variable), parental biomass, and CUE2 year i-1 (independent variables).

show that the transformations are extremely sensitive to this outlier. Under this set of conditions recruitment is inversely related to $CUE2_{i-1}$ in the case of the Ricker S/R relation and presents a sharp break (from negative to positive) in the Beverton and Holt relation (this abrupt change is also present in the Ricker case with CUE_{i-1} when Log R/S is explained by parental biomass, CUE_{2i} and $CUE2_{i-1}$). Moreover, the contribution of CUE2 $_{i-1}$ to total explained variance in both cases is considerably reduced when compared to the data set containing the year 1981.

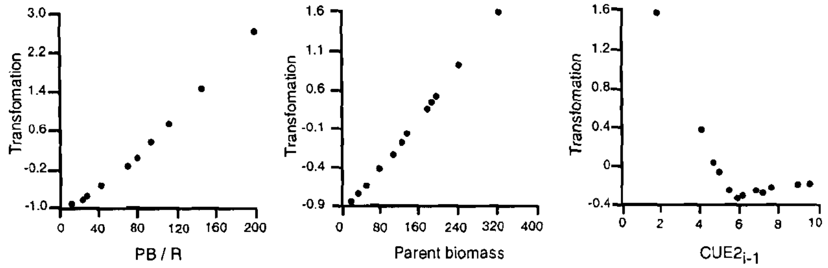


Fig. 18: Optimal transformations estimated by the ACE algorithm: PB/R (dependent variable), parental biomass and CUE2 year i-1 (independent variables).

Finally, a Stock-Recruitment relationship incorporating an environmental variable (Parrish and MacCall, 1978) was fitted to the different data sets by multiple regression. The transformations for $CUE2_{i-1}$ for the whole data set were approximated by a parabolic function and a negative exponential function for the Ricker and Beverton and Holt S/R relationships, respectively. In the case of the Ricker function the contribution of $CUE2_{i-1}$ was not statistically significant ($P<0.5$) with most of the explained variance ($R^2=0.64$) attributable to parental biomass ($P<0.001$). For the Beverton and Holt function, the environmental variable and parental biomass were statistically significant ($P<0.001$; $R^2=0.90$). However, the contribution of $CUE2_{i-1}$ to the relation depended almost exclusively on the data point representing the negative anomaly observed in 1981 (Fig. 19). The exclusion of the year 1981 did not permit to incorporate an environmental variable into a Stock-Recruitment relationship and the Y-axis transformation was explained by parental biomass only in both the Ricker ($R^2=0.69$, $P<0.001$), and Beverton and Holt ($R^2=0.59$, $P<0.003$) functions.

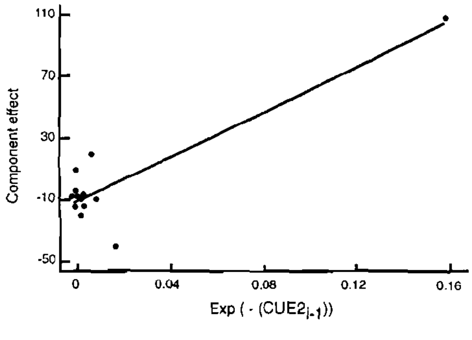


Fig. 19: Component effect of CUE2 $year_{i-1}$ in multiple regression of Log (R/PB) as a function of parental biomass and CUE2 $year_{i-1}$, showing spurious correlation due to a leverage effect.

DISCUSSION

If the *S. aurita* stock in Northeastern Venezuela is underexploited, linear positive relation between catch and effort can be expected, because we are on the left hand side of the production curve. In this case, the surplus production models will tend to underestimate the inflection point (i.e., MSY), and this problem remains in production models incorporating environmental variables (Fréon, 1988). This may explain the non-significant values of c in the model chosen by CLIMPROD. The high coefficient of determination (90%) of the multiple regression between catch, effort and upwelling index cannot be considered as proof of the validity of the regression, because the relation between catch and effort in an underexploited stock is trivial. Furthermore, as opposed to more conventional units, the measure of fishing effort used here does not allow us to observe effort without catches. However, the regression confirms the influence of the upwelling index. There is no temporal lag in the relation between mean CPUE in a fishing year and mean upwelling index in an environmental year. This does not necessarily mean that.the environmental influence affects only catchability, for there is a 5-month lag between the environmental year and the fishing year, which allows for an influence of the upwelling on natural mortality and growth. This last point is very likely, considering the high estimates of growth rate obtained in this study. As a matter of fact, a relationship between biomass and Ø' was found (Fig. 16).

This positive effect of wind on CPUE may reflect a response of school size to prey abundance through a reduction in intra-school competition. Under conditions of high prey abundance, associated with stronger upwelling events, individuals located in the posterior margin of schools would be less affected by prey scarcity. This should result in increased occurrence of larger schools under the above mentioned conditions.

It is important to underline the uncertainty of catch per set as an index of abundance. The weakness of the relation between effort and CPUE may be related to biological factors, such as the absence of a relationship between school size (weight) and abundance. Several technical factors, such as the preferential selection of certain school sizes by fishers or the partial capture of large schools, may also explain the weakness of the relationship. In this context, notwithstanding possible biases due to estimation procedures, it is interesting to recall the relationship between exploited biomass and fishing effort (Fig. 14). Fishing effort may represent exploited stock abundance more closely than CPUE if the assumption is made that abundance varies as a function of school number and not school size. In this case, the effort unit retained would act as a school counter and would be, within certain limits, proportional to stock size (Laurec and Le Guen, 1981).

The nature of the eastern Venezuela fishery imposes certain limitations on the application of length-structured VPA. Catch series compared to hydroacoustic surveys (mean biomass 800 000 t; Anon., 1989) indicate that the exploitation level is low. Under these circumstances the uncertainty associated with levels of natural mortality and different sources of variability in this parameter have considerable weight on the degree of confidence which may be placed on quantitative results. This will also depend on the level of interchange (i.e., movement) between the exploited fraction and the rest of the population at any time. The assumption of a moderate exploitation level (E = 0.33) for all cohorts implies that this interchange occurs at an intermediate rate. Moreover, the enlargement of the fishing area from 1981 towards the northern fishing grounds where large fishes are more abundant could explain the increase in biomass presently being observed.

Despite the above mentioned limitations, our results are largely compatible with existing knowledge on this resource. For example, biomass estimates from VPA suggest that from 7% to 15% of total standing stock estimated from hydroacoustics was available in the restricted fishing area at the end of the study period. These values, probably underestimates would be reduced by reducing the terminal F value. Further research and more intensive sampling is required to tune VPA with independent biomass estimates from within the fishing area. In any case, assuming no major temporal changes in natural mortality, the yearly observed trends in recruitment to the fishery and exploited total and parental biomass would remain essentially the same.

The analysis of the relationship between recruitment, parental stock and environmental conditions is not conclusive. A dome-shaped transform was observed between accumulated wind in the year i-1 and recruitment in the year i, which is compatible with the Lasker (1975) hypothesis of wind effects on larval survival (Peterman and Bradford, 1987; Cury and Roy, 1989). Nevertheless, wind appears to have a monotonic effect on condition and perhaps maturation in the adult component (Fréon *et al.*, in press) and/or postlarval and early juvenile growth. However, the data set is extremely sensitive to an outlier. As a matter of fact, this outlier represents the lowest observed cumulative wind speed in the series, in the year 1981, which resulted in the lowest observed recruitment in the year 1982 (see Fig. 3,4 and 11). Obviously this result is possible from a biological perspective, but the exclusion of this point changes considerably (in fact reverses) the interpretation of possible upwelling effect upon recruitment. Therefore, we feel that a longer data series (hopefully including more cases with extreme conditions) is necessary in order to obtain a more robust representation of the underlying relationship.

REFERENCES CITED

Anon. 1989. *Surveys of the fish resources in the shelf areas between Surinam and Colombia 1988.* Inst. Mar. Res., Bergen, Norway.

Anon. 1990. *Resultados de los talleres sobre la pesca en Venezuela*. Ministerio de Agricultura y Cría, Dirección General Sectorial de Pesca y Acuicultura, Caracas, 60 p.

Aparicio R. 1986. *Upwelling along the southern coastal boundary of the Caribbean Sea: physical characterization, variability and regional implications*. Master Thesis, Oceanography Dept, Florida Institute of Technology, 183p.

Bakun A. 1973. Coastal upwelling indexes, west coast of North America, 1946-1971. U.S. Dept. Commer. *NOAA Tech. Rep. NMFS SSRF*, 671, 103 p.

Battacharya C.G. 1967. A simple method of resolution of a distribution into Gaussian components. *Biometrics*, 23: 115-35.

Breiman L. and J. Friedman. 1985. Estimating optimal transformation for multiple regression and correlation. *J. Am. Stat. Assoc.* 80: 580-619.

Cury P. and C. Roy. 1989. Optimal environmental window and pelagic fish recruitment success in upwelling areas. *Can. J. Fish. Aquat. Sci.*, 46: 670-680.

Fréon P. 1988. *Réponses et adaptations des stocks de clupéidés d'Afrique de l'ouest à la variabilité du milieu et de l'exploitation: analyse et réflexion à partir de l'exemple du Sénégal*. ORSTOM, Etudes et Thèses, Paris, 287 p.

Fréon P., B. Kiewcinski and D. López. 1992. Utilité du système expert CLIMPROD pour la connaissance du déterminisme du recrutement. *Bull. Inst. océanogr.* Paris, 68: 193-210.

Fréon P., C. Mullon and G. Pichon. 1993. CLIMPROD: Experimental interactive software for choosing and fitting surplus production models including environmental variables. *FAO Computerized Information Series (Fisheries)*, 5, 76 p.

Fréon P., M. Khattabi, J. Mendoza and R. Guzmán. In press. An original reproductive strategy: the case of *Sardinella aurita* life cycle in the southern Caribbean, Venezuela. *Marine Biology.*

Gayanilo F.C., Jr., M. Soriano and D. Pauly. 1989. A draft guide to the compleat ELEFAN. *ICLARM Software*, 2, 70 p.

González L.W. 1985. Determinación de edad y crecimiento de la sardina *Sardinella aurita* de la región nororiental de Venezuela. *Bol. Inst. Oceanogr. Venezuela*, UDO 24 (1-2): 111-128.

Gulland J. and S. Holt 1959. Estimation of growth parameters for data at unequal time intervals. *J. Cons.*, Cons. int. Expl. Mer, 25 (1): 47-49.

Herrera L. and G. Febres. 1975. Kinematics of the wind generated velocity field in the surface waters off eastern Venezuela, Caribbean Sea, *Bol. Inst. Oceanogr. Univ. Oriente*, 14(2): 165-186.

Lasker R. 1975. Field criteria for survival of anchovy larvae: the relationship between chlorophyll maximum layers and successful first feeding. U.S. *Fish. Bull.*, 73 :453-462.

Laurec A. and J. Le Guen. 1981. Dynamique des populations marines exploitées. Tome I. Concepts et modeles. *CNEXO Rapp. Sci. Tech.*, 45, 118 p.

Mendoza J. 1993. A preliminary biomass budget for the northeastern Venezuela shelf ecosystem. *In*: V. Christensen and D. Pauly (eds.). Trophic models of aquatic ecosystems. *ICLARM Conf. Proc.*, 26.

Monente J. A. 1990. Influencia del río Orinoco. Materia en suspensión. *Mem. Soc. Cienc. Nat. La Salle*, 49-50 (131-134): 347-360.

Muller-Karger F., C. McClain, T. Fisher, W. Saias and R. Varela. 1989. Pigment distribution in the Caribbean Sea: observations from space. *Prog. Oceanog.*, 23 : 23-64.

Munro J. and D. Pauly. 1983. A simple method of comparing growth of fishes and invertebrates. *ICLARM Fishbyte*, 1 (1): 5-6.

Parrish R. and A. MacCall. 1978. Climatic variation and exploitation in the Pacific mackerel fishery. *Calif. Dept. Fish. Game, Fish Bull.*, 167: 110 p.

Pauly D. 1980. On the interrelationships between natural mortality, growth parameters, and mean environmental temperature in 175 fish stocks. *J. Cons.*, Cons. int. Expl. Mer, 39 (2): 175-192.

Pauly D. and I. Tsukayama. 1983. On the seasonal growth, monthly recruitment and monthly biomass of the Peruvian anchoveta from 1961 to 1979. *In*: G.D. Sharp and J. Csirke (eds.). Proceedings of the Expert Consultation to Examine Changes in Abundance and Species Composition of Neritic Fish Resources, San José, Costa Rica, 18-29 Abril 1983. *FAO Fish. Rep.*, 291, 3: 987-1004.

Peterman M. and M. Bradford. 1987. Wind speed and mortality rate of a marine fish, the northern anchovy (*Engraulis mordax*). *Science*, 235: 354-356.

Senior W. (in preparation). Variabilidad estacional e interanual de parámetros físico-químicos en el Golfo de Cariaco (Período 1971-1975).

Varela R., F. Carvajal and F. Muller-Karger. (in preparation). El Fitoplancton de la plataforma nororiental de Venezuela.

Global and Local Change: Penaeid Stocks in French Guyana

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ABSTRACT

This study is an attempt to estimate the impact of the Amazon River, regarded as a global change indicator, and different local environmental factors, on the recruitment of penaeid stocks in French Guyana. In particular, the authors try to determine whether the impacts of these global and local environmental factors overlap on temporal scales, or whether they intervene at distinguishable (preferential) time scales. For this purpose, two different time-scales were considered, the biannual and monthly scales. Estimation of the adult stock abundance was also included in the analyses through the commercial catch effort time series. Multiple time series models were estimated from the monthly series and stepwise regressions from the biannual series. The two linear models obtained were then re-estimated using non-linear algorithms. The results indicate that the Amazon River and the adult stock abundance have both significant impacts on stock recruitment at the biannual time scale. However, at the monthly time scale, these two impacts vanish and influence of local rivers appears predominant. These results are consistent with the general hypotheses proposed in the Theory of Hierarchy, and more precisely with the concept of scale dependence usually associated with the multiple functional scales hypothesis.

RÉSUMÉ

Cette étude analyse l'impact du fleuve Amazone combiné à celui de facteurs climatiques locaux de Guyane française sur le recrutement du stock de Penaeides présent au large des côtes guyanaises. Il s'agit plus précisément de déterminer si l'impact de l'Amazone, reconnu comme un indice de changement global, agit aux mêmes échelles de temps que les facteurs locaux, ou si, au contraire, chacun de ces deux types de facteurs agissent à des échelles temporelles distinctes. Pour cela, l'échelle mensuelle et l'échelle bi-annuelle sont considérées. L'influence de l'abondance du stock des adultes matures est, elle aussi, testée par l'introduction de la série des Captures Par Unité d'Effort (CPUE). Les séries mensuelles sont étudiées par les techniques d'analyse de séries temporelles multivariées alors que les séries bi-annuelles sont analysées par régressions multiples pas à pas. Les deux modèles linéaires obtenus sont ensuite réestimés par un algorithme d'analyse non linéaire. Les résultats indiquent que les impacts de l'Amazone et de l'abondance des adultes sont significatifs à l'échelle bi-annuelle. À l'inverse, ces impacts disparaissent à l'échelle mensuelle, et l'influence du débit des fleuves locaux apparaît cette fois prépondérante. L'ensemble de ces résultats est à rapprocher des concepts développés par la Théorie de la Hiérarchie et en particulier de celui de dépendance d'échelle généralement associé à l'hypothèse d'échelles fonctionnelles multiples.

L'interaction entre phénomènes d'échelles distinctes reste une des questions scientifiques les plus épineuses posées aux spécialistes de toutes les disciplines : on peut dire qu'elle est l'un des problèmes scientifiques les plus fondamentaux (...). Elle féconde aujourd'hui la réflexion dans tous les domaines scientifiques. Frontier, 1990.

INTRODUCTION: GENERAL CONCEPTS AND METHODOLOGICAL APPROACH ADOPTING AND APPLYING THE ESSENCE OF 'GLOBAL VERSUS LOCAL CHANGES'

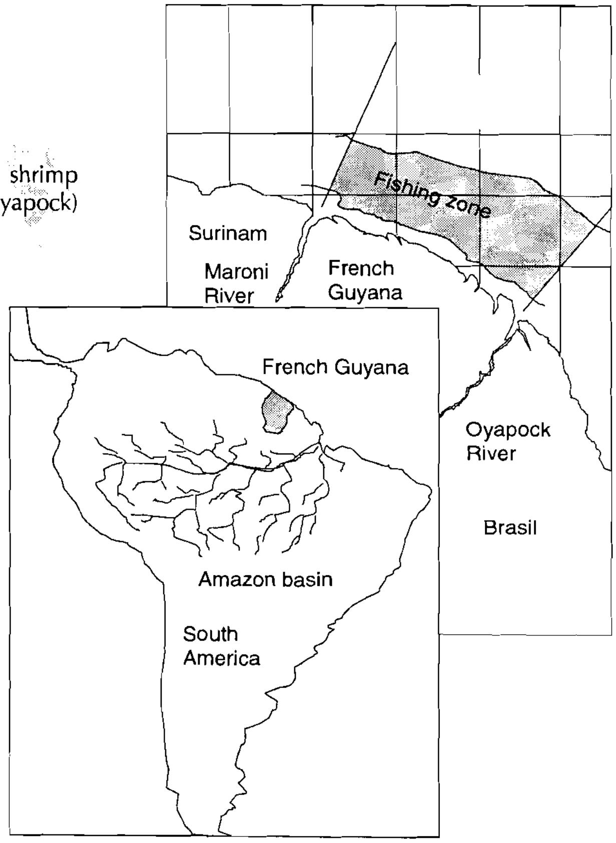
In ecology, every ecosystem analysis points out the complexity and multiplicity of nature's spatial evolution (spatial heterogeneity), and dynamics (temporal variability) and shows that the biotic and abiotic processes generally take place over overlapping spatial and temporal scales. The acknowledgment of multiple spatial and temporal scales is the essence of the approach of the present volume, devoted to 'Global versus Local Changes in Marine Ecosystems': it recalls that marine resources evolve within and because of global and local changes.

Shrimp species do not appear to be an exception: shrimp life-cycles are known to be highly environmentally-dependent (Garcia and Le Reste, 1981; Dall, 1981; Staples and Vance, 1986; Gracia, 1989; Hettler, 1992). No consensus, however, seems to emerge from the abundant literature to identify any key factor (Dall *et al.*, 1990). For illustration, the climatic factors generally assumed to have impact on shrimp recruitment includes rainfall, river flow, water temperature, sea level, salinity, turbidity, even upwelling index or solar and moon cycles (Staples *et al.*, 1984; Lam *et al.*, 1989).

This non-exhaustive list not only emphasizes the complexity of recruitment processes in marine ecosystems in general and in shrimps in particular; it also shows that only impact of locally-recorded factors have been analyzed (local rivers, local rainfall, temperature of the shrimp living area, etc.). Thus, it should be interesting to make an attempt to revisit this issue from simultaneous local and global points of view.

The French Guyana shrimp stock may represent a pertinent choice to lead this kind of investigation. Indeed, the southern limit of the area is located 450 km northwest from the Amazon River's mouth (Fig. 1), which is usually regarded as providing a global climatic index. The question which immediately arises is to know whether it would be possible to estimate the impact of the Amazon River on the dynamics of a locally-delimited process such as the recruitment of the shrimp stock off French Guyana and how this global factor interacts with other, locally-generated, environmental factors. In other words, do the global and local impacts overlap on temporal and spatial scales, i.e., do they intervene at the same spatial scale and with the same temporal frequency on the dynamics of the recruitment, or conversely, do they have specific impact scales?

Fig. 1: Geographical location of the French Guyana shrimp fishery with respect to the local rivers (Maroni and Oyapock) and mouth of the Amazon River.



1. DEPTH-DEPENDENT DISTRIBUTION OF THE RESOURCE, AND ITS IMPLICATION FOR RECRUITMENT INDEXES

When no direct estimations of recruitment are available, commercial fishery data are used. Generally, the CPUE (Catch per Unit of Effort) series of the smallest commercial category is used as proxy for recruitment. However, the analysis may be invalid if the resource distribution is depth-dependent. If it is so, and the fleet shifts its spatial distribution of effort, this inshore (or offshore) effort re-location induces a change in the pattern of the catch composition. This change introduces a subsequent modification in cpue and especially in the series that is used as a surrogate for recruitment. This shift does not correspond to any variation in the actual recruitment level, but only reflects change in the fleet fishing strategy.

Shrimp spatial distributions are depth-dependent. It is widely observed that for a given species, largest individuals are generally found in deep-water zones while the smallest individuals live in shallow-water zones (Dall *et al.*, 1990). This is a consequence of a life-cycle where juveniles develop inshore, generally in estuarine nursery grounds, and the adult migrate offshore as they grow. The occurrence of such a depth-dependent distribution has been empirically confirmed in the case of the French Guyana shrimp *Penaeus subtilis* (Venaille, 1979).

The bias in recruitment indicator induced by the depth-dependency of the resource, combined with the spatial modification of the commercial fleet effort may be partially circumvented by taking the fleet's distribution into account. In our case, this was done by introducing an indicator related to the spatial distribution of the fishing effort.

2. CHOICES OF TEMPORAL SCALES AND STATISTICAL TECHNIQUES

For the French Guyana, all climatic and/or environmental factors generally assumed to have an impact on shrimp life cycle (cf. the listed variable above) display clear-cut seasonal patterns (Fig. 2,a,c). From this, it ensues that a six-month scale might be appropriate to identify climatic inducing changes and/or biologically-induced responses involved at an intermediate temporal in the recruitment process.

However, equatorial penaeids spawn throughout the year, although spawning intensity may not be uniform in all months (Crocos, 1985; Dall *et al.*, 1990). This constancy of the spawning cycle suggests a dynamics characterized by a relatively high frequency, which might be mismatched by considering a bi-annual time scale. A shorter temporal scale (of the order of the month) is therefore also required. We thus adopted two scales, one biannual, other monthly. Based on these two different analyses were conducted, a short-term recruitment variability analysis (applied to the raw 1979-1990 monthly recorded series), and a medium-term analysis applied to the bi-annually re-scaled series. These bi-annual series were obtained by a 6-month moving average procedure applied to the monthly series. Then, we used multiple time series models for the monthly analysis and stepwise regressions for the bi-annual analysis.

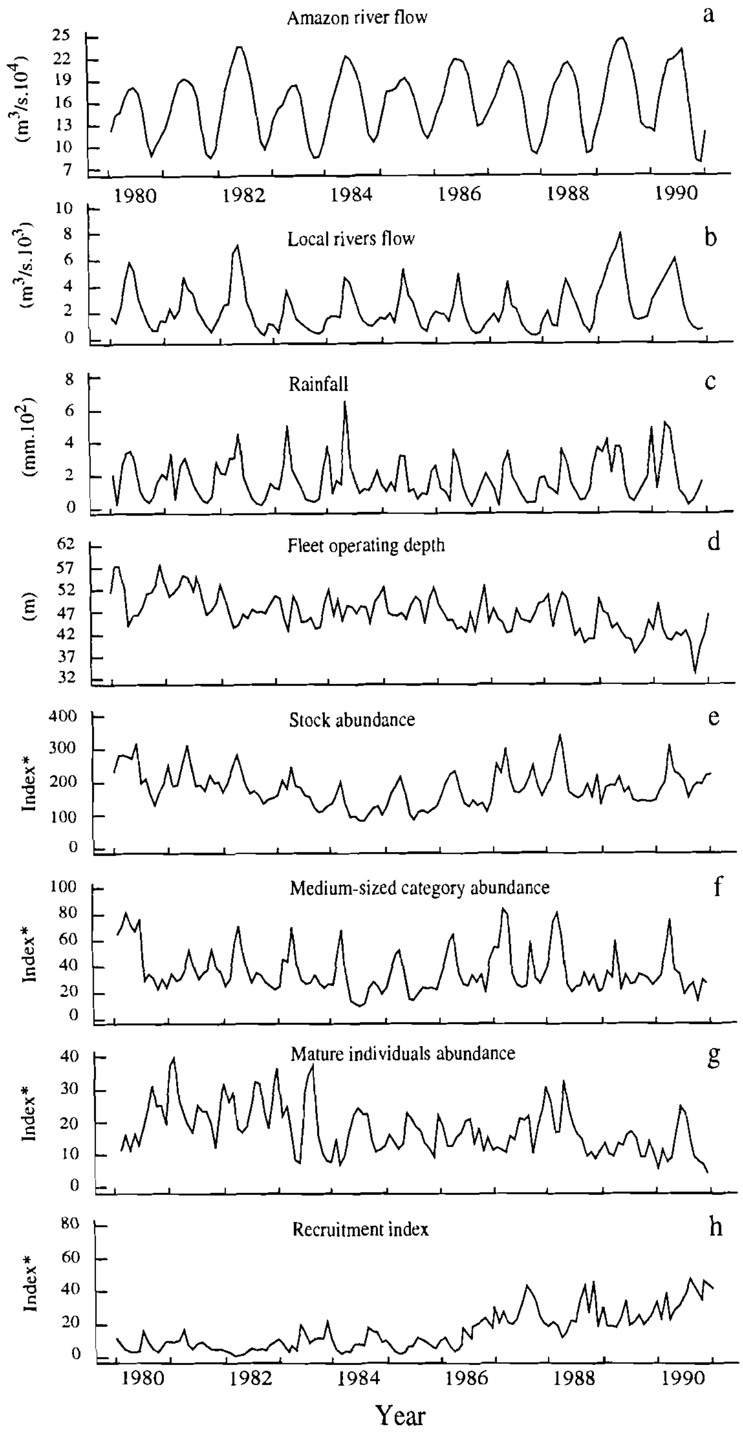


Fig. 2: Monthly time series of the variable used in the analyses, 1980-1990. Abundance and recruitment indices (*): CPUE (kg/day at sea) see Table 1 for details on series; sources : a-b: ORSTOM, c: Météo France, d-h: IFREMER.

3. CHOICES OF DEPENDENT AND EXPLANATORY DATA SERIES

The shrimp stock data was provided by (i) data sets recorded by the IFREMER station in Cayenne and (ii) captains' log-book records. The Amazon river discharge and series of environmental local factors (discharge of the French Guyana Rivers and rainfall) were provided by the stations of ORSTOM and Météo-France in Cayenne, respectively. Table 1 gives details on the explanatory variables included in the bi-annual model and Table 4 on those included of the monthly analysis. The series are shown in Figures 2 e-h. As mentioned above, in the absence of any direct estimation, the recruitment indicator is the CPUE of the smallest commercial categories of shrimps caught by the commercial fleet (i.e., the categories 61/70 + 71/80).

The presence amongst the explanatory variables of the CPUE of a medium-sized category (indicated as LogMed in Tables 1 and 4) calls for explanation. Since the fleet dynamics is likely to have an impact on catch composition (see above), one may assume the catch of mature individuals to be particularly sensible to changes in the fleet's spatial distribution. Conversely, the CPUE of the medium-sized category, distributed in middle depth-water zones, is expected to be less biased by the fleet's movements.

Indicators of	Notation	Lags	Remarks
Stock size	LogStock	t-2, t-1	total CPUE (kg/day at sea)
Mature individuals	LogLarge	t-2, t-1	CPUE of categories U10 + 11/15
Mature individuals	LogMed	t-3, t-2	CPUE of categories 31/35 + 36/40
Rainfall	LogRain	t-2, t-1	French Guyana coastal rainfall (mm)
Local rivers flow	LogRiver	t-2, t-1	Cumulated Maroni and Oyapock flows
Amazon River Flow	LogAmaz	t-2, t-1	Amazon flow
Fleet Sounding	Sound	t	Averaged fleet operating depth (m)

Table 1: Date used for stepwise regression analysis (set of biological and environmental (climatic) variables tested at the bi-annual scale). The third column indicates the different timelags at which the variables were tested in the model.

The other factors included in the model (Fig. 2 a,c) are the rainfall on the coastal zone of French Guyana, the flow of two local rivers (the Maroni and the Oyapock Rivers) (see Fig. 1) and the discharge of the Amazon River. Also, the fleet's operating depth was also included as indicator of the spatial distribution of fishing effort. All variables except fleet soundings were log-transformed to stabilize the variance.

4. MODEL IMPROVEMENT: INTEGRATING NON-LINEARITY

The estimation procedures for both time series analyses and stepwise regression are based on linear procedures. We complemented these analyses by re-estimating the models through non-linear regressions. Several algorithms [Alternative

Conditional Expectations (ACE) (Breiman and Friedman, 1985), Additivity and Variance Stabilization (AVAS) (Tibshirani, 1988), or Generalized Additive Interactive Modeling (GAIM) (Hastie and Tibshirani, 1990)] offer the possibility of this non-linear re-estimation. We used Breiman and Friedman's ACE algorithm.

5. RECRUITMENT VARIABILITY ANALYSIS

5.1. Medium term (bi-annual) variability analysis

5.1.1- Linear approach

The explanatory variables were included in the model at the different lags indicated in Table 1. Since results obtained by backward and forward stepwise multiple regressions are usually unstable when the variables are correlated (Belsey *et al.*, 1980. Koslow *et al.*, 1987), the only variables maintained in the model were those which appeared stable.

The final models obtained by backward and forward regression (F remove = F enter = 4.41, $\upsilon 1 = 1$, $\upsilon 2 = n\text{-}p$, $n = 24$) are similar (Table 2). They both indicate that, relying on linear estimations, only fleet operating depth (Sound) lagged at 0 has a significant impact on the recruitment indicator (Rec). The final linear model is thus:

$$\mathrm{LogRec}_t = f(\mathrm{Sound}_t) \qquad (1)$$

where $f()$ is a linear function with $R^2 = 41$ %

These results emphasize the impact of the fleet effort distribution on the recruitment indicator. Note that in other respects, the environmental factors which were tested have non-significant linear impact on the recruitment indicator.

Selection:	Backward	Dependent Variable:	(Log Rec_t)	
R^2 = 0.409	R^2 adj. = 0.378	M.S.E. = 0.3762	d.f. = 19	F remove = 4.41
Variables in Model	Estim. Coef.	F variables (1)		
(1) ($Sound_t$)	-0.1572	13.1682		
Selection:	Forward	Dependent Variable:	(Log Rec_t)	
R^2 = 0.409	R^2 adj. = 0.378	M.S.E. = 0.3762	d.f. = 19	F enter = 4.41
Variables in Model	Estim. Coef.	F variables (1)		
(1) ($Sound_t$)	-0.1572	13.1682		

Table 2: Final linear models after stepwise (forward and backward) regression analysis.

5.1.2- Non-linear approach

Releasing the linear constraint implies re-testing all the potential explanatory variables and identifiying the form of their optimal transformations using the ACE algorithm. The bias introduced in the recruitment series by the fleet spatial distribution can be partially removed by detrending the recruitment series. The recruitment series was thus detrended with the procedure described in Makridakis *et al.*, (1983). Two non-linear analyses were then conducted simultaneously, one with the log-transformed recruitment indicator, and one with the detrended series. They are noted as log-analysis and detrended analysis, respectively (see Table 3 for details).

Analysis	Log analysis	Detrend analysis
Log-transformation of the dep. variable	Yes	No
Detrending of the dep. variable: remove the bias induced by the fleet dynamics	No	Yes
Dependent variable:	Recruitment (LogRec)	Recruitment (RecDtrd)
(Sound) variable included	Yes	No
Explanatory variables:	Sound, LogAmaz, LogMed	LogAmaz, LogMed

Table 3: Structure of the two analyses conducted for the non-linear approach.

Results of the analysis are displayed in Figure 3. For the log-analysis, the impact of the (Sound) series on the (LogRec) variable is still significant. Amongst the other variables which appear to have non-linear, simultaneous impacts on both (LogRec) and (RecDtrd) variables, only two offer transformations which were qualitatively similar. They are the flow of the Amazon (LogAmaz) lagged at 1 (i.e., 6 months) and the CPUE of the medium-sized category (LogMed), lagged at 2 (one year). The other variables were thus removed and the final non-linear models for the log-analysis and the detrended-analysis were estimated. They have the form:

$$\varphi\,(\mathrm{LogRec}_t) = \phi_1\,(\mathrm{Sound}_t) + \phi_2\,(\mathrm{LogAmaz}_{t-1}) + \phi_3\,(\mathrm{LogMed}_{t-2}) \qquad \text{(log-analysis)} \qquad (2)$$

$$\varphi'\,(\mathrm{RecDtrd}_t) = \phi_2'\,(\mathrm{LogAmaz}_{t-1}) + \phi_3'\,(\mathrm{LogMed}_{t-2}) \qquad \text{(detrended-analysis)} \qquad (3)$$

where φ and φ' are the optimal linear transformations of the dependent variable, and ϕ and ϕ' are the optimal non-linear transformations of the explanatory variables. The R^2 are 73% and 48% for (2) and (3), respectively. The difference in these R^2 values is due to the presence of the (Sound) series in model (2), which explains a large fraction of the tLogRect.

Thus, the release from linearity allows the identification of two climatic factors (Amazon flow and the medium-sized category) which are significant. The non-linearity of their optimal transformation (i.e., the fact that straight lines would fit the optimal transformations poorly (see Fig. 3)), offers an explanation for the fact that the linear-based estimations proposed in the previous section failed to identify these variables as significant.

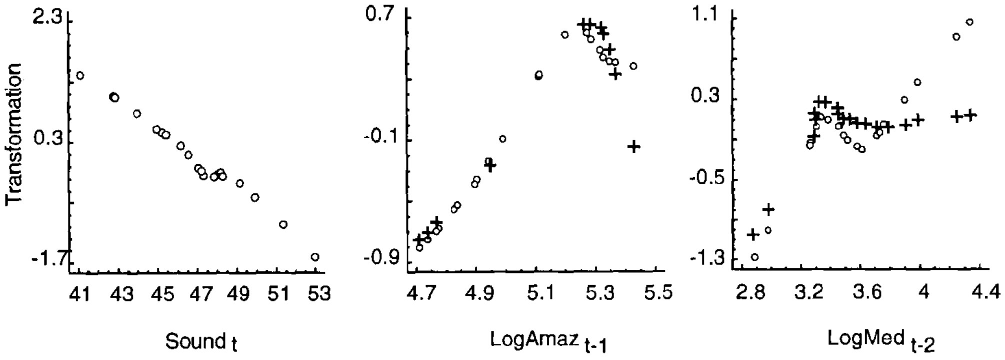


Fig. 3: Non-linear, bi-annual analyses: optimal transformations of the explanatory variables for both log-analysis and detrended analyses. (see Table 3 for details). Open dots: log-analysis ($R^2 = 0.738$). Crosses: detrended analysis ($R^2 = 0.485$).

5.2. Analysis of short term (monthly) variability

5.2.1- Linear approach

The multiple time series procedure used here is similar to the one described in Tiao and Box (1981), i.e., we used the Wisconsin Multiple Time Series program (WMTS-1) developed by Tiao *et al.* (1980). Table 4 indicates the series tested and the transformation adopted. All climatic variables (i.e., rainfall and river flow) were deseasonalized by a $(1\text{-}B^{12})$ backward shift operator for stationary purpose. The partial auto and cross-correlation analyses over 16 lags indicate that positive auto-correlation of the dependent variable (Rec) occurs at lag 1, 5, 9, 11, and 12, while negative cross-correlations with the sounding (Sound) and the local rivers flow (RiverDiff) are significant at lags 1 and 11, and 6, respectively (Table 5). The model parameters were then estimated using WMTS-1. The series parameter included in the range 2S.E. (S.E. standard error) were removed from the model (see Tiao and Box (1981) for procedural details). Table 6 shows the variables and their estimated parameters for the final linear model such as identified following the Tiao and Box's method. The R^2 coefficient reaches 75 %. The analysis of the residuals cross-correlation matrix indicates no lack of fit. The final linear model is:

$$\text{LogRec}_m = 0.78\ \text{LogRec}_{m-1} + 0.23\ \text{LogRec}_{m-12} - 0.62\text{E-}04\ \text{RiverDiff}_{m-6} \qquad (4)$$

Variable	LogStock	LogLarge	LogMed	RainDiff	RiverDiff	AmazDiff	Sound
Indicator of:	Stock	Mature	Mature	Rainfall	Local rivers	Amazone	Fleet Sound
Transf.	Log_e	Log_e	Log_e	$(1\text{-}B^{12})$	$(1\text{-}B^{12})$	$(1\text{-}B^{12})$	—

Table 4: Multiple time series analysis. Set of explanatory variables tested at monthly scale. The third row (Transf.) indicates the transformation applied to the variable. $(1\text{-}B^{12})$: backward shift operator.

(l)	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16
yy (l)	+				+				+		+	+				
yx1(l)	-										-					
yx2(l)						-										

Table 5: Sample Partial Auto and Crosscorrelation matrices yy (l) and $yx_i(l)$. The matrix is given in term of indicator symbols such as defined in Tiao and Box (1981) (a sign (+) denotes a partial coefficient value greater than $2n^{1/2}$, a sign (-) denotes a value less than $-2n^{1/2}$, a sign (.) denotes non-significant value with respect to the above criterion). y: Rec ; x_1: Sound, x_2: RiverDiff, (l): lag being tested.

Predictor series	Model specification	Parameter estimates	Estimated S.E
Rec	(1,1,1)	0.787	0.495E-01
Sound	(1,2,2)	0.573	0.731E-01
RiverDiff	(1,3,3)	0.723	0.673E-01
RiverDiff	(6,1,3)	-0.628E-04	0.285E-04
Rec	(12,1,1)	0.237	0.534E-01
Sound	(12,2,2)	0.414	0.714E-01

Table 6: Final multiple time series model identified by the WMTS-1 program. $R^2 = 75.5\%$. The variables Rec, Sound, and RiverDiff are coded 1, 2, and 3, respectively in model specification (l, i, j) (l) indicates the lag, (i) the series being regressed, and (j) the predictor series. All parameter estimates are greater than 2S.E.

5.2.2- Non-linear approach

The linear model (4) was then re-estimated using the ACE algorithm (Fig. 4). The non-linear transformation procedure resulted in an increase of the R^2 from 75 to 81%. The forced addition of the sounding series into the model (open dots in Fig. 4) improves the R^2 value by only 2%. This indicates that, at the monthly scale, the impact of this variable on the recruitment indicator vanishes. Therefore it was not maintained in the final form of the monthly model (5). All the other climatic variables were also systematically tested in the non-linear model. None of them, however, displayed a satisfactory optimal transformation. The final non-linear form of the model (crosses in Fig. 4) is therefore:

$$\varphi(\mathrm{LogRec}_m) = \phi_1(\mathrm{LogRec}_{m-1}) + \phi_2(\mathrm{LogRec}_{m-12}) + \phi_3(\mathrm{RiverDiff}_{m-6}) \qquad (5)$$

Note that in (5), the release from linearity improves the coefficient of correlation with respect to (4), but does not change the structure of the predictor function which remains $\{\mathrm{LogRec}_{m-1} : \mathrm{LogRec}_{m-12} : \mathrm{RiverDiff}_{m-6}\}$. Conversely, it may be recalled that Amazon flow and the medium-sized category were included in the non-linear model for the bi-annual analysis.

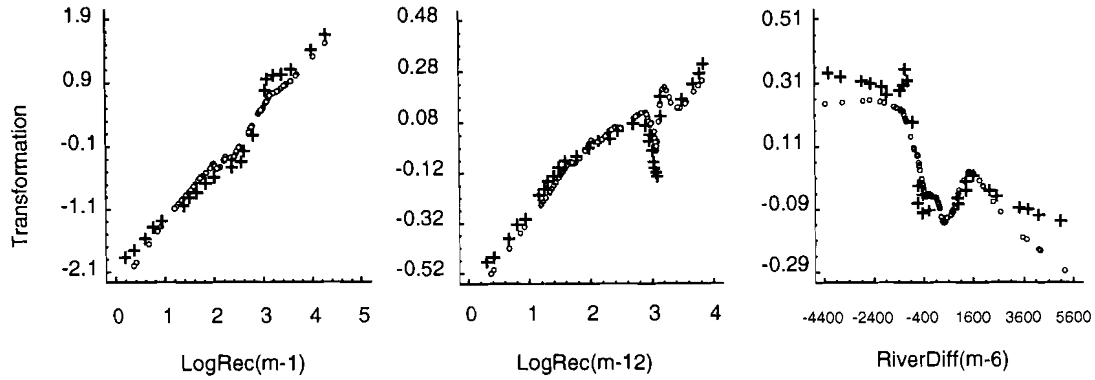


Fig. 4: Non-linear monthly analyses: optimal transformations of the explanatory variables common to the two models. Open dots: model with forced adding of (Sound), indep.var.)= (Log Rec_m), predictor function= {(Log Rec_{m-1}), (Log Rec_{m-12}), ($Sound_m$), (River $Diff_{m-6}$)}, $R^2=83.1\%$ (the (Sound) transformed curve is not shown). Crosses: model without (Sound): final model of the form (5): indep.var.= (Log Rec_m), predictor function {(Log Rec_{m-1}), (Log Rec_{m-12}), ($Sound_m$), (River $Diff_{m-6}$)}, $R^2=81.7\%$.

5.2.3- Impact of fleet dynamics on the recruitment index

In the case of the French Guyana fishery, it appears that the spatial distribution of fishing effort has an impact on the composition of the landings, and therefore on the recruitment index. This suggests that studies which do not take into account the fleet dynamics dimension when the resource is known to have spatially-structured distributions will the actual causes of long-term changes in the recruitment series. In this case, the bias might even have caused misleading conclusions concerning long term environmental and/or climatic impacts on recruitment fluctuations. Removal of this bias may be done by removing the trend in the series. In the present case, the transformation of the two climatic explanatory variables ($LogAmaz_{t-1}$) and ($LogMed_{t-2}$), with or without the detrending procedure, are similar (Fig. 3). One may therefore assume that these environmental factors actually intervene in the long term dynamics of recruitment, whereas the distribution of fishing effort impacts on the long term indicator of recruitment. The difference is slight but important.

5.3. Limits of interpretation

Biologically speaking, the above results appear easy to interpret in the context of the life cycle of *Penaeus subtilis*. The (LogMed) variable lagged at 2 in models (2) and (3) represents the abundance of the individuals about to mature, 9 to 15 months before recruitment. This one year delay corresponds to the time required to pass through the different life cycle steps separating the two stages concerned. On the other hand, the presence of ($LogAmaz_{t-1}$) in models (2) and (3) and ($RiverDiff_{m-6}$) series in model (5) are also biologically explainable. These series represent the discharge flows of the Amazon and the local rivers 6 months ahead of the recruitment, respectively. This corresponds to the periods of egg spawning and inshore migration of the larvae. Both Amazon and local rivers seem therefore to impact on the first stages of the cycle, which are usually assumed to be critical stages in penaeid life cycle. Particularly, for the Amazon River case, this impact appears to be dome-shaped. This recalls the theoretical pattern already shown by other studies, especially on pelagics (Cury and Roy, 1989).

We will however remain careful and be more deeper in biological interpretations. Several previous studies have stressed the apparent non-linear relationship between river discharge and recruitment abundance (Garcia and Le Reste, 1981; Garcia *et al.,* 1985; Staples *et al.,* 1984; Browder, 1985; Gracia, 1989; Dall *et al.,* 1990). These studies thus agree with the shape of the relationship between recruitment and the Amazon River identified here. Some other papers propose linear negative relationship between river flow and recruitment (Barrett and Gillespie, 1975; Lhomme and Garcia, 1984; etc.), while a large number of studies suggest opposite results i.e., linear, positive relationship (Racek, 1959; Le Reste, 1978; Vances *et al.,* 1985). What is therefore needed is now to perform other analyses based on similar methodologies (non-linearity combined with time series techniques, introduction of fleet effort distribution and simultaneous use of two distinct time scales) in order to generalize the present results.

6. GLOBAL VERSUS LOCAL CHANGES: A STIMULATING CONCEPT

6.1. On non-linear techniques

In the shrimp literature, linear regressions have been useful to draw attention to potential impacts of environmentally-induced factors. However, a large number of articles have stressed the non-linear (or even more non-monotonous) nature of the relationships between environmental variables and resource biological states. It is time now to move beyond the linear domain. Critics of linear techniques are not new and certainly not restricted to biology (Prigogine and Stengers, 1979; Stewart, 1992). In the present case, the changes in predictor function and the subsequent improvement of the model following the use of the non-linear transformations highlight the methodological importance of these techniques. It is admitted that present non-linear algorithms (ACE, AVAS, GAIM) have still to be improved and must be considered and used with caution (Cury *et al.*, 1995). These algorithms, however, have the advantage to exist and to be available to biologists. They have been used by pelagic specialists for several years (Mendelssohn and Cury, 1987, 1989). A similar step has still to be taken with regard to research on shrimp. It is time now to adopt non-linear techniques, even if this implies a re-questioning of the conclusions based on classical techniques.

6.2. Beyond the classical problem of pertinent observation scales

For phenomena characterized by several scales of perception, there is generally a correspondence to the main functional scales (Wiens *et al.*, 1986; Rahel, 1990; Frontier, 1990). Consequently there are usually as many models and explanatory theories as perception scales. In the case where global and local factors are involved, this issue becomes central for the methodological approach (Turner *et al.*, 1989). Furthermore, when the environmental and climatic factors impacting on the system are multiple, complex, and diversified, as is the case for penaeid stocks, thinking in terms of global versus local functional dynamics necessarily raises the question of pertinent observation scales. There are, however, no good, a priori, answers to this question. The pertinent scales can only be identified a posteriori by the natural frequencies of the phenomena studied (Urban *et al.*, 1987; Burel *et al.*, 1992). In those circumstances, ecological processes with unknown sources of variability or which are only partially understood, raise additional methodological difficulties. Some ad hoc solutions may be available. Thus, when a seasonal pattern is known to characterize a large number of the factors assumed to influence the dynamics — as it is usually the case for penaeid stock (Dall *et al.*, 1990) — this seasonality may indicate the optimal scale to adopt. In our case, this natural temporal time scale (frequency) allowed us to propose two different time scales susceptible to capture, asizeable part of shrimp variability.

6.3. The Amazon River, a global factor

The Amazon River can be viewed as an indicator of global change, for two reasons. Factors are defined as being global (or local) not in terms of their intrinsic features, but rather with respect to other factors also included in the analysis. The mouth of the Amazon River is located 450 km south of the French Guyana - Brazil border. Thus, it can be considered as a non-local factor vis-à-vis the other explanatory variables, which integrate 'locally-generated' variables.

However, the Amazon River lines up to general expectations about global factors for a second reason. A global factor should provide or contain information relevant to the Earth's global climate. With a discharge volume of $5.2 \,.\, 10^{12}$ m^3/year), the Amazon represents about 20% of the World's water discharge into the oceans (Oltman, 1968). The flow ratio Amazon/local rivers indicates, moreover, that, on the average, over the period 1979-1990, the Amazon annual discharge was 65 times stronger that the combined discharge of local rivers. The magnitude in the ratio thus justifies treating the Amazon to be qualified as a global factor with respect to the other variables, which conversely may be considered as indicators of local changes.

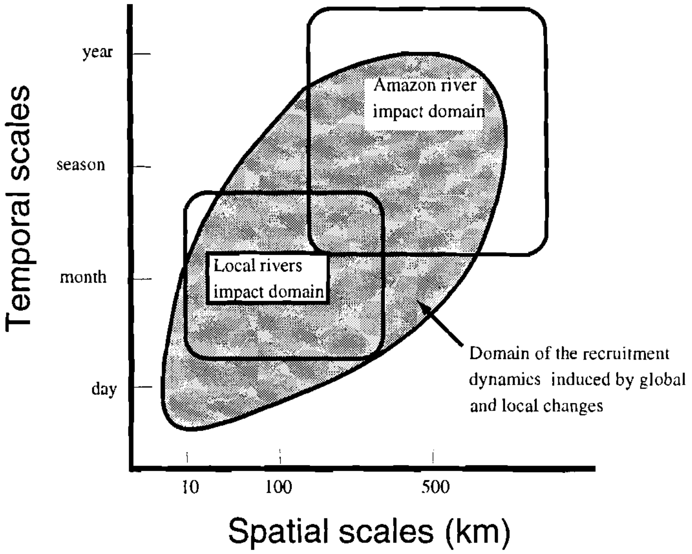
6.4. Scale dependence and the coherence of space-time scales

The fact that a river considered as a global factor appears to have a significant impact at the bi-annual but not at the monthly temporal scale, may indicate a space-time (de)limitation of its domain. Whereas the bi-annual level of shrimp recruitment dynamics is influenced by the Amazon, its impact vanishes at shorter scales. On the other hand, the discharge of the local rivers does not seem to impact the long term dynamics of shrimp abundance but is significant at the monthly scale. Shrimp recruitment dynamics thus seem to be characterized by several functional scales.

This notion of multiple functional scale is quite usual in ecology, particularly in the Theory of Hierarchy and its concept of scale dependence (Wiens, 1989; Burel *et al.*, 1992; Müller, 1992). This concept states that impacts of phenomena that spread over large spatial scales are more slower than those acting on smallest spatial scales. One may be tempted therefore to refer here to the 'concept of coherence of scales'. The term dependence when used in 'dependence of scales' implies a notion of causality and a formal relationship between space and time. On the other hand, the term 'coherence' merely refers to a logical, but not empirically established relationship between the temporal and spatial dimensions of the factors.

The observations presented here on ***Penaeus subtilis*** off French Guyana are in agreement with expectations of coherence of scales (Fig. 5): the Amazon River turns out to have an impact at a relatively long-term scale, while the impact of the local rivers is effective at higher frequencies, observable at monthly scales.

Fig. 5: Coherence of scale (scale dependence) in the case of the French Guyana shrimp recruitment dynamic: the Amazon River affects system dynamics at a longer temporal scale (the bi-annual scale), while local factors generate impacts at a smaller scale (monthly). This creates a virtual relationship between spatial and temporal scales in accordance with the classical concept of scale dependence.



6.5. Global versus local: avoiding misleading simplifications

Thinking in terms of global versus local changes is not merely tantamount to comparing or even to opposing two different spatially- or temporally-scaled impacts. First of all, the two notions (local and global) have no absolute, but only relative dimensions. They are only defined with respect to each other.

Nevertheless, it is on a more fundamental field that the view is erroneous which tends to reduce this concept to an over-simplistic opposition between two scales. Not only are the two notions relative and not absolute, but also their contrast between them is disputable. They are not two opposite poles excluding one another, as sometime asserted, but rather different parts of a continuum along scales. Furthermore, the different levels are not independent from one another. The same environmental factor may not restrict its impact to one given level but 'spread out' on several levels. One may expect, for instance, that the local rivers have a temporal domain which covers a larger scale than the monthly scale used here, probably of several months.

For these reasons, the dynamics of shrimp recruitment we observed, is the emergent result of a combination of interacting dynamics characterizing different hierarchical (space-time scaled) levels, and not merely the result of addition (superposition) of dynamics at two or more scales. The dynamics of biological systems are not simply 'piled up' at diverse scales (Fig. 6; Burel *et al.*, 1992).

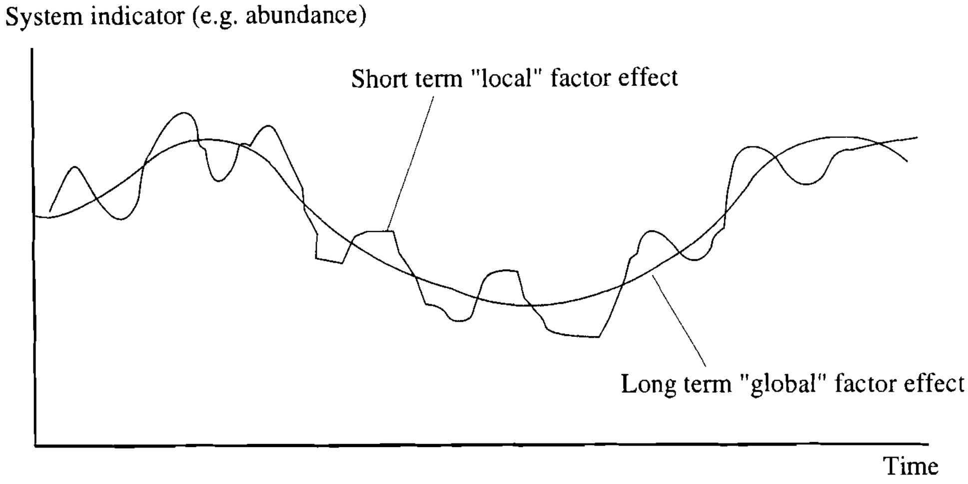


Fig. 6: Representation of the misleading notion of 'addition of effects' (instead of 'combination of effects'). This oversimplistic approach does not allow for emerging properties. We should consider systems as emergent responses to combined effects acting within and between functional levels rather than as simple addition of 'compartimentalized' responses specific to distinct functional levels.

The conclusion is therefore that one should not strive any longer to 'integrate' the dynamics of a given level by analyzing variability of this unique level. We have to widen the space-time dimension of our investigations to neighbouring levels, to identify the specific but also the interlevel mechanisms acting within and between the system levels. Within this conceptual framework, we shall not think in terms of 'Global versus Local Changes', as the two notions are in fact inseparable. Rather, we should think in terms of 'Global and Local Changes'.

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REFERENCES CITED

Barrett B. and M.C. Gillespie. 1975. Environmental conditions relative to shrimp production in coastal Louisiana. *Louisiana Wildlife and Fisheries Commission Techn. Bull.*, 15: 1-22.

Belsey D.A., E. Kun and R.E. Welsch. 1980. *Regressing diagnostics: identifying influential data and source of colinearity*. John Wiley, New-York.

Breiman L. and J.H. Friedman. 1985. Estimating optimal transformations for multiple regression and correlation. *J. Am. Stat. Assoc.*, 74: 829-836.

Browder J.A. 1985. Relationship between pink shrimp production on the Tortugas grounds and water flow patterns in the Florida Everglades. *Bull. Mar. Sci.*, 37(3): 839-856.

Burel F., J. Baudry, P. Clergeau, P. Constant and M.-C. Eybert. 1992. Approche spatiale des phénomènes écologiques: échelles et hiérarchie. *Bull. Ecol.*, 23(1-2): 93-101.

Crocos P.J. 1985. Appraisal of some factors relevant to the development of penaeid prawn population reproductive models. *In*: P.C. Rothlisberg, B.J. Hill and D.J. Staples (eds.). *Second Australian National Prawn Seminar*. Cleveland, Australia. 159-164.

Cury P. and C. Roy. 1989. Optimal environmental window and pelagic fish recruitment success in upwelling areas. *Can. J. Fish. Aquat. Sci.*, 46: 670-680.

Cury P., C. Roy, R. Mendelssohn, A. Bakun, D. Husby and R. Parrish. 1995. Moderate is better: exploring nonlinear climatic effects on the California northern anchovy (*Engraulis mordax*). *In*: R.J. Beamish (ed.). Climate and northern fish populations. *Can. Spec. Publ. Fish. Aquat. Sci.*, 121: 417-424.

Dall W. 1981. Osmoregulation ability and juvenile habitat preference in some penaeid prawns. *J. Exper. Mar. Biol. Ecol.*, 54: 55-64.

Dall W., B.J. Hill, P.C. Rothlisberg and D.J. Staples. 1990. The biology of the *Penaeidae*. *In*: J.H. Blaxter and A.J. Southward (eds.). *Advances in Marine Biology*. Acad. Press, 27, 489 p.

Frontier S. 1990. Les outils mathématiques nouveaux du transfert d'échelle. *In*: C. Mullon (ed.). Le transfert d'échelle. *Séminfor 4*, ORSTOM: 379-403.

Garcia S. and L. Le Reste. 1981. Cycles vitaux, dynamique, exploitation et aménagement des stocks de crevettes pénaeides côtières. *FAO Fish. Doc. Tech.*, 203, 210p. FAO, Rome.

Garcia S., M. Lemoine and E. LeBrun. 1985. Seasonal and long-term variability of recruitment in French Guyana shrimp fishery on *Penaeus subtilis*. *FAO Fish. Rep.*, 327, Suppl., FAO, Rome.

Gracia A.G. 1989. Relationship between environmental factors and white shrimp abundance in the southwestern Gulf of Mexico. *An. Inst. Ciec. Mary Limnol. Univ. Autom. Mexico*, 16(1): 171-182.

Hastie T. and R. Tibshirani. 1990. *Generalized additive models*. Chapman and Hall, London.

Hettler W.F. 1992. Correlation of winter temperature and landings of pink shrimp, *Penaeus duorarum*, in North Carolina. *Fish. Bull.*, U.S., 90: 405-406.

Koslow J.A., K. R. Thompson and W. Silvert. 1987. Recruitment to northwest Atlantic cod (*Gadus morhua*) and haddock (*Melanogrammus aeglefinus*) stocks: influence of stock size and climate. *Can. J. Fish. Aquat. Sci.*, 44: 26-39.

Lam C.F., J.D. Whitaker and F.S. Lee. 1989. Model for white shrimp landings for the central coast of South Carolina. *North Am. J. Fish. Manag.*, 9: 12-22.

Le Reste L. 1978. *Biologie d'une population de crevettes, Penaeus indicus, sur la côte nord-ouest de Madagascar*. Trav. Doc. ORSTOM. 99: 1-291.

Lhomme F. and S. Garcia. 1984. Biologie et exploitation de la crevette pénaeide au Sénégal. *In*: J.A. Gulland and B.J. Rothschild (eds.). *Penaeid shrimp, their biology and management*. Fishing News Books, Farnham: 111-114.

Makridakis W., S.C. Wheelwright and U.E. McGee. 1983. *Forecasting: methods and applications*. 2nd edition, John Wiley, New-York.

Mendelssohn R. and P. Cury. 1987. Fluctuations of a fortnightly abundance index of the Ivorian coastal pelagic species and associated environmental conditions. *Can. J. Fish. Aquat. Sci.*, 44: 408-421.

Mendelssohn R. and P. Cury. 1989. Temporal and spatial dynamics of a coastal pelagic species, *Sardinella maderensis* off the Ivory Coast. *Can. J. Fish. Aquat. Sci.*, 46: 1686-1697.

Müller F. 1992. Hierarchical approaches to ecosystem theory. *Ecol. Model.*, 63: 215-242.

Oltman R.E. 1968. Reconnaissance investigations of the discharge and water quality of the Amazon River. U.S. Geol. Survey. Circ., 552, Washington D.C.

Prigogine I. and I. Stengers. 1979. *La nouvelle alliance*. Gallimard, Paris, 439 p.

Racek A.A. 1959. Prawn investigations in eastern Australia. *Res. Bull. State Fish.*, New South Wales, 6: 1-57.

Rahel F. 1990. The hierarchical nature of community persistence: a problem of scale. *Am. Nat.*, 136: 328-344.

Staples D.J., W. Dall and D.J. Vance. 1984. Catch prediction of the banana prawn, *Penaeus merguiensis*, in the south-eastern Gulf of Carpentaria. *In*: J.A. Gulland and B.J. Rothschild (eds.). *Penaeid shrimps: their biology and management*. Fishing New Books Ltd: 259-267.

Staples D.J. and D.J. Vance. 1986. Emigration of juvenile banana prawns *Penaeus merguiensis* from a mangrove estuary and recruitment to offshore areas in the wet-dry tropics of the Gulf of Carpentaria, Australia. *Mar. Ecol. Prog. series*, 27: 239-252.

Stewart I. 1992. *Dieu joue-t-il aux dés? Les nouvelles mathématiques du chaos*. Flammarion, Paris, 441 p.

Tiao G.C., G.E.P. Box, M.R. Grupe, G.B. Hudak, W.R. Bell and I. Chang. 1980. *The Wisconsin Multiple Time Series (WMTS-1) program. A preliminary guide*. Dep. Stat. Univ. Wisconsin, 75 p.

Tiao G.C. and G.E.P. Box. 1981. Modeling multiple time series with applications. *J. Amer. Stat. Assoc.* 76: 802-816.

Tibshirani R. 1988. Estimating transformations for regression via additivity and variance stabilization. *J. Am. Stat. Assoc.*, 83: 394-405.

Turner M.G., V.H. Dale and R.H. Gardner. 1989. Predicting accross scale: theory development and testing. *Landscape Ecol.*, 3: 245-252.

Urban D.L., R.V. O'Neill, and H.H.jr Shugart. 1987. Landscape ecology. *Biosci.*, 37: 119-127.

Vances D.J., D.J. Staples and J. Kerr. 1985. Factors affecting year-to-year variation in the catch of banana prawn (*Penaeus merguensis*) in the Gulf of Carpentaria, Australia. *J. Cons.*, Cons. int. Expl. Mer, 42: 83-97.

Venaille L. 1979. La pêcherie de crevettes pénéides du plateau guyano-brésilien. *Bull. Inst. Pêches marit.*, 297: 1-18.

Wiens J.A. 1989. Spatial scaling in ecology. *Functional Ecology*, 3: 385-397.

Wiens J.A., J.F. Addicott, T.J. Case and J. Diamond. 1986. Overview: the importance of spatial and temporal scale in ecological investigations. *In*: J. Diamond and T.J. Case (eds.). *Community Ecology*. Harper & Row, New York: 145-153.

Changes in the Dynamics and Biology of small Pelagic Fisheries off Côte-d'Ivoire and Ghana: an Ecological Puzzle

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GHANA

ABSTRACT

Spatio-temporal changes in the dynamics of small pelagic fisheries in the Ghanaian-Ivoirian coastal marine ecosystem and changes in the biology of the fish are examined. The abundance of the *Sardinella aurita* population appears to show a transition from a depleted to a prosperous state over the last two decades. These drastic changes is puzzling as it does not appear to be in conformity with previous knowledge on the fish and fisheries of the western Gulf of Guinea ecosystem. The strengthening of minor upwelling appears to be the most likely cause for these observed changes.

RÉSUMÉ

Les dynamiques spatiales et temporelles des petits pélagiques côtiers de l'écosystème ivoiro-ghanéen et les changements dans la biologie des poissons sont examinés. Durant les deux dernières décennies l'abondance de la population de *Sardinella aurita* est passée d'un état en déplétion à un état prospère. Ces changements drastiques n'apparaissent pas en conformité avec les précédentes connaissances acquises sur les espèces et les pêcheries de l'ouest du Golfe de Guinée. Cependant, le renforcement du petit upwelling apparaît comme la seule cause probable responsable des changements observés.

INTRODUCTION

Coastal pelagic fisheries in the western Gulf of Guinea (between Côte-d'Ivoire and Benin) exploit several fish stocks. Between 1983 and 1990, total annual landings were estimated at 200-260.10^3 t in the whole sub-region (FAO, 1992). Four species are particularly important, namely: anchovy *Engraulis encrasicolus* (Linnaeus, 1758), chub mackerel *Scomber japonicus* (Houttuyn, 1782), round sardinella *Sardinella aurita* (Valenciennes, 1847) and flat sardinella *S. maderensis* (Lowe, 1839; Whitehead, 1967). Annual landings of *E. encrasicolus* and *S. aurita* attain 100.10^3 t but the landings of *S. japonicus* and *S. maderensis* are much smaller. A third sardinella species *S. rouxi* (Poll, 1953), is also fished in the region. However, because of its small size (generally less than 15 cm), the species is confused with juvenile *S. maderensis* and is not separated in the statistics except in Ghana (Mensah and Koranteng, 1988). Since the 1980s, there has been a substantial increase in the landings of *S. aurita*. Changes in the distribution and abundance of the species have also been noticed (Pezennec and Bard, 1992). This evolution of the fishery contradicts most of the knowledge acquired in the 1960s and 1970s about this resource. The abundance of the other species of this pelagic ecosystem have also fluctuated, but not as much as *S. aurita*. Significant changes in some aspects of the biology of *S. aurita* have also been observed. Size of fish caught and size at first maturity have increased and spawning activity outside the known main spawning season has intensified.

These and other recorded changes in the biology and dynamics of *S. aurita* in the western Gulf of Guinea ecosystem in the last two and a half decades, constitute what may be described as the 'Sardinella puzzle'. This paper presents some pieces of the puzzle and discusses the merits and demerits of hypotheses that have been put forward to explain the observed changes.

1. AVAILABLE DATA AND ANALYSIS

The data used in this paper were obtained from the landings of purse-seiners and canoes in Côte-d'Ivoire and Ghana. They are as follows:

- Total annual catch of the Ghanaian and Ivoirian sardinella fishing crafts from 1966 to 1993;
- Fortnightly catch, effort (in days of search), catch per unit of effort (CPUE) for the Ivoirian purse seiners in seven fishing areas (delimited by degrees of longitude) off Côte-d'Ivoire and Ghana for the same time period;
- Annual catch, effort (in trips) and CPUE in Ghana from 1972 to 1993 and for four fishing area (administrative areas from West to East: Western, Central, Greater Accra and Volta Region);

- Selected length-frequency data on sardinellas in Ghana and Côte-d'Ivoire, since 1963 and 1968, respectively;
- Maturity stage, gonad weight and body weight of female fishes obtained from two periods: 1964-1970 (in both countries) and 1988-1991 (in Côte-d'Ivoire).

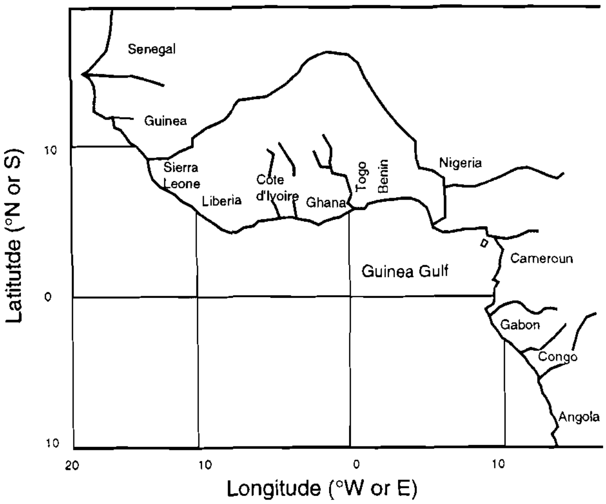

Fig. 1a: West Africa from Senegal to Angola (from Binet, 1983).

To fish for Sardinella, the canoes use a gillnet called 'Ali', and beach seines and purse seine-type nets called 'Poli' and 'Watsa' in both Ghana and Côte-d'Ivoire. However, these three gears are lumped for statistical purposes and in this paper their catch, effort and CPUE are labeled as APW in the figures.

In spite of its limitation for assessment of pelagic fish stocks, CPUE is used here as the index of abundance. As pelagic fish are usually found in schools, their abundance has two components: the size of the school and the number of schools per unit area (spatial density).

The gonado-somatic index GSI, defined as GW/aL^n where GW is the gonad weight, L is the fork length of the fish, and n is the exponent in the length-weight relationship, was used to describe spawning activity. Following Ni and Sandeman (1984), length at first maturity (L_m) was estimated from a logistic relationship of the form:

$$P = 1/(1+e^{-(a+bL)})$$

where P is the estimated proportion of mature fish at fork length L, and a and b are constants. The logit of the equation, i.e.

$$\text{Logit } P = \text{Ln}\,(P/(1-P)) = a + bL$$

gives the length at first maturity, L_m, for $P = 0.5$.

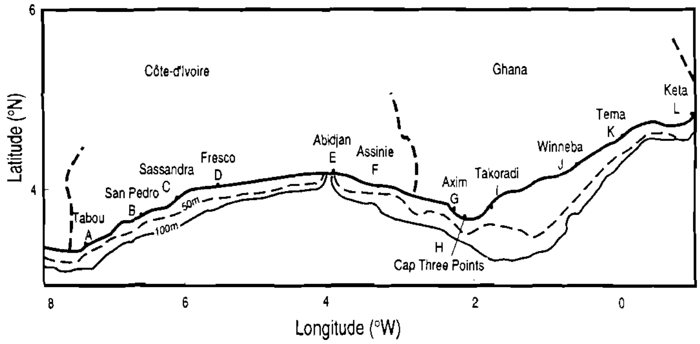

Fig. 1b: Ivoirian and Ghanaian continental shelves and coastal stations.

2. OBSERVED CHANGES

2.1. Catch, abundance and dynamics

2.1.1- *Evolution of fishing effort*

The activity of the small-scale fishing fleets (canoes and beach seines) increased in both countries from the mid 1970s to the mid 1980s (Fig. 2). From 1983 to 1989, the number of fishing trips by canoes fishing for small pelagics in Ghana first declined, then increased. In Côte-d'Ivoire, the effort of the Ivoirian purse-seiners decreased between 1969 and 1975; there was a fifty percent reduction in the number of boats in 1973. Effort began to rise in 1976, reaching a maximum in 1979 and then declined again afterwards. There has been a steady growth in the effort of this fleet since 1985.

2.1.2- *Trends in the landings and abundance of* S. aurita

Until 1972, total landings of the two sardinella species in the whole of the western Gulf of Guinea never exceeded 50.10^3 t. During the 1972 fishing season, over 70.10^3 t of *S. aurita* was caught off Ghana alone, leading to an apparent "overfishing". Between 1973 and 1975, catches dropped to an average of 4 400 t from the whole sub-region. In 1976, a recovery was noticed with the Ghanaian catch alone reaching about 14 000 t (Fig. 3). In subsequent years, catches fluctuated with an underlying increasing trend. During the same period, catches off Côte-d'Ivoire increased

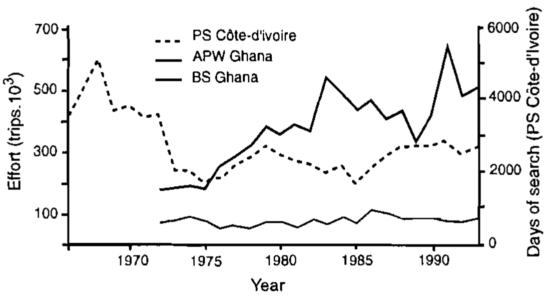

Fig. 2: Annual effort of the Ghanaian beach seine (BS) and Ali-Poli-Watsa nets (APW) and of Ivoirian purse seiners (PS), 1972 (or 1966) to 1993.

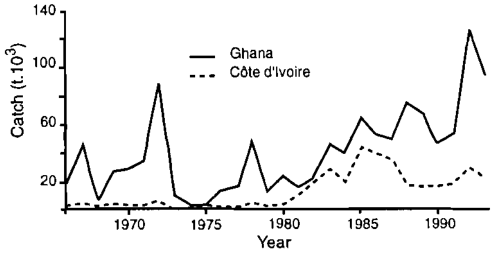

Fig. 3: Annual catch of *S. aurita* off Côte-d'Ivoire and Ghana, 1966 to 1993.

ten fold. Since 1983 high catch and abundance have been observed in both countries, and catches recorded after 1985 have either been similar to, or exceeded those of 1972. The highest total catch, in excess of 154.10^3 t, was in 1992.

2.1.3- Catch of the other small pelagic fish species

Landings of *S. maderensis* remained relatively stable from 1972 to 1992 (20 - 40.10^3 t per year) in the whole sub-region, except in 1987 when 48 200 t were landed (Fig. 4). There was also a steady increase in the landings of anchovy (*Engraulis encrasicolus*) during the last two decades, with relatively low landings in some years (1973, 1986). Over 90.10^3 t were caught in both countries in 1987. Large fluctuations in the landings of chub mackerel (*Scomber japonicus*) were observed. The combined effect is a global increase of catches of coastal pelagic species of this ecosystem in the period for which data are available.

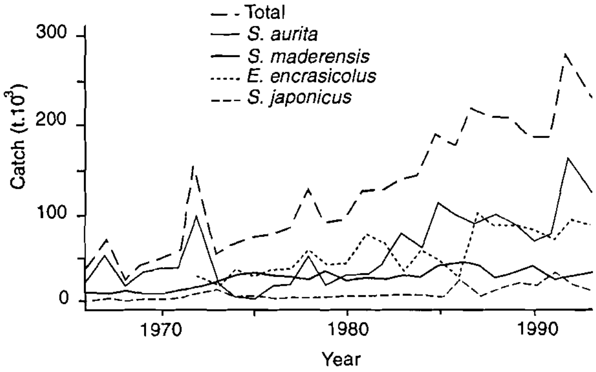

Fig. 4: Total annual landings of major small pelagic species in Ghana and Côte-d'Ivoire (*Sardinella aurita, S. maderensis, Engraulis encrasicolus, Scomber japonicus*).

2.1.4- Variation of catch and abundance with fishing effort

For *S. aurita*, the trend of catch per unit effort (CPUE) of APW canoes or beach seines in Ghana and for purse seiners and APW canoes in Côte-d'Ivoire are presented on Figure 5. Catch and CPUE of *S. aurita* are distributed in accordance with the state of the resource (Fig. 6): for the Ivoirian seiners, the inter-annual variability of total catch or CPUE with effort is very important, especially in view of the lower level of effort. Before 1981, catch and CPUE were low and increased with fishing effort. After 1981 catch and CPUE, which were much higher than in previous years, decreased with effort. The analysis of the Ghanaian data showed that in the case of *S. aurita* a situation is quite similar to that in Côte-d'Ivoire. Here, in the period 1973-1980, there were generally low values of CPUE with increasing fishing effort. With the exception of 1986, high values of CPUE have been recorded since 1985. For *S. maderensis*, in Côte-d'Ivoire, the years are randomly distributed and both catch and CPUE are highly variable given an average level of effort (Pezennec, 1994). Similar analysis of the Ghanaian data for this species showed that catch and CPUE decreased with increasing canoe effort.

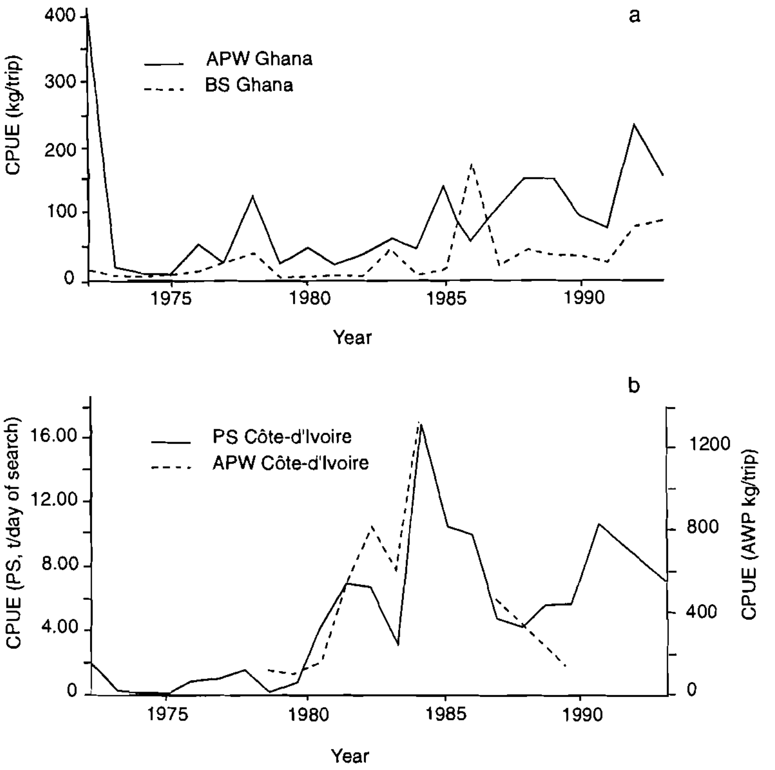

Fig. 5: Catch per unit of effort (CPUE) of *Sardinella aurita* for (a) the Ghanaian and (b) Ivoirian fleets, 1972 to 1993.

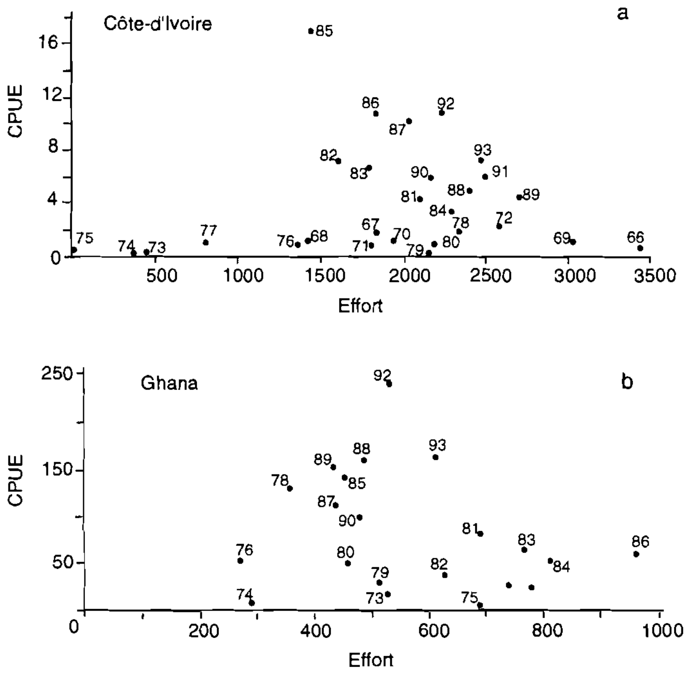

Fig. 6: Annual abundance (catch per unit of effort) of the *Sardinella aurita* off (a) Côte-d'Ivoire and (b) Ghana and theoretical effort (catch/CPUE).

Côte-d'Ivoire: CPUE: tonnes per day of search; effort: days of search.

Ghana: CPUE: kg per trip; effort: thousands of trips. For Ghana the year 1972 is not represented (CPUE= 400).

2.1.5- Development of S. aurita abundance in Côte-d'Ivoire and changes in the species composition of catch

In Côte-d'Ivoire, the average abundance (CPUE) of *S. aurita* observed during the eighties was ten times higher than during the previous years (Fig. 7). Indeed, this species became more important than *S. maderensis* and *Brachydeuterus auritus* (Pezennec, 1994), which had dominated the catch of small pelagics in the 1960s and 1970s in this country.

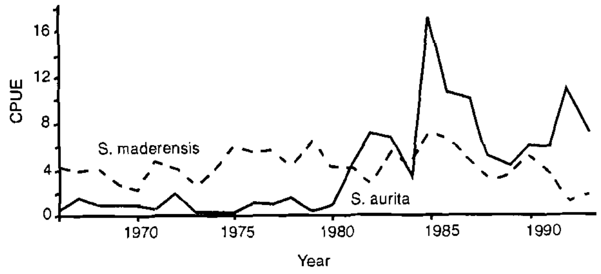

Fig. 7: Annual abundance (CPUE) of *Sardinella aurita* and *S. maderensis* off Côte-d'Ivoire from 1966 to 1993 (t per day of search for the purse seiners).

2.1.6- Extension of the spatial distribution of S. aurita

The increase of the abundance of *S. aurita* off Côte-d'Ivoire was accompanied by a spectacular extension of its distribution to the western part of the country. Since 1980, the CPUE of purse seine operations in western Côte-d'Ivoire have exceeded those from the east except for four years (Fig. 8). A similar increase was seen in the western part of Ghana where, although landings in the western areas always exceeded those from the east, the difference has widened since 1987. There were no similar changes in the distribution of the other small pelagic species in either country.

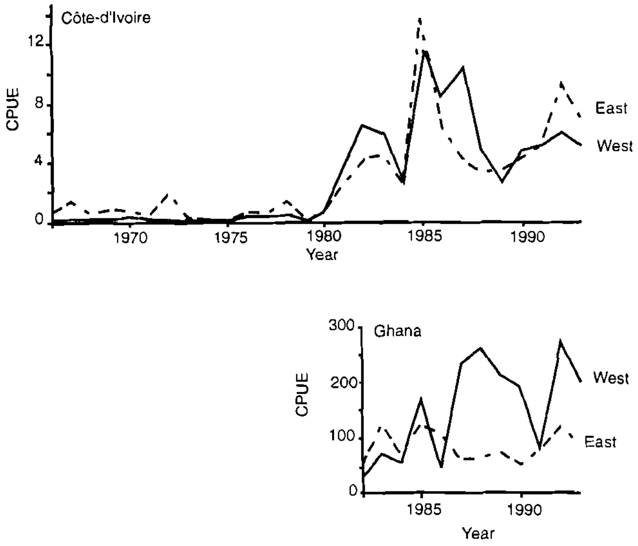

Fig. 8: Abundance of *Sardinella aurita* off the western and eastern parts of Côte-d'Ivoire (1966-1993) and of Ghana (1982-1993). Côte-d'Ivoire: t per day of search for purse seiners. Ghana: kg per trip for APW nets.

2.1.7- Importance of the S. aurita *abundance during the minor upwelling season*

Figure 9 presents CPUE values recorded during two periods, the major upwelling season and the minor upwelling season in Côte-d'Ivoire and Ghana. Whereas, in Ghana, CPUE values in the major upwelling are always higher than those in the minor upwelling, the situation is different in Côte-d'Ivoire. In the latter country, CPUE values for the GSF and PSF were equally important. Values in the GSF increased dramatically in 1981 and in subsequent years. The PSF has assumed greater importance since 1983-84, and in 1987, the CPUE recorded during this season exceeded that of the GSF. Also in Côte-d'Ivoire, there is a difference between the western and eastern parts of the country. In western Côte-d'Ivoire, the minor upwelling is as important as the major upwelling for the sustainability of the species (Pezennec, 1994).

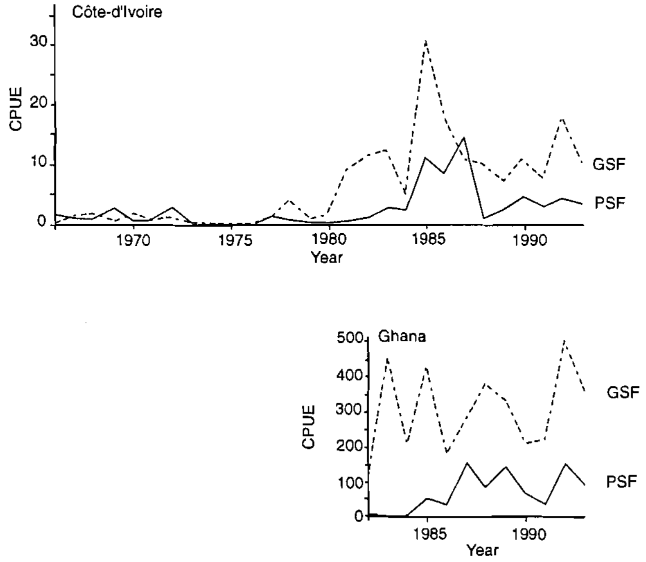

Fig. 9: Annual abundance (CPUE) of *Sardinella aurita* during the minor (PSF) and major (GSF) upwelling seasons off Côte-d'Ivoire (1966-1993) and off Ghana (1982-1993). Côte-d'Ivoire: t per day of search for purse seiners. Ghana: kg per trip for APW nets.

In all these, the limitation on the use of CPUE in pelagic resource assessment, as discussed in many studies (e.g., Saville, 1980) need not to be overlooked. One such limitation is that of the spatial distribution of the stock and (or) the fleet is reduced, the CPUE could remain constant (or even increase) even though the biomass have decreased. In this case, the abundance of *S. aurita* has increased as well as his spatial distribution.

2.2. Biological changes

2.2.1- Increase in sizes of fish caught

In the early 1960s and 1970s, the modal size (fork, length) of *S. aurita* caught off Côte-d'Ivoire was between 15 and 18 cm (ORSTOM/FRU, 1976; Fig. 10). During the 1980s, this modal size was between 18 and 24 cm and a similar increase of the maximum size of the fishes caught was also observed. In Ghana, an increase of the modal size was also observed, from 14-17 in the early 1960s to 17-21 in the 1980s.

Also observed is an increase in the length at first maturity of *S. aurita* in Côte-d'Ivoire from 15-16 cm in 1969 to 19-20 cm in 1990 (Fig. 11). Quaatey (1993) similarly noted an increase for female fish caught in Ghanaian waters, from 14.5 cm to 17.1 cm.

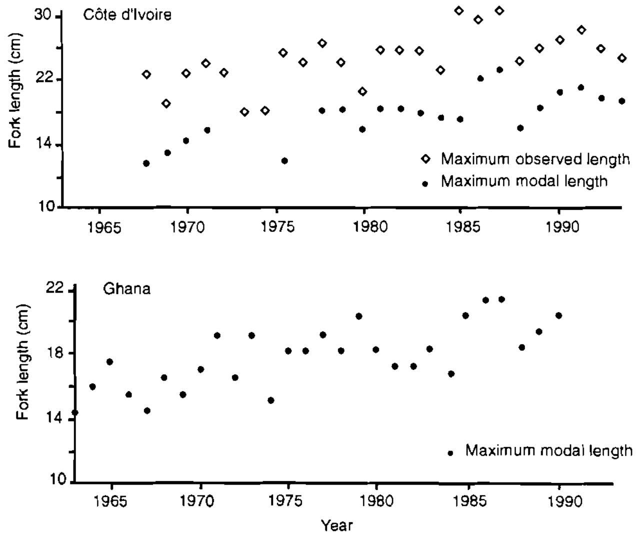

Fig. 10: Maximum modal length and maximum observed length (fork length, in cm) of *Sardinella aurita* caught off Côte-d'Ivoire and Ghana from 1963 to 1990.

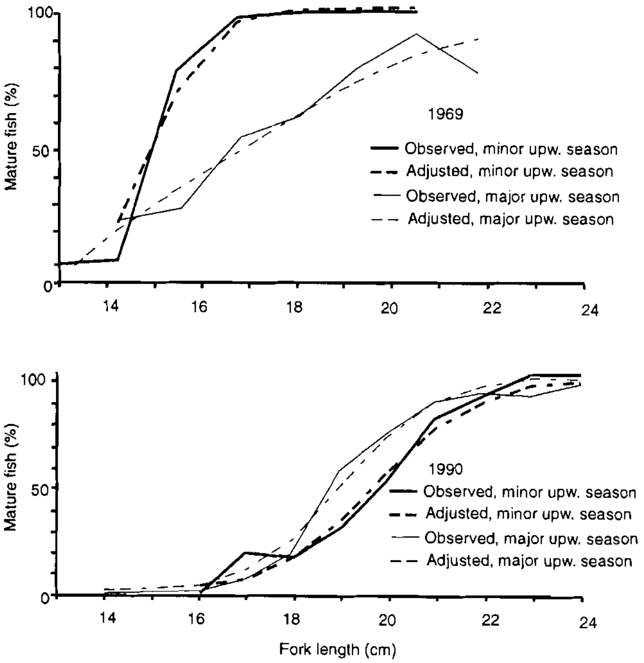

Fig. 11: Sexual maturity of the females of *Sardinella aurita* caught off Côte-d'Ivoire during the 1969 and 1990 upwelling seasons: percentage of mature fishes observed and adjusted values (logistic function).

2.2.2- Changes in spawning activity

S. aurita was known to spawn mainly during the upwelling seasons (ORSTOM/FRU, 1976), especially during the major upwelling. In Côte-d'Ivoire, observed GSI were during the minor upwelling season and part of the warm season (March, April), as large as during the major upwelling season (Fig. 12). In recent years, it has become clear that both cold periods occurring off Côte-d'Ivoire are fully utilized by *S. aurita* for spawning. Quaatey (1993) also reported an increased gonadal development and spawning activity of the *S. aurita* outside the major upwelling season. No such changes were observed for *S. maderensis* (Pezennec, 1994).

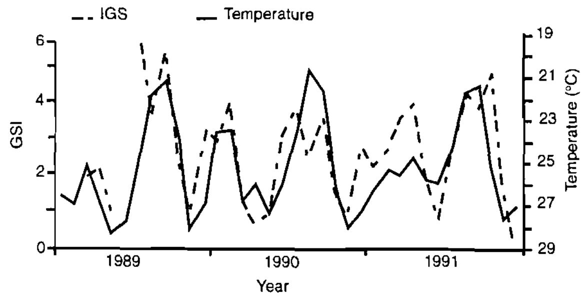

Fig. 12: Gonado-somatic index of *Sardinella aurita* caught off Côte-d'Ivoire and mean temperature (from warmer to colder) off Tabou and Abidjan. Monthly means, 1989-1991.

2.3. Influence of the biological changes on the dynamics of fish and fishery

The general increase in size of fish has effect on the total weight of fish landed. In Côte-d'Ivoire, for example, similar numbers of *S. aurita* individuals were caught during the 1986 (120 millions) and 1988 (140 millions) fishing seasons, but the landed weight in 1986 was double that of 1988 (Pezennec, 1994).

All things being equal, the increase in size at first maturity and modal size should result in increase in the fecundity of the fish. A fish of 23 cm long is expected to release a quantity of eggs twice as high as a 18 cm long fish (Fontana and Pianet, 1973; Boëly, 1982). This increase in fecundity may result in an increase of recruitment and hence, of the total biomass of the fish.

3. DISCUSSION

3.1. Hypotheses

The observed changes in the dynamics and biology of *S. aurita* surely constitute a puzzle, the solution of which possibly requires a deeper understanding of the fishery and the nature of changes in the physico-chemical parameters of the

Ivoiro-Ghanaian ecosystem. Some of these changes in the past led to certain hypotheses being proposed by researchers. These hypotheses were based on observations of the fluctuations in the biotic and abiotic components of the ecosystem.

One of the earliest suggestions attributed the decline of *S. aurita*, in part, to the increase of triggerfish *Balistes capriscus*, a semi-pelagic fish in coastal waters off Côte-d'Ivoire, and especially off Ghana (ORSTOM/FRU, 1976). *B. capriscus* drastically declined since 1988 (FAO, 1992). It is obvious now that, although the rise and fall of *B. capriscus* was observed between 1970 and 1988, and the decline of *S. aurita* occurred during the early part of this period, the recovery of the round sardinella began before the decline of the triggerfish. Furthermore, except perhaps for their juveniles, the two species do not have the same ecological requirements (Caverivière, 1991).

Various models developed to facilitate understanding of the dynamics of the pelagic resources of Côte-d'Ivoire and Ghana (Binet, 1982; Cury and Roy, 1987) failed to explain the increase in abundance of *S. aurita* in the 1980s (Pezennec, 1994).

Increase in wind speed has been suggested to lead to an increase of upwelling off Côte-d'Ivoire and Ghana (Roy, 1992). However, these upwellings are not entirely related to the wind and in fact, the annual values of mean temperature and wind speed or Ekman transport.are positively correlated during the GSF and showed no relationship during the PSF (Pezennec and Bard, 1992). Thus, increase of wind speed has not led to an increase of upwelling. However, an increase in this environmental factor leads to increase of superficial mixing and turbulence, which have been hypothesized to increase productivity only if wind speed does not exceed 6 $m.s^{-1}$ (Cury and Roy, 1989).

Binet *et al.*, (1991) and Herbland and Marchal (1991) have attributed the increase of abundance of *S. aurita* off Côte-d'Ivoire to changes in water currents and (or) intensity of the upwelling in the western and eastern regions off this country. The 'current hypothesis' is based on the notion that an increase of the westward circulation may have increased the drift of *S. aurita* larvae from the Ghanaian shelf and their retention off Côte-d'Ivoire, resulting in increased recruitment off the latter country. This hypothesis thus implies displacement of the Ghanaian stock of *S. aurita* towards Côte-d'Ivoire and a decrease of recruitment of the species off Ghana. Following this hypothesis, a decline in abundance of *S. aurita* should occur off Ghana. However, catches and abundance off Ghana have increased just as in Côte-d'Ivoire. Another hypothesis postulated a displacement of the centre of the upwelling off Côte-d'Ivoire from west to east. This, however, is based on a short time series of coastal sea surface temperature and obviously contradicts the observed increase in catch and abundance of *S. aurita* in the western part of Côte-d'Ivoire.

The above hypotheses have failed to explain the dynamic changes in the Ivoiro-Ghanaian ecosystem and in the biology of sardinella, particularly on its Ghanaian side. These changes constitute a puzzle of observed facts which need to be explained by a hypothesis that would take into consideration the dynamics of the fishery and of the ecosystem, and the biology of the species.

3.2. Ecological importance of the minor upwelling season

A new hypothesis, which deals with the part played by the second or minor upwelling season in the changes observed in the Ivoiro-Ghanaian coastal pelagic ecosystem was proposed by Pezennec and Bard (1992). This ecosystem is characterized by two independent upwellings. However, the influence of the minor upwelling has never been taken into consideration as an important event for the productivity of the ecosystem and for the dynamics of the pelagic species. This hypothesis gives greater importance to the minor upwelling in the sustenance of the Ivoiro-Ghanaian pelagic ecosystem, and the role that it plays regarding the biology of the *Sardinella aurita* and dynamics of the small pelagic fisheries. The hypothesis in question assumes that the intensity of the minor upwelling may have been underestimated and that the difference between the intensities of the two upwellings exhibited a decreasing trend between 1970 and 1990, as shown by Pezennec and Bard (1992) and Koranteng and Pezennec (this vol.).

3.2.1- Favourable and unfavourable periods

Outside of the major upwelling season, the pelagic species of the ecosystem studied here are faced with unfavourable condition. Several ecological theories insist on the necessity of a global approach to the population-environment system (Barbault, 1981). Taking qualitative approach to the problem of food limitation, one notes that it may be seen as sufficient on a global (annual) basis, but insufficient during a critical period or season. In this case, production of food during this period will be a limiting factor.

3.2.2- The minor upwelling season and productivity of the pelagic ecosystem

Studies into the productivity of the upwelling ecosystem have shown the importance of cooling periods outside the main upwelling season. Zooplanctonic biomass is highly correlated with these coolings (Binet, 1983). The minor upwelling season and the other cooling events occuring outside the main upwelling season are low productivity periods for the pelagic ecosystem, and may function as a 'bottlenecks' in term of productivity. So, an increase of the strength of the minor upwelling season in the ecosystem should be of great importance.

3.2.3- Importance of the minor upwelling season for S. aurita

It has been shown that the spawning activity of *S. aurita* is similar during the minor and major upwelling seasons. This provides *S. aurita* with extended opportunities for exploitation of the ecosystem in terms of spawning and recruitment. The Guinea Current creates on the eastern side of Cape Palmas and Cape Three Points two areas of cyclonic circulation which favours larval retention (Marchal and Picaut, 1977). Thus, the western part of the Ivoirian continental shelf (where the minor upwelling season is most intense) is a favourable area for larval survival.

The parallel changes of maximum length and length at first maturity are in conformity with the usual relationship between these two lengths (Beverton and Holt, 1959). According to Pauly (1984), the increase of these sizes should correspond to changes in key environmental factors (decrease of temperature or increase of the availability or density of food) which limit the growth of fish in an ecosystem.

Further, the increase of the abundance of *S. aurita* in Côte-d'Ivoire, first during the major upwelling season, and later during the minor upwelling season, may be explained by MacCall's theory (1990) of density-dependent geographic distribution of biomass.

3.2.4- Recovery from a depleted state

Figure 6 shows that the stock of *S. aurita* recovered from its previous depleted state (see Peterman *et al.* (1979) and Cury (1991)).

There have been significant changes in the dynamics of small pelagic fisheries in the Ivoiro-Ghanaian coastal marine ecosystem in the last two decades. After the decline of the fisheries in the early 1970s, total catches of the principal small pelagic species in this ecosystem (especially of the round sardinella, *Sardinella aurita*) increased in the 1980s and early 1990s. The stock of *S. aurita* appears to have recovered from its depleted state, especially off Côte-d'Ivoire. Also observed are changes in some aspects of the biology of *S. aurita*. These changes are not in conformity with earlier hypotheses put forward to explain the dynamics of small pelagics in the western Gulf of Guinea or other ecosystems. However, most of the observed changes in the biology and dynamics of *S. aurita* resources can be attributed to the increasing impact of the minor upwelling on the ecosystem. This minor upwelling, which is more intense off Côte-d'Ivoire than off Ghana, occurs during an environmentally unfavourable period of the year for the productivity of the pelagic ecosystem, and which acted as a 'bottleneck'.

No comparable changes have been observed in the biology and dynamics of the other small pelagic species of this ecosystem. Cury and Fontana (1988) have shown, for example, that *S. aurita* and *S. maderensis* have different demographic and adaptive strategies. According to these authors *S. aurita* is more sensitive to environmental fluctuations and could take advantage of them. Therefore, utilization of the relative changes in the intensity of the two upwelling seasons could be an illustration of this difference between the two sardinella species.

The stocks of the Indian oil sardine (*Sardinella longiceps*; Longhurst and Wooster, 1990) and sardinellas in the Benguela system (*S. aurita* and *S. maderensis*; Crawford *et al.*, 1987), have experienced similar changes in abundance to those observed in the Ivoirian and Ghanaian ecosystem. It would be very interesting and useful to do a comparative study of these ecosystems and their populations.

ACKNOWLEDGMENTS

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REFERENCES CITED

Barbault R. 1981. *Ecologie des populations et des peuplements*. Masson, 200 p.

Beverton R.J.H. and S.J. Holt. 1959. A review of the lifespans and mortality rates of fish in nature, and their relation to growth and other physiological characteristics. p. 142-177. *In*: G.E.W. Wolstenholmen and M. O'Connor (eds.). Ciba Found Colloquium on Ageing: the lifespan of animals. Vol. 5, Churchill, London.

Binet D. 1982. Influence des variations climatiques sur la pêcherie des *S. aurita* ivoiro-ghanéennes: relation sécheresse-surpêche. *Oceanol. Acta*, 5 (4): 443-452.

Binet D. 1983. Zooplancton des régions côtières à upwellings saisonniers du golfe de Guinée. *Océanogr. trop.*, 18 (2): 357-380.

Binet D., E. Marchal and O. Pezennec. 1991. *Sardinella aurita* de Côte-d'Ivoire et du Ghana. Fluctuations halieutiques et changements climatiques. *In*: P. Cury and C. Roy (eds.). *Pêcheries ouest-africaines. Variabilité, instabilité et changement*. ORSTOM, Paris: 320-342.

Boëly T. 1982. Etude du cycle sexuel de la sardinelle ronde (*Sardinella aurita* Val. 1847) au Sénégal. *Océanogr. trop.*, 17 (1): 3-13.

Caverivière A. 1991. L'explosion démographique du baliste (*Balistes carolinensis*) en Afrique de l'ouest et son évolution en relation avec les tendances climatiques. *In*: P. Cury and C. Roy (eds.). *Pêcheries ouest-africaines. Variabilité, instabilité et changement*. ORSTOM, Paris: 354-367.

Cury P. 1991. Les contraintes biologiques liées à une gestion des ressources instables. *In*: P. Cury and C. Roy (eds.). *Pêcheries ouest-africaines: variabilité, instabilité et changement*. ORSTOM, Paris: 506-518.

Cury P. and C. Roy. 1987. Upwelling et pêche des espèces pélagiques côtières de Côte-d'Ivoire: une approche globale. *Oceanol. Acta*, 10 (3): 347-357.

Cury P. and A. Fontana. 1988. Compétition et stratégies démographiques comparées de deux espèces de sardinelles (*Sardinella aurita* et *Sardinella maderensis*) des côtes ouest-africaines. *Aquat. Living. Ressour.*, 1: 165-180.

Cury P. and C. Roy. 1989. Optimal environmental window and pelagic fish recruitment success in upwelling areas. *Can. J. Fish. Aquat. Sci.*, 46: 670-680.

Crawford R.J.M., L.V. Shannon and D. E. Pollock. 1987. The Benguela ecosystem. Part IV. The major fish and invertebrate resources. *Oceanogr. Mar. Biol. Ann. Rev.*, 25: 353-505.

FAO. 1992. *Rapport du groupe de travail ad hoc sur les stocks de pélagiques côtiers du golfe de Guinée ouest* (Côte-d'Ivoire-Ghana-Togo-Bénin). 10-16 Décembre 1990, Abidjan.

Fontana A. and R. Pianet. 1973. Biologie de *Sardinella eba* (Val.) et *Sardinella aurita* (Val.) des côtes du Congo et du Gabon. *Doc. scient. Cent. ORSTOM Pointe-Noire*, 430, 21 p.

Herbland A. and E. Marchal. 1991. Variations locales de l'upwelling, répartition et abondance des sardinelles en Côte-d'Ivoire. *In*: P. Cury and C. Roy (eds.). *Pêcheries ouest-africaines. Variabilité, instabilité et changement*. ORSTOM, Paris: 343-353.

Longhurst A.R. and W.S. Wooster. 1990. Abundance of oil sardine (*Sardinella longiceps*) and upwelling on the southwest coast of India. *Can. J. Fish. Aquat. Sci.*, 47: 2407-2419.

MacCall A., 1990. *Dynamic geography of marine fish populations*. Washington Sea Grant, University of Washington, 153 p.

Marchal E. and J. Picaut. 1977. Répartition et abondance évaluées par échointégration des poissons du plateau continental ivoiro-ghanéen en relation avec les upwellings locaux. *J. Rech. Océanogr.*, 2(4): 39-57.

Mensah M.A. and K.A. Koranteng. 1988. A review of the oceanography and fisheries resources in the coastal waters of Ghana, 1981-1986. *Marine Fishery Research Reports*, 8. Fisheries Department, Research & Utilization Branch, Tema, Ghana.

Ni I.H. and E.J. Sandeman. 1984. Size at maturity for northwest Atlantic redfishes (*Sebastes*). *Can. J. Fish. Aquat. Sci.*, 41: 1753-1762.

ORSTOM/FRU 1976. *Rapport du groupe de travail sur la Sardinelle (Sardinella aurita) des côtes ivoiro-ghanéennes*, Abidjan 28 juin-3 juillet 1976.

Pauly D. 1984. A mechanism for the juvenile-to-adult transition in fishes. *J. Cons.*, Cons. int. Explor. Mer, 41: 280-284.

Peterman M.R., W.C. Clark and C.S. Holling. 1979. The dynamics of resilience: shifting stability domains in fish and insect systems. *In*: R.M. Anderson, B.D. Turner and L.R. Taylor (eds.). *Population dynamics*. Blackwell Scientific Publications: 321-341.

Pezennec O. 1994. *Instabilité et changements dans l'écosystème pélagique côtier ivoiro-ghanéen. Variabilité de la ressource en sardinelles: faits, hypothèses et théorie.* Thèse de Doctorat. Océanologie Biologique. Université de Bretagne Occidentale, Brest.

Pezennec O. and F.X. Bard. 1992. Importance écologique de la petite saison d'upwelling ivoiro-ghanéenne et changements dans la pêcherie de *Sardinella aurita*. *Aquat. Living Resour.*, 5:249-259.

Quaatey S.N.K. 1993. *Long-term changes in the reproductive cycle and population parameters of Sardinella aurita in Ghanaian waters.* M.Sc. Dissertation, University of Wales, U.K.

Roy C. 1992. *Réponses des stocks de poissons pélagiques à la dynamique des upwellings en Afrique de l'ouest: analyse et modélisation.* Thèse dr. Univ. Bretagne Occid., Brest, 149 p.

Saville A. (ed.). 1980. The assessment and management of pelagic fish stocks. *Rapp. P.-v. Réun. Cons. int. Explor. Mer*, 177, 517 p.

Stock Assessment of Sprat and Whiting in the Western Black Sea in Relation to Global and Local Anthropogenic Factors

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ABSTRACT

Historical stock assessments of the Black Sea sprat (1957-1992) and whiting (1976-1992) have been performed using Virtual Population Analysis. Relationships between fish stock parameters (recruitment, spawning biomass, mortality rates) and environmental variables (wind speed and duration, sea temperature, light, phyto- and zooplankton biomasses) have been analyzed using multiple regression models. Strong correlation has been found between sprat recruitment and western winds during November-December and January-March. The western winds force the upwelling of deep waters and their progress shorewards. As the upwelled waters are rich in nutrients and organic matter, they contribute to the intense productivity in the Black Sea. The role of the other variables appears to be less significant. The need for including more reliable data on plankton and ctenophore *Mnemiopsis maccradii* in the analysis is pointed out.

RÉSUMÉ

L'évaluation à long terme du stock du sprat *Sprattus sprattus* L pour la période 1957-1992 et du merlan *Merlangius merlangus euxinus* de 1976 à 1992 en mer Noire a été effectuée par l'analyse des cohortes (VPA, analyse virtuelle des populations). Les relations entre les paramètres des stocks de poisson (recrutement, biomasse féconde et taux de mortalité) et des variables environnementales (vitesse du vent et durée des événements de vent d'ouest, température de la mer, activité solaire, biomasses du phyto- et du zooplancton) ont été analysées avec des modèles de régression. Une corrélation importante a été trouvée entre le recrutement du sprat et les données du vent d'ouest pour novembre-décembre et janvier-mars. Le vent d'ouest est responsable d'un upwelling côtier qui apparaît à certains endroits en fonction de la topographie. La remontée d'eau enrichie en éléments nutritifs et en matière organique, qui contribue aux taux de production, augmente dans ces régions. La contribution des autres variables est moins significative. L'importance d'analyser des données de meilleure qualité sur le plancton et sur le cténophore *Mnemiopsis maccradii* est soulignée.

INTRODUCTION

During the last 30-35 years, the Black Sea ecosystem has been subjected to dramatic changes due to the increased pollution of the basin and the overexploitation of the main commercial fish species. The period of eutrophication dating back to the early 1970s is characterized by structural and functional alterations in the ecosystem as a result of the intensification and spreading of both local and regional phytoplankton blooms. These blooms over the last decade attain their maximum intensity in late spring-summer, a period abnormal for the Black sea, where peak production normally occurred in early spring and autumn. Changes have also been registered in the taxonomic composition of bloom-producing phytoplankton species with succession shifted towards the predominance of Dinophyta and since 1989 — towards an increasing importance of *Chrysophyta* species — *Emiliania huxleyi* and *Phaeocystis pouchettii* (Moncheva, 1991, 1992). Recently some new phyto- and zooplankton species for the Black Sea ecosystem have invaded the basin resulting in dramatic alterations in the food web (Moncheva *et al.*, 1995). During the period under consideration, the abundance of the most common carnivores has sharply decreased: bonito (*Sarda sarda* Bloch), bluefish (*Pomatomus saltator*) and mackerel (*Scomber scombrus*) have almost become extinct in the Black Sea since 1986. This has been the period of rapid intensification of fishing particularly of sprat, horse mackerel (*Trachurus mediterraneus ponticus*) and anchovy (*Engraulis encrasicolus ponticus*) catches of which have been extended from 3.1, 4.9 and 193.3 10^3 t (1970) up to 105.2 (1989), 147.7 (1985) and 502.6 (1984) thousand t, respectively. Shljakhov *et al.* (1990) claim that the rapid decline of sprat stock is related both to the deteriorated environmental conditions and to overfishing. In 1982, the ctenophore *Mnemiopsis leidyi* invaded the Black Sea (Zaitsev, 1994; Konsulov and Konsulova, 1993) with a biomass attaining its maximum in 1990-1991 and decreasing thereafter. In 1991 and 1992, the ctenophore biomass was 40.9 and 18.6 million t, respectively. This has resulted in a reduction in the biomass of zooplankton consumed by fish, and of copepod species in particular (Vinogradov *et al.*, 1989; Zaika and Sergeeva, 1991). Taking into account the fact that *M. leidyi* feeds on eggs and larvae of spawning fish, although at less significant rate (Eremeev and Chudinovsky, 1990) it is reasonable to assert that the sharp reduction in sprat, anchovy and horse mackerel stocks is due mainly to the complex impact of the four above mentioned factors: pollution, eutrophication, structural alterations in the ecosystem and intensification of exploitation. All four factors are of local origin and should be distinguished from factors such as global climatic changes, and their impact on the hydrology and hydrochemistry of the basin (Brjantzev, 1989). An example of such global effects is that of sunlight on phytoplankton (Petrova-Karadjova, 1993; Petrova-Karadjova and Apostolov, 1988).

The results of virtual population analyses (VPA) are reported; they aimed at the assessment of sprat abundance and biomass dynamics over the period 1957-1992. Based on these results, an attempt is made to highlight the impact of some abiotic and biotic factors related to global and local anthropogenic causes.

1. MATERIAL AND METHODS

The sprat data for VPA to be applied over the period 1957-1992 were collected and analyzed in conformity with the research program of the international project Environmental management of Black Sea fish resources and their rational exploitation, funded by the Central European University Foundation. Experts from Bulgaria, Romania, Ukraine and Turkey participate in this project, which facilitated the integration of available data, including that of fishery statistics. Thus, it became possible for the first time to perform a retrospective assessment of sprat stock in the western part of Black Sea, where most of the catch originates.

The age composition of sprat catches in the abovementioned regions are presented in Table 1 and Figure 1. Until 1974, the fishery was carried out mostly by coastal fishing gear (trap nets), while thereafter, it was carried out mainly from ships. Thus, after 1974, the catch by coastal fishing gear does not exceed 5% of total catch. That is why the calculated fishing effort for the 1975-1992 period is based on the catch/effort of the fishing fleet and those for the preceding period, on the number of trap nets in the Black Sea countries. Another peculiarity that was considered is the space distribution of the different age groups, as the 3, 4 and 5 years old fishes normally line further offshore, which is why trap net catches are dominated by 1- and 2-year old individuals. With the beginning of the fishing fleet operation deeper waters became exploited, from 20-25 down to 80-110m which resulted in considerable changes in the age composition of the catch (Table 1, Fig. 1). Still, the 1- and 2-year old fishes dominate over the 3-year old individuals, and especially on the 4- and 5-year old fishes (integrated in the age group 4+). The explanation lies in the fact that trawl sprat fishing is of highest intensity in spring-summer months (April-July and in some years in August) at 20-40m depth, when the young-age groups (1- and 2-years), move towards the coastal zone for feeding. During this period the thermocline is located at 15-30m. That is why the older age groups, which prefer colder waters, may be found in deeper waters, although food availability there is

Years	0+	1+	2+	3+	4+	5+	Total	Catch in weight (C)
1957	281.63	2216.94	91.52	7.91	0.00	0.00	2598.00	6534
1958	214.06	1459.66	257.17	4.99	0.00	0.00	1935.88	5793
1959	74.70	410.25	822.50	75.98	0.00	0.00	1383.43	5917
1960	0.00	781.81	254.61	127.75	0.00	0.00	1164.17	4541
1961	612.95	493.98	372.50	36.56	0.00	0.00	1515.95	4228
1962	246.46	557.74	605.77	89.53	4.72	0.00	1504.22	5342
1963	0.00	749.36	334.88	93.91	4.41	0.00	1182.56	4418
1964	42.44	1772.23	442.88	55.84	7.58	0.00	2320.97	7640
1965	0.00	2739.56	335.34	35.15	6.51	0.00	3116.56	9480
1966	0.00	783.46	94.20	0.00	0.00	0.00	877.66	2704
1967	89.85	507.88	210.08	21.78	1.77	0.00	831.36	2669
1968	84.65	848.15	313.46	64.98	6.91	0.00	1318.50	4597
1969	27.67	316.19	179.44	27.74	1.89	0.00	552.93	2560
1970	37.60	646.78	77.26	10.43	1.07	0.00	773.14	3068
1971	36.98	497.49	440.44	16.74	1.40	0.01	993.06	4662
1972	59.62	407.22	586.71	110.33	1.49	0.00	1165.37	6142
1973	54.91	512.79	513.68	145.92	1.92	0.02	1292.24	6483
1974	32.83	1401.73	175.90	20.68	1.04	0.00	1632.18	6253
1975	0.63	320.08	973.40	134.55	53.18	4.81	1486.65	7127
1976	1.01	209.81	758.46	399.49	110.94	7.78	1487.49	10420
1977	45.92	555.45	715.81	551.63	253.33	4.58	2126.72	16917
1978	222.54	1771.58	1282.85	939.46	234.73	34.87	4486.03	34893
1979	422.41	4309.72	3432.60	1543.36	355.96	13.77	10077.82	73732
1980	15.40	8464.69	4055.19	757.59	410.88	100.07	13803.82	84450
1981	39.16	7981.03	4190.29	953.01	288.69	193.60	13644.78	96284
1982	19.23	8048.58	2562.35	336.67	115.31	75.08	11157.82	75876
1983	13.50	5477.16	800.38	381.61	165.07	58.09	6895.81	40913
1984	19.67	6926.63	915.52	195.22	87.14	9.17	8153.35	42515
1985	27.78	7179.45	1872.86	240.56	31.11	0.00	9351.76	51271
1986	18.18	9112.10	2540.13	1044.34	185.99	0.00	12900.74	63610
1987	22.04	6550.62	5487.69	1149.77	92.71	0.00	13302.83	79591
1988	1.48	9181.94	1433.27	885.91	262.81	0.00	11765.41	66819
1989	22.29	9349.17	5268.56	2176.05	902.64	0.00	17718.71	105170
1990	64.97	4613.33	2734.95	2060.84	319.30	0.00	9793.39	53896
1991	28.26	2761.78	470.08	36.08	20.29	0.00	3316.49	18405
1992	10.06	1602.65	1274.40	320.37	58.32	4.43	3270.23	19431

Table 1: Age composition ($N.10^6$) of sprat catches in the western part of Black Sea, 1957-1992.

lower. The two periods (1957-1973 and 1974-1992) differ by their predator abundances, which dropped sharply after 1971-1972, with favorable effect on their prey: sprat, anchovy and horse mackerel. Stoyanov (1966) estimated a total mortality rate of 1.14 $year^{-1}$ in 1959 for 1- and 2-year old sprats. The same author, however noted that this figure may be an underestimate, due to the underestimation of 1- year old fish abundance. The analysis of sprat catch suggests that, in that particular year, total mortality was almost equal to natural mortality, e.g. in the range 1.15-1.20 $year^{-1}$. Our estimation of sprat natural mortality for the period 1957-1973, based on indirect estimates of the biomass of their predators (mackerel, bonito, bluefish), are presented in Table 2.

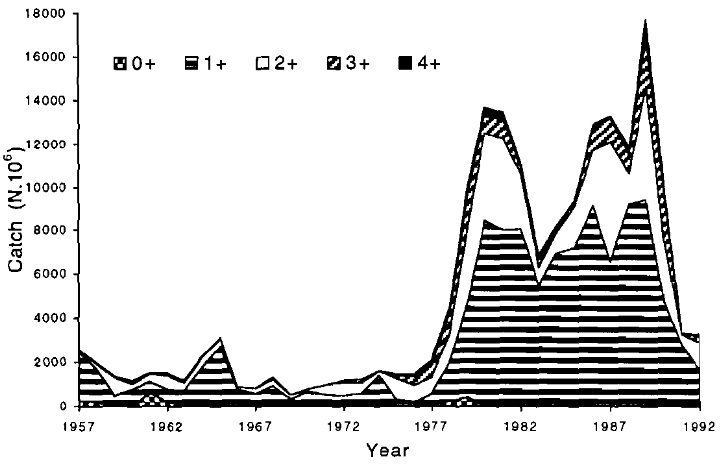


Fig. 1: Bulgarian sprat catches by age groups (N 10^6) from 1957 to 1992.

Year	M	Year	M	Year	M	Year	M
1957	1.27	1961	1.32	1965	1.22	1969	1.31
1958	1.17	1962	1.29	1966	1.27	1970	1.25
1959	1.18	1963	1.25	1967	1.36	1971	1.13
1960	1.32	1964	1.15	1968	1.34	1972	1.06
—	—	—	—	—	—	1973	0.98

Table 2: Estimates of natural mortality coefficient for sprats (M . $year^{-1}$).

After 1973, a constant M of 0.95 $year^{-1}$ value was assumed (Domashenko and Ijurev, 1978). The relationship between spawning biomass ($B_{1\text{-}4+}$) and recruitment abundance (R) is determined by the equations of Ricker (1975) and Ivanov (1977):

$$R = aB\,e^{-bB} \qquad (1)$$

$$R = aB - bB^2 \qquad (2)$$

The influence of environmental factors on sprat recruitment was evaluated by applying linear and nonlinear relationships as well as multiple linear regression.

The correlation coefficients (r) for the corresponding equations were calculated from:

$$r = [1-\Sigma(R_{Ti} - R_{Fi})^2/(R_{Fi})^2]^{1/2} \qquad (3)$$

where : R_{Ti} = theoretical value of R_i; R_{Fi} = the observed value of R_i; R_F = mean value of R_i.

The coefficient of determination (D%) as a measure of the extent of the variability in R_i value related to the variability of the examined factors is defined by:

$$D\,\% = 100\,r^2 \qquad (4)$$

The coefficient of indetermination (S%) is a measure of the extent of the variability in R_i due to random factors, and is defined by:

$$S\,\% = 100\,(1-r^2) \qquad (5)$$

Equation (3) is applicable both in linear and nonlinear correlations.

2. RESULTS AND DISCUSSION

The changes sprat in spawning standing stock biomass ($B_{1\text{-}4+}$) from 1957-1992 in the western part of Black Sea are depicted on Figure 2. During the 1967-1992 period, sprat biomass was determined by trawling, and hydroacoustics. The results of these surveys can be compared with the VPA estimates(Table 3).

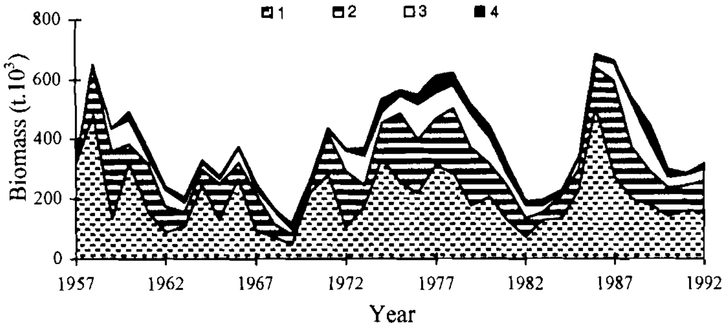


Fig. 2: Sprat spawning biomass (by age groups) in the western part of the Black Sea during 1957-1992.

Year	Surveys	VPA	Year	Surveys	VPA
1967	145.0	253.2	1980	1327.5	447.5
1968	187.0	166.7	1981	540.5	322.8
1969	210.0	114.8	1982	—	190.6
1970	152.0	271.0	1983	104.4	195.1
1971	218.0	436.0	1984	187.4	226.5
1972	134.0	326.8	1985	20.9	336.0
1973	157.0	370.7	1986	300.0	684.4
1974	370.0	534.3	1987	480.0	663.6
1975	490.0	566.0	1988	108.9	540.3
1976	400.0	546.6	1989	109.0	448.0
1977	240.0	613.4	1990	78.0	295.9
1978	633.9	623.1	1991	95.0	286.5
1979	792.5	515.9	1992	475.0	316.4

Table 3: Sprat biomass (10^3 t) in the western part of the Black Sea during 1967-1992, as estimated by hydroacoustic surveys and by VPA.

The biomass estimated by hydroacoustics refer to the entire Black Sea. As obvious in some specific years the differences between the two estimates are considerable, particularly in 1980 and 1986 (880 and 384 t.10^3, respectively). Similar differences occur between the VPA estimates of recruitment and the fingerling abundances estimated by ichthyoplankton surveys conducted in May-June (Table 4).

Year	Surveys	VPA	Year	Surveys	VPA
1967	30.9	75.9	1980	51.3	103.0
1968	51.3	45.0	1981	68.7	56.8
1969	22.0	199.0	1982	368.3	104.0
1970	74.2	229.0	1983	86.9	108.0
1971	6.1	82.8	1984	276.6	179.0
1972	163.1	137.0	1985	215.3	400.0
1973	31.5	263.0	1986	22.1	215.0
1974	32.0	201.0	1987	92.1	160.0
1975	52.0	173.0	1988	23.9	141.0
1976	28.9	247.0	1989	38.1	112.0
1977	30.5	225.0	1990	440.9	128.0
1978	60.1	140.0	1991	93.4	121.0
1979	48.6	163.0	1992	193.1	Ñ

Table 4: Estimated (N.10^9 of sprat fingerlings (0+) during 1967-1992, from ichthyoplankton surveys and VPA.

The sources for the differences in the survey and VPA estimates in Table 3 and 4 are not obvious, and, pending detailed study assumed to be due to the heterogeneity of the data we used.

The estimates of the parameters of equation (1) and (2) and their corresponding values for B_{opt} and R_{max} are presented in Table 5.

Equations	a	b	r	D%	S%	B_{opt}	R_{max}
1	0.85262	0.00185	0.535	28.62	71.38	540.1	169.4
2	0.89169	0.00124	0.543	29.48	70.52	400.6	198.6

Table 5: Parameters estimates of equations (1) and (2), and the corresponding values for B_{opt} (t.10^3) and R_{max} (N.10^{-9}).

The multiple regression model used to investigate the impact of various factors on sprat recruitment (R) has the form

$$R = a\,B+b\,Z+c\,X_1+d\,X_2+e\,X_3+f\,X_4+g\,X_5+h\,X_6 \qquad (6a)$$

Where:

B is the parental biomass;
Z the total mortality;
X_1 the phytoplankton standing stock;
X_2 the zooplankton standing stock;
X_3 the sea surface temperature;
X_4 the amount of sunlight;
X_5 the intensity of cosmic rays; and
X_6 an index of the Earth's geomagnetism.

These variables were introduced one at a time, starting with R=f(B) and ending with the full model in (6a). Table 6 summarises the results thus obtained.

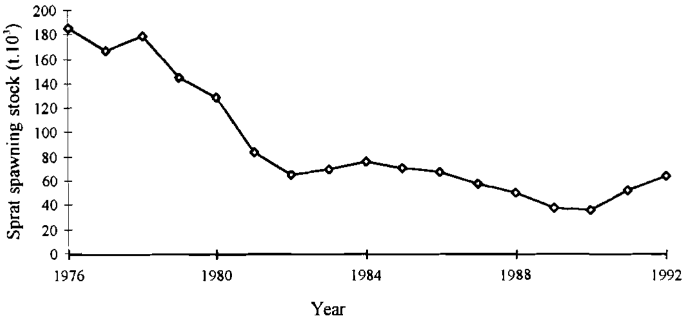
Sprat biomass along the Bulgarian Black Sea coast from 1952 to 1992 is illustrated in Figure 3. The overall trend has a maximum in the period 1974-1979, and decreases to about 35.10^6 t after some fluctuations in 1990, after which biomass again increases. The variability in sprat biomass seems mainly dependent on the number of its predators. Their sharp decrease after 1968-1971 resulted in an increase in sprat standing stock, which coincided with a period (1975-1978) of sprat fishery intensification. In 1981 the Bulgarian catches reached the figure 19.10^9 t, where after a decline occurred, especially during 1990-1991. The latter period coincides with the invasion of the new ctenophore whose biomass attained its peak in this particular period. The present trend of sprat biomass recovery may be related to the decrease in ctenophore abundance and a decrease of fishing effort.

During 1984-1990 regular hydroacoustic assessment of sprat biomass have been conducted in Bulgarian waters, in June-September, excepting the last three years, when the surveys were conducted in June. The results of these investigations together with the VPA estimates are presented in Table 7.

R =	f(B...	+ Z	$+ X_1$	$+ X_2$	$+ X_3$	$+ X_4$	$+ X_5$	$+ X_6$
a	139.4	144.1	170.3	754.2	775.1	947.0	1494.6	1746.7
b	0.068	0.072	0.050	0.067	-0.064	-0.083	-0.034	-0.111
c		-0.0073	-0.0045	-0.0043	0.0443	0.0491	0.0528	0.0310
d			-0.2217	-0.3274	-0.3007	-0.4464	-0.4536	-0.2797
e				-32.65	-24.00	-28.51	-27.00	-25.32
f					-1.30	-1.22	-1.67	-1.36
g						-3.67	-5.60	-5.67
h							-0.12	-0.14
r	0.13	0.14	0.20	0.32	0.66	0.68	0.68	0.71
D%	1.9	2.1	4.3	10.4	44.5	46.6	47.2	50.7
S%	98.1	97.9	95.7	89.6	55.5	53.4	52.8	49.3

Table 6: Parameters values in equation (6), reflecting the relationships between the abundance of sprat recruits in the western part of Black Sea and environmental factors added one at a time.

Fig. 3: Sprat spawning stock (age 1-4+) along the Bulgarian Black Sea coast from 1976 to 1992.



Year	1984	1985	1986	1987	1988	1989	1990	Mean
Surveys	24.0	69.0	77.0	16-28	74.0	25.0	70.0	51.6
VPA	76.2	71.3	67.8	57.6	50.1	37.9	35.6	56.6

Table 7: Hydroacoustic and VPA estimates of sprat biomass (t.10^3) along the Bulgarian Black Sea coast from 1984 to 1990.

From 1957 to 1992, the sprat biomass along the Bulgarian Black Sea coast comprised about 23% of total sprat biomass in the western Black Sea, but in 1989 and 1990, it represented only 8.5 and 12.0% respectively.

The values of the parameter of equation (1) and (2) concerning the relationship between sprat biomass and recruitment off the Bulgarian coast are presented on Table 8.

Equations	a	b	r	D%	S%	B_{opt}	R_{max}
1	0.98834	0.00607	0.390	15.2	84.8	164.8	59.9
2	0.49872	0.00093	0.565	31.9	68.1	268.4	66.9

Table 8 : Parameter estimates for equations (1) and (2).

The impact of fishing mortality rate during 1973-1989 is estimated by the equations:

$$R = aB - bB^2 + cBF \qquad (7)$$

$$R = aB - bB^2 + cBF + dB^2F \qquad (8)$$

The estimated parameters of these equations are presented on Table 9. This shows that fishing mortality exerts a strong impact on the stock-recruitment relationships.

Equations	a	b	c	d	r	D%	S%
7	1.1356	0.0041	1.4732	—	0.771	59.5	40.5
8	1.1082	0.0035	0.9109	0.0092	0.796	63.4	36.6

Table 9: Parameters estimates for equations (7) and (8).

The second multiple regression model used to investigate the impact of various factors on sprat recruitment (R) has the form:

$$R= aB + bF + cX_1 + dX_2 + eX_3 + fX_4 + gX_5 + hX_6 \qquad (6b)$$

where

B is the parental biomass;
F the fishing mortality;
X_1 the duration of the western wind component in November-December;
X_2 the mean speed of the western wind component in November-December;
X_3 the duration of the western wind component in January-March;
X_4 the mean speed of the western wind component in January-March;
X_5 the intensity of cosmic rays; and
X_6 the amount of sunlight.

As for equation (6), these variables were introduced one at a time, starting with R=f(B) and ending with the full model in (6b).

It is known that the western winds generate an upwelling of deep waters and their shoreward progression. As these waters are rich in nutrients they contribute to phytoplankton bloom in summer. Because of their low temperature and low O_2 content they may also be responsible, however, for regional zoobenthic mortality, including of fish species (Rozhdestvenski, 1969; Kolarov, 1970; Dimitrov and Yaneva, 1992).

During the winter similar upwelling of deep waters occurs, but unlike in summer, their temperature is higher than at the surface. For species that reproduce in winter, such as sprat, the upwelling of the deep waters towards the shelf is very dangerous such that this tends to lower the survival of the eggs and larvae.

That is why the wind factor is represented by four variables: X_1 (western wind duration in November-December with a speed above 5m/sec - in hours); X_2 (average wind speed in November-December) with X_3 and X_4 as the corresponding values for January-March.

As is apparent from the results (Table 10), the influence of wind speed is higher than that of wind duration. Wind velocity has a favorable effect while wind duration has a negative one. The joint impact of these variables on recruitment survival is considerable with r = 0.843 (D% =73.0%; S% = 27.0%).

The stock-recruitment relationship of sprat, depends both on the predator abundance and on the number of the days with water temperature below 6°C during the reproduction period (November-March). The same author points to the fact that the influence of water temperature is indirect and occurs via the food web. Similar conclusions are drawn by Feldman (1986) who has reported a strong correlation between water temperature and the recruitment of sprat and cod (*Gadus morbua*) in the Baltic Sea. During severe winters sprat recruitment is less abundant while that of cod, increases. In warmer

R =	f(B...	+ Z	+ X_1	+ X_2	+ X_3	+ X_4	+ X_5	+ X_6
a	41.9	-73.0	-55.8	-192.6	-187.0	-152.4	-153.7	75.6
b	-0.00	-0.068	-0.06	-0.021	-0.018	-0.020	-0.020	-0.017
c		16.29	15.52	8.77	8.01	7.913	7.90	4.16
d			-0.023	-0.065	-0.05	-0.052	-0.052	-0.062
e				21.31	20.16	17.95	17.91	21.68
f					0.048	-0.007	-0.008	0.093
g						-39.26	-39.13	-14.48
h							0.00	-0.052
r	0.25	0.54	0.55	0.84	0.84	0.85	0.85	0.86
D%	6.2	29.4	31.1	71.0	71.4	73.0	73.0	75.4
S%	93.7	70.5	68.8	28.9	28.5	26.9	26.9	24.5

Table 10: The parameter values in equations (6), reflecting the relationships between the abundance of sprat fingerlings along Bulgarian Black Sea coast and the investigated factors.

winters this relationship is inversed. The same author claims that low temperatures in February-March restrict zooplankton reproduction rate in the North and Baltic Sea.

Gapishko and Malyshev (1990) documented that small sprat (2.5-3.0 cm of length) feeds principally on *Calanus* and *Pseudocalanus nauplii.* According to these authors the number of individuals with empty stomach depends on the stability of the ratio between nauplii, copepodites and adult forms, as well as on the availability of other nutritive and non-nutritive zooplankton.

Prodanov and Konsulov (1987) established that sprat recruitment along the Bulgarian coast is strongly influenced by status of the food web and by whiting biomass, whose reproduction occurs during the same months and at the same depths for sprat reproduction. During its reproductive period, whiting still actively feeds on sprat and large decapod crustaceans. Small whiting has almost the same food spectrum as small sprat, which implies a high food competition. Since 1985, the recruitment of both species declined resulting in a reduction in their standing stocks.

Table 11 presents the numbers and total biomasses of sprat and whiting for the period 1976-1991, and estimates of whiting recruits (0+) in the Western Black Sea. As might be seen, the sprat abundance decreased by a factor of two from the beginning to the end of the series, while that of whiting declined by 1.4. In this particular case the critical factor seems to be the expansion of ctenophores, which, after their introduction in 1982, sharply expanded in biomass. The estimates of sprat biomass from 1957 to 1992 show great fluctuations, as it has already been stated this may be due to a variety of reasons. Until 1971-1972, environmental conditions and predators play a decisive role. During 1978-1989 the key factors are the intensification of the fishery and environmental alterations, especially the invasion by ctenophores. After 1989 a lowering of pollution of the basin occurred as a result of the economical recession in the former USSR, Romania and Bulgaria followed by a reduction of their industrial production: the chemical industry in particular is operating at present at only 30% of its total capacity. As a consequence during the last 1-2 years, a decline in the phytoplankton blooms occurred, along with a decline of their adverse effects: toxicity, O_2 deficiency, asphyxia, etc. (Moncheva *et al.*, 1995). Since 1991, the ctenophores also exhibit a decreasing trend. As a consequence a recovery in sprat stock has occurred. The reduction in fishing effort after 1990 is also thought to here contribute positively to this recovery.

Year	Sprat biomass	Sprat recruits	Whiting biomass	Whiting recruits	Whiting recruits*
1976	186.1	52.7	27.3	1.55	40.0
1977	167.7	75.9	25.3	1.00	10.0
1978	179.0	38.1	25.2	1.45	3.0
1979	145.2	47.0	25.1	0.73	12.0
1980	129.2	18.3	21.6	1.03	23.0
1981	84.6	29.6	17.9	0.74	-
1982	65.6	33.1	15.7	0.97	19.4
1983	69.7	34.5	13.5	0.85	10.5
1984	76.2	29.4	14.7	0.87	3.1
1985	71.3	30.2	14.6	0.66	4.5
1986	67.8	20.7	14.0	0.60	3.8
1987	57.6	20.9	12.8	0.45	0.3
1988	50.1	11.0	10.9	0.90	2.7
1989	37.9	17.5	12.1	0.94	5.1
1990	35.6	26.9	14.5	0.64	20.7
1991	52.4	26.3	15.4	0.51	6.0
1992	64.3	-	-	-	12.6
Mean	90.6	29.85	17.5	0.87	11.1

* abundance of whiting recruits in the entire Black Sea, as estimated from ichthyoplankton surveys.

Table 11: Estimates of sprat and whiting biomass (t.10^3) and abundance of 0+ groups (from ichthyoplankton surveys; 10^9) along Bulgarian Black Sea coast (and entire Black Sea for whithings recruits).

CONCLUSION

Fish recruitment abundance depends on numerous natural and anthropogenic factors and its dynamics are difficult to predict. Among the natural variables, the strongest correlation is found between recruitment and the western wind average velocity during November-December and January-March when sprat is actively spawning, at 25-100m depth. The western winds force the upwelling of deep waters and their shorewards progress. As they are rich in nutrients and organic matter, they contribute to the intensive productivity in these regions. The role of the other variables is less important. The comparatively low correlations in equations (6) could be explained to a certain extent by the fact that there is no term in the equation accounting for role of the ctenophore (which is impossible at this stage as there is no long-term data set). The same is valid for phytoplankton bloom data except for the data reported by Moncheva *et al.* (1995). In the case of phytoplankton, the great interannual variability of the species producing blooms restricts the possibility to collect statistically significant long-term data reliable enough to be included in equation (6). Because they were unsure about the relative importance of various factors they considered, Brjantzev (1989) considered the correlations they established as too risky to rely upon for the determination of sprat recruitment. This is similar to the situation with equations (6a, b) which leaves much variance unexplained. The task is now to reduce this unexplained variance and thus to obtain better predictions for the factor that determines biomasses.

REFERENCES CITED

Brjanzev V.A. 1989. Long-term variability of the environment and some problems of fishery prognoses. *Coll. Rep. VNIRO*, Moscow: 282-291 (in Russian).

Dimitrov P. and A. Yaneva. 1992. On some negative impact of upwelling phenomenon upon the Black Sea coastal ecosystem. *Rep. Conf. Ecological Problems of the Black Sea*, Bourgas: 244-254 (in Bulgarian).

Domashenko G.P. and G.S. Ijurev. 1978. On the problem of sprat total allowable catch. *Coll. Rep. VNIRO*, 128: 57-60 (in Russian).

Eremeev V.N. and T.V. Chudinovsky. 1990. Hydrobiology of the Black Sea. Applied Ecology of Sea Regions. The Black Sea, Kiev: 57-106 (in Russian).

Feldman V.N. 1986. Interannual variations of sprat growth and recrutment of commercial stock in relation to temperature regims of the North Sea. Dynamics of the commercial fish abundance. *Science*, Moscow: 103-112 (in Russian).

Gapishko A.I. and V.I. Malyshev. 1990. Calculating daily rations for sprat under natural conditions at the time of spawning and feeding migration. Living resources of Black Sea. *Coll. Rep. VNIRO*: 39-45 (in Russian).

Ivanov L.S. 1977. A symetric curve on the reproduction of fish populations. *Proceedings of the Institute of Fisheries-Varna*, 15: 7-15 (in Bulgarian).

Kolarov P. 1970. On some biological peculiarities of the Black Sea lichnus. *Proc. NIORS-Varna*, 10: 91-92 (in Bulgarian).

Konsulov A. and Tz. Konsulova. 1993. Biodiversity on the Black Sea plankton and benthos. *National Biological Diversity Conservation Strategy, Sofia*: 473-514 (in Bulgarian).

Moncheva S. 1991. *Eutrophication, phytoplankton blooms, hypoxia*. International workshop on the Black Sea, Varna, 30 Sept. - 04 Oct. 1991.

Moncheva S. 1992. *Ecology of common Black Sea phytoplankton species under the influence of anthropogenic eutrophication*. Ph.D thesis (in Bulgarian).

Moncheva S., V.J. Petrova-Karadjova and A. Palasov. 1995. Harmful algal blooms along the Bulgarian Black Sea coast and possible patterns of fish and zoobenthic mortalities. *In*: P. Lassus, G. Arzul, E. Erard-Le-Denn, P. Gentien and C. Marcaillou-Le Baut (eds.). *Proceedings of 6th Int. Conf. Toxic Marine Phytoplankton*, 18-22 Oct.1993, Nantes, France, Lavoisier, Paris: 193-198.

Petrova-Karadjova V.J. and E.M. Apostolov. 1988. Influence of solar activity upon the diatoms of Black Sea plankton. *Rapp., P.-v. Réun. Cons. int. Explor. Mer*, 31 (2).

Petrova-Karadjova V.J. 1993. Solar control upon the phytoplankton in the Black Sea. *Rapp. P.-v. Réun. Cons. int. Explor. Mer*, 33.

Prodanov K. and A. Konsulov. 1987. On some factors determine the abundance of 0+ year old fish (fingerlings) of whiting off Bulgarian Black Sea coast. *Hydrobiology, Sofia*, 30: 44-55 (in Bulgarian).

Ricker W.E. 1975. Computation and interpretation of biological statistics of fish populations. *Bull.Fish.Res.Board. Canada*, 191.

Rozhdestvenski A. 1969. Hydrochemical and meteorological characteristics of the year 1968 regarding the Black Sea fishing activities. *Fish Farm*, 5: 4-6.

Shljakhov V.A., A.K. Chashchin and N.I. Korkosh. 1990. Fishing intensity and dynamics of the Black Sea anchovy stock. *Coll. Rep. VNIRO*, Moscow: 80-92 (in Russian).

Vinogradov M.E., E.A. Shushkina, E.I. Musaeva, P.Yu. Sorokin. 1989. Ctenophore *Mnemiopsis leidyi* (A. Agassiz) (*Ctenophora:Lobata*)- new settlers in the Black Sea. *Oceanology, Acad. Sci. USSR*, 29 (2): 293-299 (in Russian).

Zaika V.E. and N.G. Sergeeva. 1991. Diurnal variations in populations structure and vertical distribution of jellyfishes *Mnemiopsis McCradyi Mayer (Ctenophora)* in the Black Sea. *Hydrobiol. J.*, 27 (2): 15-19 (in Russian).

Zaitsev Yu.P. 1994. Impact of eutrophication on the Black Sea fauna. General fish. Council for the Mediterranean. Studies on fish and env. in the Black Sea basin. Rome, Italy, FAO. 64: 63-88.

Variability of Fish Catches in Different Ecosystems

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ABSTRACT

The effect of the number of years over which catch variability is calculated was determined for different fish species/genus in different FAO subareas (Atlantic, Pacific, Mediterranean) for the 1970-1991 period. Overall, 109 species/subarea catch series, making up more than 40% of the annual world marine catch, were analyzed. The results indicated that for the vast majority of the catch series, variability increases with the length of time over which it is calculated. The increasing variability with time indicates that most of the species/subarea catches show long-term trends and, hence, 'reddened' spectra. As a result, fishery managers and scientists are confronted with variables that do not explore quickly their size limits but rather wander and reach new extreme values continually. Such a pattern suggests that there is not any equilibrium yield, though the latter is at the basis of most models presently used for fisheries management. The results also indicated that between-species/genus variability is a function of species' life history. Moreover, the results revealed that within-species/genus, variability is higher in the four major upwelling areas of the world, especially in the Peruvian one, and lower in the Mediterranean Sea. Within-species/genus, differences in variability (i.e., spatial) are found to be a function of the community/ecosystem characteristics of the marine region of concern.

RÉSUMÉ

La variabilité des captures en fonction du temps (nombre d'années considérées) a été déterminée pour différentes espèces/genres de poissons dans différentes sous-zones FAO (Atlantique, Pacifique, Méditerranée) pour la période 1970-1991. Globalement, 109 séries de capture par espèce/sous-zone, réalisant plus de 40 % des captures marines annuelles mondiales, furent analysées. Les résultats indiquent que pour la grande majorité des séries de capture la variabilité s'accroît avec la période de temps considérée. La variabilité croissante avec le temps indique que la plupart des captures d'espèces/sous-zones présentent une tendance à long terme et, par conséquent, un spectre « rouge ». Un premier résultat est que les aménageurs et les scientifiques sont confrontés à des variables qui n'explorent pas rapidement leur limite extrême, mais au contraire se promènent entre des bornes sans cesse fluctuantes. Un tel pattern suggère qu'il n'existe pas d'équilibre, qui constitue cependant la notion fondamentale de la plupart des modèles présentés en aménagement des pêches. Les résultats indiquent aussi que pour les mêmes espèces/genres, la variabilité est plus grande dans les quatre grandes zones d'upwelling mondiales, principalement au Pérou ; et plus faible en Méditerranée. Pour les mêmes espèces/genres, les différences observées dans la variabilité (c'est-à-dire spatiale) apparaissent comme une fonction des caractéristiques de la communauté/écosystème de la région marine considérée.

INTRODUCTION

Pimm and Redfearn (1988) showed that the variability of a simulated 'red' population density series, formed by summing sine waves with random phases and amplitudes that increase linearly with period, differs greatly from the variability of a simulated 'white' population density series, formed by choosing densities randomly with uniform probability over the same range as those densities in the 'red' model. Pimm and Redfearn (1988) showed that for the 'red' series, variability increases with an increase in the length of period over which variability is estimated. Consequently, Pimm and Redfearn (1988) estimated the standard deviation of logged catch (SDL) of the abundance of 42 farmland bird species, 32 woodland bird species, 22 other bird and mammal species and four insect species over different time periods (i.e., 2, 4, 8 and 16 years for the first two groups and 2, 4, 8, 16, 32 and 50 years for the last two groups). They found that SDL increases with the length of time over which it is calculated for all groups with the exception of insects for which SDL leveled off at very long periods (>8 years). Fisheries catches are generally highly variable. Caddy and Gulland (1983) distinguished empirically four classes of fisheries in terms of pattern of their species catch variability: steady-state, cyclical, irregular and spasmodic fisheries and similar classification was provided by Kawasaki (1983). In addition, it is well known that the major upwelling areas of the world sustain some of the most productive and irregular fisheries (Bakun, 1985). Yet, these and related issues of fish catch variability have not so far been approached quantitatively.

In the present study, the effect of the number of years over which catch variability is calculated as well as between-species and within-species variability were determined for a variety of species in different FAO subareas (Atlantic, Pacific, Mediterranean). The following species/genus were considered: *Engraulis* spp., *Trachurus* spp., *Sardinops* spp., *Scomber japonicus* and *Merluccius* spp. (the main species found in the four major upwelling areas of the world: Bakun, 1985) as well as *Sardinella* spp., *Sardina pilchardus*, *Mallotus villosus*, *Scomber* spp., *Clupea* spp., *Micromesistius poutassou*, *Pleuronectes platessa*, *Hippoglossoides platessoides*, *Gadus* spp., *Theragra chalcogramma*, *Thunnus albacares*, *Katsuwonus pelamis*, *Xiphias gladius* and Elasmobranchii. The above mentioned species make up more than 40% of the annual world marine catch.

1. MATERIAL AND METHODS

Data was extracted using FISHSTAT-PC (FAO Fisheries department, Release 1993A, April 1993). Overall, 109 species per FAO-subarea catch records, referring to the 1970-1991 period, were analyzed. Catch records of species/subarea including many zero values were not taken into account. Scientific names of species are according to FAO Bulletins. The methodology used has been described by Pimm and Redfearn (1988). The measure of variability (standard deviation of logged catch: SDL) and time scales over which SDL was calculated were both selected such that the results presented here could be directly comparable with those of Pimm and Redfearn (1988). For all species/subarea catch records analyzed, SDL was calculated over 2, 4, 8, 16 and 22 years (i.e., the maximum period available) and calculations refer to nested data (i.e., first two years, first four years, etc.).

2. RESULTS

The results indicated that for the majority of species/subarea catches analyzed, variability increases with the length of time over which it is calculated (Tables 1 and 2; Fig. 1). Hence, the slopes of the regressions between SDL and time period over which SDL was calculated, were significantly ($P<0.05$) different from zero and positive for 63 (58%) species/subarea catches when only 2, 4, 8 and 16 years were considered (i.e., 4-point regressions) as well as when regressions also included SDL calculated over the total period (i.e., 22 years, 5-point regressions; Table 1). Overall, slope values were negative for five species/subarea catch series (4-point regressions: *Katsuwonus pelamis* in SW and SE Pacific and *Xiphias gladius* in SE Pacific; 5-point regressions: *Katsuwonus pelamis pelamis* in SW and SE Pacific and *Xiphias gladius* in SE Pacific; 5-point regressions: *Katsuwonus pelamis* in SW Pacific and *Thunnus albacares* in NW Pacific: Table 1). The arithmetic values of the slopes (excluding the negative ones) ranged from 0.0024 to 0.0590, for the 4-point regressions, and from 0.0016 to 0.1590, for the 5-point regressions (Table 1).

Species	FAO Subarea	(2, 4, 8, 16)		(2,4,6, 8, 16, 22)					
		r	b	r	b	min	max	mean	max/min
Engraulis anchoita	Atlantic, Southwest	0.46	-	0.32	-	10137	41100	20565	4.1
Engraulis capensis	Atlantic, Southeast	0.73	-	0.89	0.006	167657	969401	436983	5.8
Engraulis encrasiculus	Atlantic, Northeast	0.93	0.015	0.91	0.011	5423	59674	25985	11
Engraulis encrasiculus	Atlantic, Eastern central	0.95	0.007	0.96	0.011	22000	347247	97539	15.8
Engraulis encrasiculus	Mediterranean	0.94	0.0032	0.96	0.0028	63988	152413	98991	2.38
Engraulis japonicus	Pacific,Northwest	0.94	0.004	0.95	0.003	296428	500614	381820	1.7
Engraulis mordax	Pacific, Eastern central	0.92	0.008	0.95	0.012	5993	424397	170652	70.8
Engraulis ringens	Pacific,Southeast	0.88	0.031	0.82	-	93654	1,3E+07	3423358	139.4
Merluccius bilinearis	Atlantic, Northwest	0.95	0.016	0.88	0.011	53332	434900	139013	8.2
M.capensis, M.paradox	Atlantic, Southwest	0.96	0.009	0.96	0.007	229547	1122000	566920	4.9
Merluccius gayi	Pacific, Southeast	0.91	0.015	0.88	0.011	31260	382439	133845	12.2
Merluccius hubbsi	Atlantic, Southwest	0.93	0.013	0.89	0.009	108100	521312	314790	4.8
Merluccius merluccius	Atlantic, Eastern Central	0.52	-	0.41	-	2900	13810	8172	4.8
Merluccius merluccius	Atlantic, Northeast	0.49	-	0.62	-	49555	117100	76953	2.4
Merluccius merluccius	Mediterranean	0.95	0.007	0.95	0.057	16809	47985	30213	2.85
Merluccius productus	Pacific, Northeast	0.96	0.009	0.98	0.009	31312	297966	153365	9.5
Merluccius senegalensis	Atlantic, Eastern Central	0.71	-	0.69	-	8425	102241	36239	12.1
Sardina pilchardus	Atlantic, Eastern Cenral	0.57	-	0.65	-	319500	1118084	636149	3.5
Sardina pilchardus	Atlantic, Northeast	0.47	-	0.42	-	136014	236370	182921	1.7
Sardina pilchardus	Mediterranean	0.99	0.0044	0.98	0.0035	148801	284411	213820	1.91
Sardinella aurita	Atlantic, Eastern Central	0.93	0.0198	0.95	0.0176	18800	328035	129296	17.4
Sardinella aurita	Atlantic, Western Central	0.81	-	0.89	0.0042	24344	86585	53274	3.6
Sardinella brasiliensis	Atlantic, Southwest	0.61	-	0.86	-	32081	228000	125822	7.1
Sardinella gibbosa	Pacific, Westen Central	0.94	0.014	0.92	0.0103	24000	127890	79638	5.3
Sardinella lemuru	Pacific, Western Central	0.96	0.0175	0.94	0.0131	12500	107160	51936	8.6
Sardinella maderensis	Atlantic, Eastern Central	0.94	0.0341	0.96	0.0301	194	38938	11503	200.7
Sardinops caeruleus	Pacfic, Eastern Central	1	0.0197	0.98	0.02	35500	509248	268553	14.3
Sardinops melanostictus	Pacific, Northwest	0.93	0.0324	0.87	-	16900	5428922	2816178	321.2
Sardinops ocellatus	Atlantic, Southeast	0.93	0.022	0.92	0.0171	62981	677093	265247	10.8
Sardinops sagax	Pacific, Southeast	0.92	0.0496	0.86	-	11400	6509301	2834290	571
Scomber japonicus	Pacific, Northwest	0.98	0.004	0.97	0.006	611744	2238781	1393759	3.7
Scomber japonicus	Atlantic, Southeast	0.97	0.013	0.96	0.011	16352	201556	57631	12.3
Scomber japonicus	Atlantic, Northeast	0.98	0.017	0.9	0.011	1749	39000	10484	22.3
Scomber japonicus	Pacific, Eastern Central	0.99	0.059	0.95	0.043	200	77986	30338	389.9
Scomber japonicus	Altantic, Southwest	1	0.018	0.94	0.012	4724	71968	18611	15.2
Scomber japonicus	Pacific, Western Central	0.98	0.018	0.95	0.014	534	4287	1213	8
Scomber japonicus	Atlantic, Western Central	0.23	-	0.1	-	113	1200	497	10.6
Scomber japonicus	Atlantic, Eastern Central	0.9	0.007	0.94	0.006	87173	326193	179894	3.7
Scomber japonicus	Pacific, Southeast	0.87	0.022	0.76	-	51800	835958	313876	16.1
Scomber spp.	Mediterranean	0.98	0.0078	0.98	0.0068	9740	26468	17112	2.7
Trachurus capensis	Atlantic, Southeast	0.82	-	0.7	-	64900	686943	446810	10.6
Trachurus japonicus	Pacific,Northwest	0.89	0.008	0.89	0.006	56742	283400	161632	5
Trachutus murphyi	Pacific, Southeast	0.98	0.03	0.97	0.024	108700	3852928	1606507	35.4
Trachurus picturatus	Atlantic, Southwest	0.72	-	0.7	-	81	2004	673	24.7
Trachurus symmetricus	Pacific, Eastern Central	0.61	-	0.82	-	1745	49957	17292	28.6

Table 1 (to be continued on next two pages): Minimum, maximum, mean and (maximum/minimum) ratio values of the 107 species/FAO-subarea catches over the 1970-1991 period examined in the present study together with the correlation coefficient (r) and the slope (b) values of the regressions of SDL versus the length of period for 4 data points (i.e., 2, 4, 8, and 16 years) and 5 data points (i.e., 2, 4, 8, 16 and 22 years). Slopes not shown were not significantly different from 0 (P>0.05).

Species	FAO Subarea	(2, 4, 8, 16)		(2,4,6, 8, 16, 22)					
		r	b	r	b	min	max	mean	max/min
Trachurus trachurus	Atlantic, Eastern Central	0.7	-	0.57	-	0	3118	846	-
Trachurus trachurus	Atlantic, Northeast	0.93	0.008	0.1	0.006	136721	440292	258597	3.2
Trachurus trecae	Atlantic, Southeast	0.32	-	0.35	-	31298	378255	135484	12.1
Trachurus spp.	Mediterranean	0.93	0.0055	0.88	0.0039	25998	49438	34570	1.9
Clupea harengus	Atlantic, Northwest	0.95	0.0122	0.85	-	165720	849100	342812	5.1
Clupea harengus	Atlantic, Northeast	0.91	0.0092	0.85	-	632515	1494100	1088537	2.4
Clupea pallasii	Pacific, Northwest	0.99	0.0177	0.96	0.0132	86799	525800	252822	6.1
Clupea pallasii	Pacific, Northeast	0.74	-	0.76	-	65903	155800	92668	2.4
Mallotus villosus	Atlantic, Northwest	0.39	-	0.22	-	5900	367215	118687	62.2
Mallotus villosus	Atlantic, Northeast	0.78	-	0.89	0.0023	777112	3773808	1969124	4.9
Mallotus villosus	Pacific, Northwest	0.97	0.02258	0.98	0.0023	1039	38984	8062	37.5
Micromesistius poutassou	Atlantic, Northeast	0.98	0.032	0.93	0.0227	30512	1106448	471433	36.3
Pleuronectes platessa	Atlantic, Northeast	0.99	0.003	0.95	0.0022	133750	203308	174231	1.5
Hippoglossoides platessoides	Atlantic, Northwest	0.91	0.0027	0.96	0.0036	42887	117400	84971	2.7
Gadus morhua	Atlantic, Northwest	0.73	-	0.65	-	422625	1161500	680057	2.7
Gadus morhua	Atlantic, Northeast	0.95	0.0024	0.96	0.0034	916208	2019978	1538198	2.2
Gadus macrocephalus	Pacific, Northwest	0.96	0.0086	0.98	0.0079	60218	271591	134256	4.5
Gadus macrocephalus	Pacific, Northeast	0.55	-	0.75	-	38800	262881	126186	6.8
Theragra chalcogramma	Pacific, Northwest	0.28	-	0.37	-	2E+06	5153770	3797126	2.6
Theragra chalcogramma	Pacific, Northeast	0.5	-	0.6	-	679022	1714473	1175066	2.5
Katsuwonus pelamis	Atlantic, Northeast	0.92	-0.0133	0.87	-	124	13789	3395	111.2
Katsuwonus pelamis	Atlantic, Western Central	0.99	0.0233	0.92	0.0157	1673	20875	7053	12.5
Katsuwonus pelamis	Atlantic, Eastern Central	0.79	-	0.88	0.0016	40786	172223	87121	4.2
Katsuwonus pelamis	Atlantic, Southwest	1	0.0529	0.97	0.0408	87	25198	10243	289.6
Katsuwonus pelamis	Atlantic, Southeast	0.97	0.0232	0.98	0.0204	109	4472	1712	41
Katsuwonus pelamis	Indian Ocean, Western	0.97	0.012	0.97	0.0157	25329	218952	81881	8.6
Katsuwonus pelamis	Indian Ocean, Eastern	0.95	0.0147	0.95	0.012	2300	19348	9316	8.4
Katsuwonus pelamis	Pacific, Northwest	0.2	-	0.38	-	99905	226955	148691	2.3
Katsuwonus pelamis	Pacific, Western Central	0.95	0.0071	0.98	0.0073	90450	859307	381378	9.5
Katsuwonus pelamis	Pacific, Eastern Central	0.84	-	0.75	-	32540	141815	81856	4.4
Katsuwonus pelamis	Pacific, Southwest	0.98	-0.0399	0.99	-0.036	0	17932	6048	-
Katsuwonus pelamis	Pacific, Southeast	0.7	-	0.72	-	9870	47361	25985	4.8
Thunnus albacares	Atlantic, Western Central	0.99	0.0163	0.88	0.008	5350	31977	15895	6
Thunnus albacares	Atlantic, Eastern Central	0.82	-	0.63	-	53581	148111	104457	2.8
Thunnus albacares	Atlantic, Southwest	0.83	-	0.72	-	915	5209	2895	5.7
Thunnus albacares	Atlantic, Southeast	0.86	-	0.78	-	1468	7648	2959	5.2
Thunnus albacares	Indian Ocean, Western	0.99	0.0134	0.99	0.0109	21610	166253	64221	7.7
Thunnus albacares	Indian Ocean, Eastern	0.83	-	0.73	-	3292	18181	10316	5.5
Thunnus albacares	Pacific, Northwest	0.76	-	0.9	-0.0013	11343	45304	32038	4
Thunnus albacares	Pacific, Western Central	0.99	0.0095	0.95	0.0058	59000	356755	169720	6
Thunnus albacares	Pacific, Eastern Central	0.2	-	0.83	-	109250	282595	195137	2.6
Thunnus albacares	Pacific, Southwest	0.43	-	0.45	-	940	16233	5622	17.3
Thunnus albacares	Pacific, Southeast	0.69	-	0.9	0.0049	18260	88176	37153	4.8
Xiphias gladius	Atlantic, Northwest	0.82	-	0.83	-	401	5856	2987	14.6
Xiphias gladius	Atlantic, Northeast	0.97	0.0085	0.99	0.0089	2612	12138	5189	4.6
Xiphias gladius	Atlantic, Western Central	0.94	0.0156	0.93	0.012	284	5212	1966	18.4
Xiphias gladius	Atlantic, Eastern Central	0.99	0.0079	0.99	0.0072	1294	4354	2261	3.4
Xiphias gladius	Atlantic, Southwest	0.82	-	0.52	-	629	6403	2134	10.2

Table 1 (continuation)

Species	FAO Subarea	(2, 4, 8, 16)		(2,4,6, 8, 16, 22)					
		r	b	r	b	min	max	mean	max/min
Xiphias gladius	Atlantic, Southeast	0.92	0.0106	0.96	0.139	317	9308	2145	29.4
Xiphias gladius	Pacific, Northwest	0.73	-	0.63	-	5574	10839	8483	1.9
Xiphias gladius	Pacific, Western Central	0.91	0.0057	0.94	0.0051	1931	4997	3281	2.6
Xiphias gladius	Pacific, Eastern Central	0.77	-	0.54	-	2697	8463	5474	3.1
Xiphias gladius	Pacific, Southwest	0.81	-	0.75	-	383	1865	1091	4.9
Xiphias gladius	Pacific, Southeast	0.96	-0.0131	0.34	-	500	8403	2177	16.8
Elasmobranchii	Atlantic, Northeast	0.91	0.0286	0.93	0.023	895	14200	6183	15.9
Elasmobranchii	Atlantic, Western Central	0.99	0.0116	0.98	0.0097	3100	17642	9229	5.7
Elasmobranchii	Atlantic, Eastern Central	0.86	-	0.58	-	14544	32942	23876	2.3
Elasmobranchii	Atlantic, Southwest	0.71	-	0.71	-	2300	29864	16635	13
Elasmobranchii	Atlantic, Southeast	0.92	0.0149	0.88	0.0102	1230	9538	3683	7.8
Elasmobranchii	Pacific, Northwest	0.87	-	0.92	0.0023	54834	96888	80602	1.8
Elasmobranchii	Pacific, Western Central	1	0.0066	1	0.0065	19900	53317	33033	2.7
Elasmobranchii	Pacific, Eastern Central	0.92	0.0062	0.92	0.0048	9430	22218	15813	2.4
Elasmobranchii	Pacific, Southwest	0.5	-	0.83	-	1800	7601	3860	4.2
Elasmobranchii	Pacific, Southeast	0.93	0.0076	0.9	0.0088	300	3255	1652	10.9

Table 1 (concluded).

For the different species/genus considered in the present study, the percentage of catch/subarea for which SDL increases over the different time periods examined ranged between 55% and 100%, with the following exceptions: (a) *Merluccius* spp., *Sardina pilchardus*, *Sardinops* spp., *Scomber japonicus* and *Clupea* spp. for the 16- versus 22-year comparison, for which the percentage ranged between 0 and 44%; and (b) *Trachurus* spp. and *Mallotus villosus* for the 8- versus 16-year comparison, for which the percentage was 38 and 33%, respectively (Table 2). Overall, 78% of the total species/subarea catch records showed an increase in SDL from 2 versus 4 years, 75% from 4 versus 8 years, 76% from 8 versus 16 years and 57% from 16 versus 22 years (Table 2). The percentages for the successive changes in SDL in the first three time periods were generally higher for the relatively small-sized pelagic and demersal species (*Engraulis* spp., *Sardinops* spp., *Sardinella* spp., *Sardina pilchardus*, *Mallotus villosus*, *Clupea* spp., *Scomber* spp., *Trachurus* spp., *Merluccius* spp. and 'other') than for the relatively large-sized pelagic and demersal ones (*Gadus* spp., *Thunnus albacares*, *Katsuwonus pelamis*, *Xiphias gladius* and *Elasmobranchii*). The opposite was true of the percentages of catch records showing changes in SDL from 16 to 22 years (Table 2).

All regressions between the mean SDL of the catches of each genus/species over the different subareas and time period over which SDL was calculated, had positive slopes, significantly ($P<0.05$) different from zero with the only exception of *Mallotus villosus* (Fig. 1). However, when the catch record of *Mallotus villosus* in the NE Atlantic was extended back to 1918 (72 years; data from Stergiou (1984)), SDL was found to increase linearly with time over all time scales (Fig. 1). When the logged slopes of the 4-point mean-SDL/time regressions per species/genus (shown in Fig. 1) were regressed against the logged maximum body size per species/genus (Fig. 2), the resulting regression had a negative slope significantly ($P<0.05$) different from zero.

The mean slope of all 4-point SDL-time regressions (Table 1) was higher in the four major subtropical eastern boundary regions (FAO subareas: eastern-central and SE Pacific and Atlantic, corresponding roughly to California, Peru, Canary and Benguela upwelling regions) than in non-upwelling ones (0.0198 ± 0.0031 and 0.0141 ± 0.0017, respectively) but the difference was not significant (t-test, $P>0.05$).

Species	N	2 *versus* 4	4 *versus* 8	8 *versus* 16	16 *versus* 22	Size Category
	Number					
Sardinops	4	3	4	4	1	small
Scomber japonicus	9	9	7	9	4	small
Trachurus	8	6	8	3	5	small
Sardinella	6	5	5	4	6	small
Sardina pilchardus	3	2	2	2	1	small
Clupea	4	3	3	4	0	small
Engraulis	8	6	6	8	5	small
Merluccius	9	6	6	7	3	small
Mallotus villosus	3	3	3	1	2	small
Other[a)]	7	6	7	7	5	small
Thunnus albacares	11	11	7	8	6	large
Xiphias gladius	11	6	6	6	7	large
Gadus	4	4	3	3	3	large
Katsuwonus pelamis	12	9	9	8	8	large
Elasmobranchii	10	6	6	9	6	large
	Percentages					
Sardinops	—	75	100	100	25	small
Scomber japonicus	—	100	78	100	44	small
Trachurus	—	75	100	38	63	small
Sardinella	—	83	83	67	100	small
Sardina pilchardus	—	67	67	67	33	small
Clupea	—	75	75	100	0	small
Engraulis	—	75	75	100	63	small
Merluccius	—	67	67	78	33	small
Mallotus villosus	—	100	100	33	67	small
Other*	—	86	100	100	71	small
Thunnus albacares	—	100	64	73	55	large
Xiphias gladius	—	55	55	55	64	large
Gadus	—	100	75	75	75	large
Katsuwonus pelamis	—	75	75	67	67	large
Elasmobranchii	—	60	60	90	60	large
Total	109	85	82	83	62	both
% of Total	100	78	75	76	57	both
Total 1	61	49	51	49	32	small
%	—	80	84	80	52	small
Total 2	48	36	31	34	30	large
%	—	75	65	71	63	large

a) consisting of *Micromesistius poutassou*, *Pleuronectes platessa*, *Hippoglossoides platessoides* and *Theragra chalcogramma*.

Table 2: Number and percentages of species/FAO-subarea catches for which SDL increases were examined over different time periods.

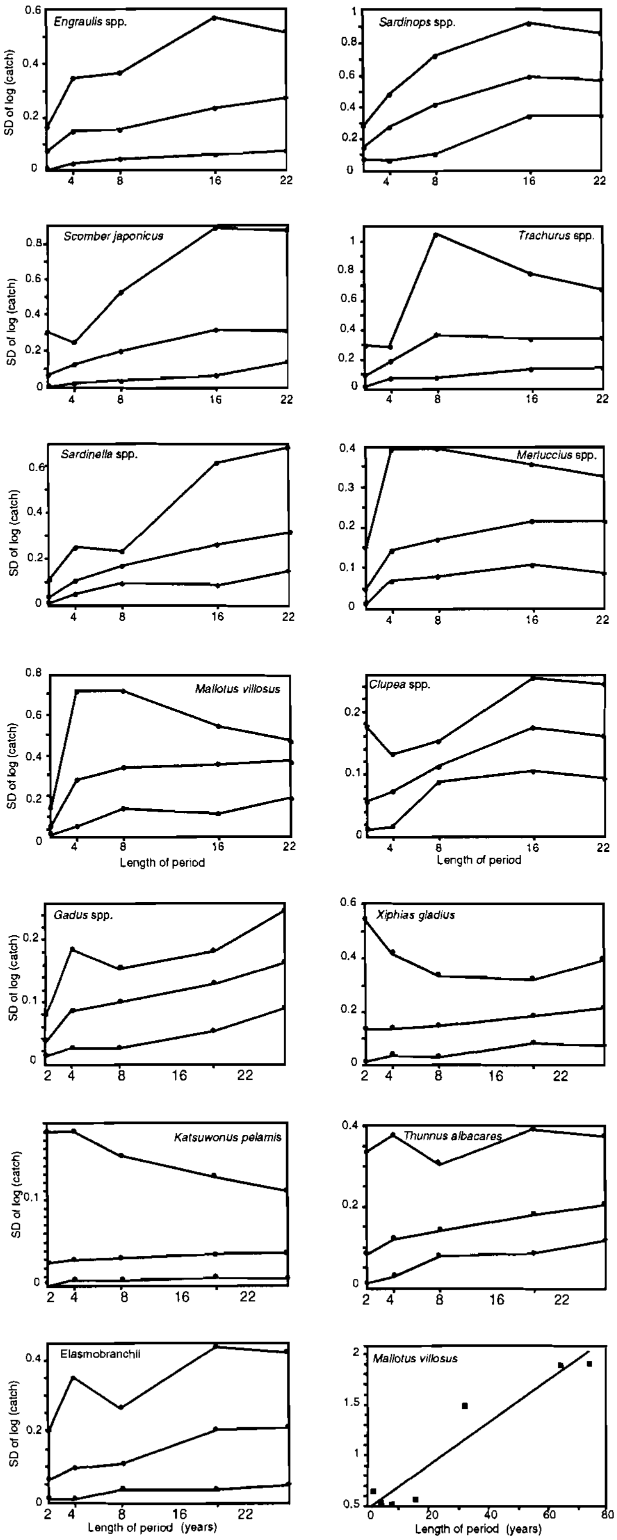


Fig. 1: Variability of catches (standard deviation of logged catches, SDL) versus the number of years over which SDL was calculated for a variety of fish species/ genus/ groups. On each graph, the middle line joins the mean SDL values among the different species over all subareas considered whereas the top and bottom lines join the maximum and minimum values, respectively. With the exception of *Mallotus villosus*, all regressions, between mean SDL and length of the time period over which SDL was calculated, are significant at $P<0.05$ ($n=4$; 2, 4, 8 and 16 years). The last graph (bottom right) refers to the catches of *Mallotus villosus* in the NE Atlantic for the period 1918-1991(data from Stergiou (1984)) and SDL is plotted against 2, 4, 8, 16, 32, 64 and 72 years; the slope of the regression line (=0.0216) is significantly ($P<0.05$) different from zero.

Fig. 2: Regression between the logged slopes of the 4-point SDL-time regressions (graphs shown in Fig. 1) and the logged maximum body length in cm (maximum body length values taken from Whitehead *et al.* (1984)).

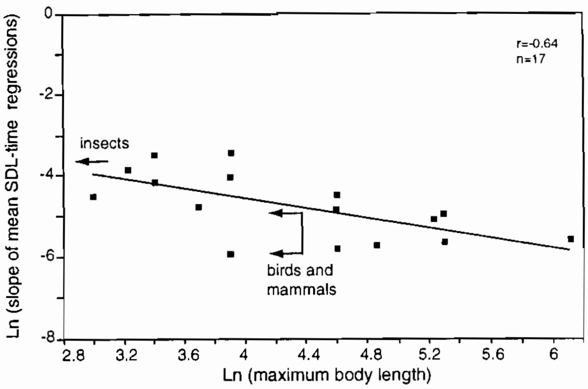
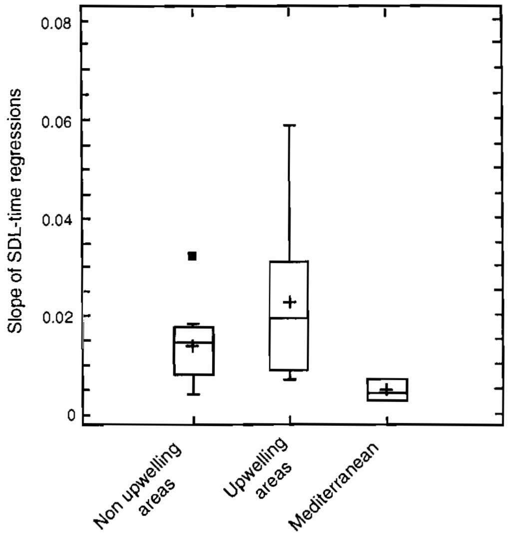


Fig. 3: Box-Whiskers plots of the slopes of the SDL-time regressions of all species considered in the present study in three different ecosystems: non-upwelling areas (NE, SE, western-central, NW Atlantic and Pacific); major upwelling areas (FAO subareas: eastern-central and SE Pacific and Atlantic, corresponding roughly to California, Peru, Canary and Benguela upwelling regions); and Mediterranean Sea. The central box encloses the middle 50% of the values, the horizontal line inside the box shows the median value of the data, the cross inside the box shows the mean value of the data, and the vertical lines extending from each end of the box (i.e., whiskers) enclose 75% of the values; one outlier is marked by a black square.



In addition, the values of the slopes of the SDL-time regressions for *Engraulis encrasicolus*, *Sardina pilchardus*, *Trachurus* spp., *Scomber* spp. and *Merluccius merluccius* in the Mediterranean Sea were by one order of magnitude smaller than the corresponding ones in the Atlantic and Pacific Oceans (Table 1). The mean value of the slopes of all 4-point SDL-time regressions differed significantly (ANOVA, $P<0.05$) between regions attaining the highest value for all major upwelling regions combined and lower ones for the Mediterranean Sea (see Fig. 3). In addition, when the major upwelling species as well as their non-upwelling counterparts thriving in similar latitudinal zones were considered alone (i.e., *Engraulis* spp., *Trachurus* spp., *Sardinops* spp., *Scomber* spp., *Merluccius* spp., *Sardinella* spp. and *Sardina pilchardus*), the mean value of the slopes of the above mentioned regressions differed significantly (ANOVA, $P<0.05$) between regions in the following order: Peruvian > remaining upwelling areas > non-upwelling Atlantic and Pacific areas > Mediterranean Sea (see also Fig. 4). In addition, in both cases, the minimum, maximum and median slope values displayed differences similar to those of the mean slopes (Fig. 3 and 4).

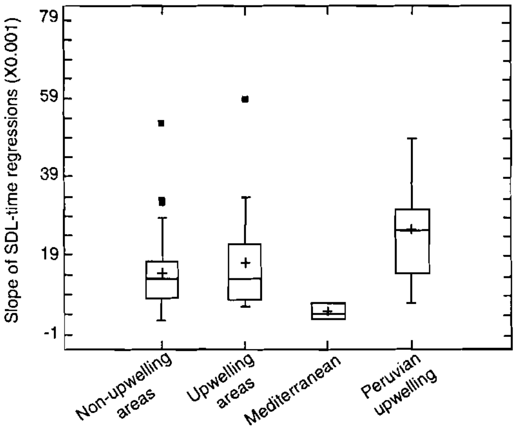


Fig. 4: Box-Whiskers plots of the slopes of the SDL-time regressions for the major upwelling fish species as well as their non-upwelling counterparts occurring in similar latitudinal zones (i.e., *Engraulis* spp., *Trachurus* spp., *Sardinops* spp., *Scomber* spp., *Merluccius* spp., *Sardinella* spp. and *Sardina pilchardus*), in four different ecosystems: non-upwelling areas (NE, SE, western-central, NW Atlantic and Pacific); Peruvian upwelling (FAO subarea: SE Pacific); remaining major upwelling areas (FAO subareas: eastern-central Pacific and eastern-central and SE Atlantic, corresponding roughly to California, Canary and Benguela upwelling regions); and Mediterranean.

DISCUSSION

The results indicated that for the majority of species/subarea catches analyzed, variability increases with the length of time over which it is calculated. The increasing variability with time indicates that most of the species/subarea catches examined here exhibit long-term trends and, hence, 'reddened' spectra. In other words, fishery managers and scientists are confronted with variables that do not explore quickly their size limits but rather wander and reach new extremes. The results have important implications which were stressed by Pimm and Redfearn (1988) for terrestrial populations and are directly applicable to fisheries. Such a pattern in fish catch variability suggests that there is no 'equilibrium yield', even though they are assumed by most models presently used for fisheries management; steady yield seems to be the exception rather than the rule (Caddy and Sharp, 1986; Hilborn and Walters, 1992). Yet, long-term trends and cycles in commercial catches can be incorporated into various fishery models (Taylor and Prochaska, 1984).

The negative relationship between variability and body size most probably indicates that between-species/genus variability is a function of species' life history (i.e., trophic position in the food web, natural rate of population increase and natural mortality, all of which are size-related processes (Kawasaki, 1983; Caddy and Sharp, 1986; Pimm, 1991). This is consistent with the results of Warner *et al.* (1994) who, after estimating the Hurst exponent for a variety of terrestrial and aquatic population series, found a significant ($P<0.003$) negative correlation between the values of the Hurst exponent and species' body size. It is worthy to point out that the degree of risk accepted by fishery managers tend to be generally higher for small-sized rather than large-sized fish species.

It is interesting to compare the results presented here with those of Pimm and Redfearn (1988). The slope values of the 4-point SDL-time regressions of the 94 farmland and woodland bird and mammal species (estimated by the present author from Pimm and Redfearn's (1988) data) ranged between 0.003 (logged value = -5.81) and 0.008 (logged valued = -4.83) whereas the slope value of the four insect species was 0.026 (logged value = -3.65) (Fig. 2), a fact indicating that the former are ecologically equivalent, in terms of variability, to small-sized fish and the latter to large-sized ones.

Catch variability differs between regions in the following order: Peruvian upwelling > other upwelling areas > non upwelling Atlantic and Pacific areas > Mediterranean. This suggests that in the case of within-species/genus, spatial differences in variability are a function of the community/ecosystem characteristics of the marine region in concern, such as the trophic potential and complexity of the food web (i.e., primary production and number of trophic levels) and the environmental dynamics affecting community characteristics. Indeed, the four major upwelling ecosystems are generally controlled by similar environmental dynamics and inhabited by similar communities of exploited fisheries stocks that most probably have adapted to similar environmental/community characteristics (Bakun, 1985, 1990). Yet, the Peruvian upwelling region is characterized, when compared with the remaining major upwelling areas, by: (a) a longer effective upwelling period, i.e., more or less throughout the year; (b) more intense effect of ENSO events (Mann and Lazier, 1991); and (c) the highest fishery catch densities (Cury, 1995; Faure and Cury, this vol.). In contrast, there is a pronounced oligotrophy in the surface waters of the Mediterranean Sea, especially so in its eastern part (Aegean and Levantine Seas) because of the low nutrient concentration in the trophogenic layer. The latter is attributed to: (a) the lack of significant upwelling areas, resulting to upwelling of 'new' nutrients from deep waters in the euphotic zone, the key to high biological productivity; (b) the relatively small amounts of discharge from land; and (c) the fact that in the Mediterranean Sea, where total evaporation exceeds precipitation and river runoff (Hopkins, 1978), the conservation of mass and salinity is maintained by the balance of a two-layer flow through the Strait of Gibraltar: surface, nutrient-poor Atlantic waters inflow in the upper layer whereas Mediterranean deeper waters outflow in the lower layer. In addition, in the Mediterranean Sea, especially in the south-eastern part, the importance of picoplankton increases, a fact which presumably increases the number of trophic levels and, hence, may limit the potential production at higher trophic levels (Azov, 1991). As a result of this, the Mediterranean Sea is characterized by a low fish catch density (1.4 t/km^2 of continental shelf), which is many times lower than that in upwelling as well as some other non-upwelling ones areas (Stergiou and Christou, this vol.). The low trophic potential of the Mediterranean sets an upper limit in the carrying capacity of the region and, hence, in the level of the catch variability of a given species at a given time (i.e., lower maximum slope values: Fig. 3 and 4).

There remain the questions of whether catch trends reflect abundance trends of similar scales and of what causes trends in fish catches. With respect to the first question, one may assume that fish abundance may exhibit trends similar to those of their catches for the following reasons: (a) although zero catches do not imply zero abundance (e.g., closed fisheries, impossibility to completely fish out a population/species from a given geographic area), annual catches are usually smaller than biomasses; (b) all or most species examined here have been traditionally fished in most FAO subareas and, since catches refer to years following 1970, one may assume that most of the fisheries examined were not in the initial stage of development, at which catch is not related to abundance (Hilborn and Walters, 1992); and finally, (c) many of the catch series used here possibly reflect, at least to a certain extent, management measures that were set based on forecasted abundance level.

With respect to what causes trends in fish catches, climate, predation and its special form of fishing, species' dynamics and life-history, managerial decisions, economic and social factors may all, in a synergetic dynamic fashion, affect fisheries catches (Caddy and Sharp, 1986; Hilborn and Walters, 1992). The effect of climate cannot be distinguished from that of fishing inasmuch as fisheries managers will tend to respond to catch declines by assuming that fishing is the main factor and, hence, both effects will be reflected in catch records (Hilborn and Walters, 1992). However, it is worthy to mention that the fact that the majority of the catch records examined in the present study are characterized by 'reddened' spectra, as is also true of marine physical parameters (Steele, 1985), probably reflects the effect of the such parameters on fish catches.

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REFERENCES CITED

Azov Y. 1991. Eastern Mediterranean - a marine desert? *Mar. Pollut. Bull.*, 23: 225-232.

Bakun A. 1985. Comparative studies and the recruitment problem: searching for generalizations. *CalCOFI Rep.*, 26: 30-40.

Bakun A. 1990. Global climate change and intensification of coastal ocean upwelling. *Science*, 247: 198-201.

Caddy J.F. and J.A. Gulland. 1983. Historical patterns of fish stocks. *Mar. Policy*, 7: 267-278.

Caddy J.F. and G.D. Sharp. 1986. An ecological framework for marine fishery investigations. *FAO Fish. Tech. Pap.*, 283, 152 p.

Cury P. 1995. Comparison of the Ivoiro-Ghanaian fishery with other exploited upwelling systems of the world. *In*: F.X. Bard and K.A. Koranteng (eds.). *Dynamics and use of sardinella resources from upwelling off Ghana and Ivory Coast*. ORSTOM, Paris: 169-193.

Hilborn R. and C.J. Walters. 1992. *Quantitative fisheries stock assessment: choice, dynamics and uncertainty*. Chapman and Hall, New York, 570p.

Hopkins T.S. 1978. Physical processes in the Mediterranean basin. *In*: B. Kjerfve (ed.) Estuarine transport processes. Bell W. Baruch Lib. in Mar. Sci.,7.

Kawasaki T. 1983. Why do some pelagic fishes have wide fluctuations in their numbers? Biological basis of fluctuation from the viewpoint of evolutionary ecology. *In*: G.D. Sharp and J. Csirke (eds.). Proceedings of the Expert Consultation to Examine Changes in Abundance and Species Composition of Neritic Resources. San José, Costa Rica, 18-29 April 1983. *FAO Fish. Rep.*, 291(2): 1065-1080

Mann K.H. and J.R.N. Lazier. 1991. *Dynamics of marine ecosystems: biological-physical interactions in the oceans*. Blackwell Scientific Publications, Boston, 466p.

Pimm S.L. 1991. *The balance of nature? Ecological issues in the conservation of species and communities*. The University of Chicago Press, Chicago, 434p.

Pimm S.L. and A. Redfearn. 1988. The variability of population densities. *Nature*, 334: 313-314.

Steele J.H. 1985. A comparison of terrestrial and marine ecological systems. *Nature*, 313: 355-358.

Stergiou K.I. 1984. *Capelin and climatic change in the Barents Sea*. MSc Thesis, McGill University, Montreal, Canada, 225p.

Taylor G.T. and F.J. Prochaska. 1984. Incorporating unobserved cyclical stock movements in fishery catch equations: an application to the Florida blue crab fishery. *N. Am. J. Fish. Manage*, 4: 67-74.

Warner S., K.E. Limburg, A.H. Arino, M. Dodd, J. Dushoff, K.I. Stergiou and J. Potts. 1994. Comparisons of time series across the land-sea gradient. *In*: J. Steele and T. Powell (eds.). *Ecological time series*. Chapman and Hall, New-York.

Whitehead P.J.P., M.L. Bauchot, J.C. Hureau, J. Nielsen and E. Tortonese (eds.). 1984. *Fishes of the north-eastern Atlantic and the Mediterranean*. UNESCO, Paris, Vol. 1, 2 and 3.

Desperately Searching for Natural Eutrophication: the Case of the NE Mediterranean

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ABSTRACT

In the present work, we review and analyse the major features of the Greek marine fisheries (catch species composition and densities) for the 1982-1989 period and the results are discussed in the context of the trophic potential of the Greek seas (phytoplankton and zooplankton productivity and abundance) and compared with those of other upwelling and non-upwelling areas of the world ocean. Multivariate analyses (classification and ordination) performed on the mean (1982-1989) commercial catch weight of 66 species (or groups of species) from 16 fishing subareas indicated that the 16 subareas fall into three main groups, generally representing the S-SE Aegean (and NW Levantine Seas), the Ionian and central Aegean Seas, and the N-NW Aegean Sea, respectively. The species compositions of the mean catches of the groups identified by multivariate analyses differed considerably. The mean catch of S-SE Aegean was dominated by pickerel and bogue and, to a lesser extent, by horse mackerels, that of the central Aegean and Ionian Seas by sardine, horse mackerel, bogue and pickerel, whereas that of N-NW Aegean Sea by anchovy and sardine. The mean pelagic, demersal and total fisheries catch densities between 1982 to 1989 all decrease from 1.3, 0.83 and 2.13 t/km^2 in N-NW Aegean Sea to 0.25, 0.37 and 1.23 t/km^2 in S-SE Aegean Sea, respectively, with the latter densities being comparable to those in the Ionian Sea. In addition, such an increase goes along with a decrease in the relative importance of demersal species. The mean pelagic catch density in the Ionian and S-SE Aegean Seas is from 3 to 150 times lower than those in other marine areas of the world ocean. In contrast, the mean pelagic catch density in the N-NW Aegean Sea is: (a) comparable to that in the California coast (22-38°N), (b) higher than those in the Gulf of California and Indian waters (7-25°N) and (c) 2 to 30 times lower than those in the major upwelling areas of the world. Natural eutrophication processes are responsible for such a geographical differentiation in catch species composition and densities, namely the gradient in eutrophy, river runoff, temperature and salinity of the Greek marine waters along a NNW to SSE axis. In contrast to other areas where seasonal upwelling takes place (e.g., Ivoirian and Ghanaian coasts), seasonal upwelling along the E Aegean coast, driven by the Etesian winds (dry and cool N-NE-E winds blowing over the Aegean Sea in summertime) probably has no significant impact on primary production and fisheries catch densities, most probably because upwelled waters reach the surface from layers immediately below the seasonal thermocline, its depth in the E Aegean Sea generally being <50 m, and, hence, are already poor in nutrients.

RÉSUMÉ

Dans ce travail, nous analysons les principales caractéristiques des pêcheries marines grecques (composition des captures et densités) pour la période 1982-1989 ; les résultats sont discutés en termes de potentiel trophique des eaux maritimes grecques (abondance et productivité du phytoplancton et du zooplancton) et comparés à ceux obtenus dans d'autres zones (d'upwelling ou non). Des analyses multivariées (classification et hiérarchisation) sont faites sur les captures commerciales moyennes de 66 espèces (ou groupes d'espèces) de 16 zones de pêche appartenant à trois groupes : la zone S-SE de la mer Egée (et NW de la mer du Levantin), la mer Ionienne et la zone centrale de la mer Egée, et le N-NW de la mer Egée. La composition des captures diffère beaucoup d'une zone à l'autre. La capture moyenne de la zone S-SE de la mer Egée est dominée par les brochets et les bogues et, dans une moindre mesure, par les chinchards ; celle de la partie centrale de la mer Egée et de la mer Ionienne par les sardines, les chinchards, les bogues et les brochets ; et celle de la zone N-NW de la mer Egée par les anchois et les sardines. Les densités moyennes des captures de poissons pélagiques, démersaux et des captures totales diminuent entre 1982 et 1989 de 1.3, 0.83 et 2.13 t/km^2 respectivement dans le N-NW de la mer Egée, à 0.25, 0.37 et 1.23 t/km^2 dans le S-SE de la mer Egée, ces dernières valeurs se retrouvent aussi dans la mer Ionienne. De plus, un tel accroissement va de pair avec une décroissance de l'importance relative dans chacune des zones des espèces démersales. La densité des captures de poissons pélagiques dans la mer Ionienne et dans le S-SE de la mer Egée est de 3 à 150 fois plus faible que celle d'autres zones marines. Par exemple, la capture moyenne des pélagiques dans le N-NW de la mer Egée est (a) comparable à celle de la Californie (22-38 °N), (b) plus importante que celle du golfe de Californie et de l'Inde (7-25 °N) et (c) de 2 à 30 fois plus faible que celle des principales zones d'upwelling mondiales. Les processus d'eutrophisation naturelle que sont le gradient d'eutrophisation, le débit des rivières, la température, la salinité des eaux le long de l'axe N-NW à S-SE, sont responsables de ces différences de composition des captures et des densités. Par comparaison avec les autres upwellings saisonniers d'autres zones (par exemple Côte-d'Ivoire-Ghana), celui des côtes orientales de la mer Egée, soumis aux vents Etésiens secs et froids, N-NE-E, qui soufflent sur la mer Egée en été, n'a probablement pas d'impact sur la production primaire et sur les captures. Les eaux upwellées atteignent la surface depuis des couches situées juste en dessous de la thermocline dont la profondeur dans l'est de la mer Egée est généralement inférieure à 50 m. De ce fait, elles sont généralement pauvres en sels nutritifs.

INTRODUCTION

The Mediterranean Sea has a maximal depth of 5 140 m, maximal width of 800 km, an area of 2.5 million km^2 (0.8% of the total marine area of the world) and a mean depth of 1 470 m (Azov, 1991). There is a pronounced oligotrophy in the surface waters of the Mediterranean Sea, especially so in its eastern part (Aegean and Levantine Seas). The lack of significant upwelling areas resulting from upwelling of 'new' nutrients from deep waters in the euphotic zone, an important key to high biological productivity, and the relatively small amounts of discharge from land, results in low nutrient concentration in the trophogenic layer. In addition, the Mediterranean Sea is a concentration basin in which total evaporation exceeds precipitation and river runoff (Hopkins, 1978) and the conservation of mass and salinity is maintained by the balance of the two-layer flow through the Strait of Gibraltar: surface, nutrient-poor Atlantic waters inflowing in the upper layer and Mediterranean deeper waters outflowing in the lower layer. The low concentration of phosphates in deeper waters, reflect the restricted exchange of the landlocked water with the waters of the adjacent Atlantic Ocean. The oligotrophy of the Mediterranean Sea is also reflected in the level of fisheries catches (300 kg/km^2 for all areas and 1,400 kg/km^2 over the continental shelf, Ben Tuvia, 1983).

The marine waters of Greece include the Aegean Sea and a part of the Ionian and NW Levantine Seas. The Greek part of the Ionian Sea comprises a part of a larger area in which the existing stocks are fished by a number of other major fishing nations (especially Albania, Italy, Libya, Malta and Tunisia). The mean Greek catch from the Ionian Sea over the period 1982-1987 represented only 7% of the total Ionian Sea catch (FAO, 1989). The Greek part of the Levantine Sea also comprises a part of a larger area in which the existing stocks are fished by a number of other major fishing nations (Lebanon, Turkey, Israel, Syria, Cyprus, Egypt and Gaza Strip). The mean Greek catch from the NW Levantine Sea over the period 1982-1987 represented less than 1% of the total Levantine catch. In contrast, the Aegean Sea is mainly fished by the Greek fleet. Although the Turkish fleet fishes along the eastern Aegean coast, the Turkish catch from this area is relatively insignificant when compared with that of the Greek Aegean Sea fisheries; it comprised about 20% of the mean total Aegean catch over the period 1982-1987 (FAO, 1989).

In the present work, we analyse the major aspects of the Greek marine fisheries (catch species composition and density) for the 1982-1989 period. The results are discussed in the context of the trophic potential of the Greek Seas (phytoplankton and zooplankton productivity and abundance) and compared with those of other upwelling and non-upwelling areas of the world ocean.

1. MATERIAL AND METHODS

Fisheries statistics for the waters of Greece have been recorded on a monthly basis since January 1964 by the National Statistical Service of Hellas (NSSH Bulletins, 1965-1990). For a better evaluation of the available data, the waters fished by Greek vessels have been divided into 18 statistical fishing subareas (Fig. 1). Fishing subareas 1 and 2 (not shown in Fig. 1) refer to the Atlantic Ocean and the northern coast of Africa, respectively. Catch data are collected directly from a sample of fishing vessels (stratified random sampling) that are surveyed by local customs authorities. For each vessel surveyed, a statistical questionaire is completed showing the quantities of each major fish species (or group of species) caught during the previous month (or that the vessel did not work during that period). Details on the validity of the NSSH data have been presented by Stergiou *et al.* (1994).

In general, the Greek fishing fleet includes: (a) fishing vessels operating in distant waters (Atlantic Ocean and northern African coast, and thus of no concern to the present study); (b) trawlers operating in Greek open-sea waters; (c) purse seiners operating in Greek open-sea and coastal waters; (d) beach seiners operating along the Greek coasts; and (e) 'other coastal boats' (including small ring netters, drifters, liners, etc.) operating along the Greek coasts. Since 1969 the catches of the smaller inshore ring netters, drifters and liners (i.e., boats with engine horsepower of less than 20HP) have not been recorded by the local customs authorities. In addition, the catches from the marine sport fisheries, which locally may be relatively important (e.g., 11.8% and 4.5% of the total catches from subareas 9 and 5, respectively; Stergiou *et al.,* 1989) are not included in the totals.

For the period 1964-1981, separate catch statistics are available for 23 species or groups of species only whereas for the years following 1981 separate catch statistics have been available for 66 species (or groups of species) of commercially important fishes, cephalopods and crustaceans (Stergiou *et al.*, 1994). In the present study, the annual landed catches of the 66 species (or groups of species) in the 16 statistical fishing subareas (Fig. 1) for the years 1982-1989 inclusive, were analysed using two main categories of statistical techniques, as follows.

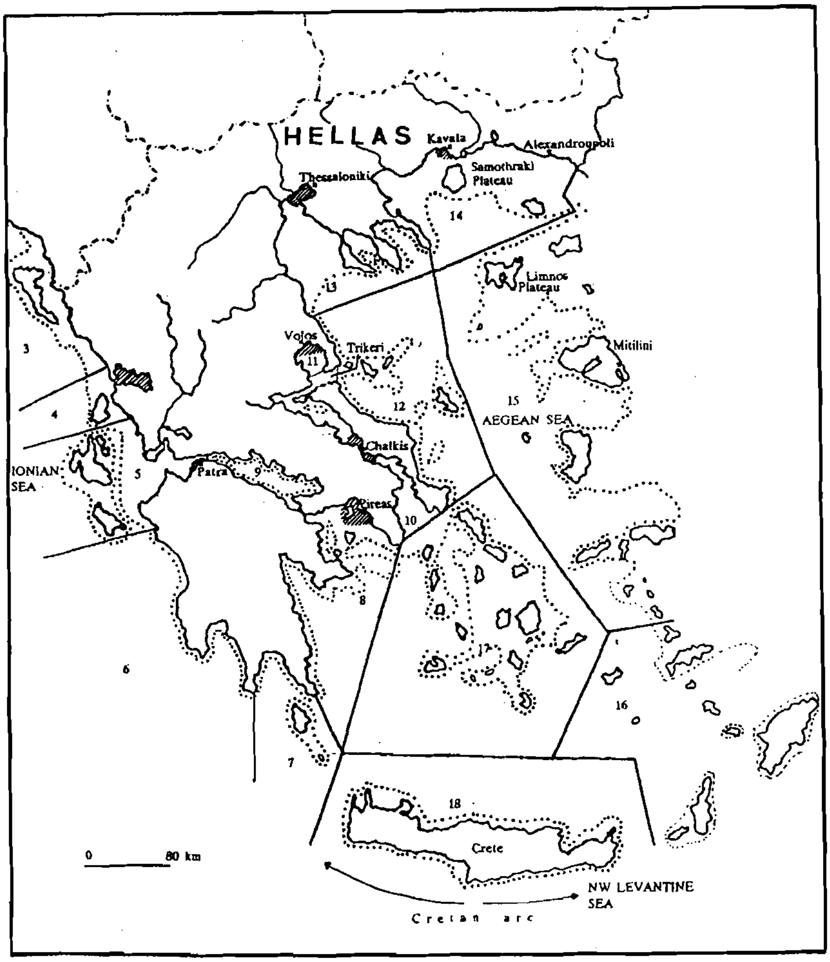

Fig. 1: Map showing the 16 fishing subareas of Greece (Hellas). The dotted line represents the 200 m isobath; hatchings show areas where anthropogenic eutrophication is locally important.

The following univariate measures were computed: mean number of species, species diversity, richness and eveness for each subarea over the 1982-1989 period. Diversity was calculated using the Shannon-Wiener diversity index H', species richness using Margalef's D, and eveness using Pielou's J (Maguran, 1988). All computations were carried out using the PRIMER algorithms (Clarke and Warwick, 1989).

A matrix comprising the mean landed commercial catch weight of each species (or groups of species) from each subarea over the 1982-1989 period was compiled. From that matrix, a triangular matrix of similarities between all pairs of subareas was computed using the Bray-Curtis coefficient (Bray and Curtis, 1957). Prior to this computation, the data was standardized by the mean total landed catch per subarea in order to compensate for between-subarea differences in fishing effort, for which data per subarea is not provided in the NSSH Bulletins. Subsequently, the similarity matrices were subjected to both clustering (employing group-average linking) and ordination (employing non-metric multi-dimensional scaling, MDS) analysis techniques. The adequacy of the ordination in two, rather than more than two, dimensions is expressed by a 'stress coefficient' (Field *et al.*, 1982). In general, stress values <0.1 imply good representation (Clarke and Warwick, 1989). Discontinuities between subareas may be accepted as real when the results of the two methods agree (Field *et al.*, 1982; Clarke and Green, 1988; Gray *et al.*, 1988). All multivariate analyses were carried out using the PRIMER algorithms (Clarke and Warwick, 1989).

2. RESULTS

Overall, the two pelagic species anchovy and sardine were dominant, comprising 18.5% and 11.4% of the mean total Greek catch, respectively, over the 1982-1989 period (Fig. 2). In addition, bogue, horse mackerel, pickerel, hake and chub mackerel comprised 8.2%, 8.0%, 7.3%, 3.3% and 3.3% of the mean catch, respectively (Fig. 2). All remaining species each contributed less than 3%. However, catch species composition differs greatly between fishing subareas and component fisheries.

The species composition of the mean catch per component fishery over the 1982-1987 period is shown in Table 1. The mean trawl catch was dominated by hake, pickerel, horse mackerel and red mullet; the mean purse seine catch mainly by anchovy and, to a lesser degree, by sardine, horse mackerel and bogue; the mean beach seine catch mainly by pickerel and, to a lesser degree, by sardine and bogue; and, finally, the mean 'other coastal boats' catch by bogue, pickerel and grey mullets.

The mean annual commercial catch weights per fishing subarea over the 1982-1989 period are shown in Table 2. The mean annual Greek catch was 92 841 t, of which 86 584 t were caught in the Aegean Sea (less than 1% was derived from the NW Levantine Sea) and 6 257 t in the Ionian Sea. Fish made up 94.2% of the mean total Aegean catch, cephalopods 3.2% and crustaceans 2.6%. In the Ionian Sea, fish made up 95.7% of the mean total catch, cephalopods 3.2% and crustaceans 1.1%.

The mean annual catch weight, mean number of species comprising the catch, and the mean diversity (Shannon-Wiener diversity, evenness and richness) over the 16 fishing subareas are shown in Table 3. The total number of species ranged from 56 (in subarea 6) to 66 (in subareas 8, 10 and 12 to 16). Richness ranged between 6.39 (in subarea 13) and 12.05 (in subarea 6), diversity between 1.67 (in subarea 11) and 3.38 (in subarea 6) and evenness between 0.41 (in subarea 11) and 0.84 (in subarea 6). The following significant regression was found between the log-transformed mean catch weights (C) and number of species (N) comprising mean catches for each subarea over the 1982-1989 period: $Ln(C) = -92.83 + 24.25Ln(N)$, SE(slope)=3.75, $r2=0.75$, $n=16$, $P<0.01$.

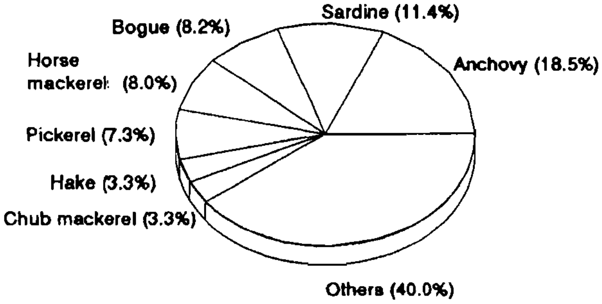

Fig. 2: Species composition of the mean total Greek marine catch, 1982-1989, in % of total weight.

Common name	Scientific name	T	P	S	O
FISHES					
Anchovy	*Engraulis encrasicolus* (L.)	1.9	95.4	0.9	1.8
Anglerfish	*Lophius* spp.	94.9	0.4	0.6	4.0
Annular sea bream	*Diplodus annularis* (L.)	8.8	13.3	0.8	77.1
Black sea bream	*Spondyliosoma cantharus* (L.)	13.7	6.8	6.0	73.6
Blotched pickerel	*Spicara flexuosa* Rafinesque, 1810	49.5	7.6	11.6	31.2
Blue whiting	*Micromesistius poutassou* (Risso, 1826)	93.8	0.5	3.3	2.4
Bluefin tuna	*Thunnus thynnus* (L.)	0.3	39.7	0.6	59.4
Bluefish	*Pomatomus saltator* (L.)	6.0	36.5	2.0	55.5
Bogue	*Boops boops* (L.)	11.0	51.8	11.8	25.4
Bonito	*Sarda sarda* (Bloch, 1793)	1.4	64.5	2.1	32.0
Brill	*Scophthalmus rhombus* (L.)	83.4	2.8	0.2	13.6
Chub mackerel	*Scomber japonicus* (Houttuyn, 1782)	3.3	82.7	3.8	10.3
Comber	*Serranus cabrilla* (L.)	32.6	5.8	2.1	59.6
Common dentex	*Dentex dentex* (L.)	9.3	2.6	5.3	82.8
Common sea bream	*Pagrus pagrus* (L.)	6.9	1.7	2.1	89.2
Dogfishes	Squalidae	37.0	4.3	0.6	58.1
Dusky grouper	*Epinephelus guaza* (L.)	3.5	5.2	1.5	89.8
European eel	*Anguilla anguilla* (L.)	2.2	5.1	0.7	92.0
European sardine	*Sardina pilchardus* (Walbaum, 1792)	1.7	77.9	9.0	11.4
European sea bass	*Dicentrarchus labrax* (L.)	24.6	14.4	3.0	58.0
Garfish	*Belone belone gracilis* (Lowe, 1839)	0.9	11.3	10.3	77.5
Gilt sardine	*Alosa falax nilotica* (Geoffroy Saint-Hilaire, 1808) and *Sardinella aurita* (Valenciennes, 1847)	5.4	70.2	2.1	22.2
Gilthead sea bream	*Sparus aurata* L.	71.6	7.8	2.8	17.8
Greater amberjack	*Seriola dumerili* (Risso, 1810)	21.5	24.0	4.0	50.5
Grey mullet	Mugilidae	9.5	17.3	0.7	72.5
Guitarfish	*Rhinobatos* spp.	65.5	1.1	4.7	28.7
Gurnard	Triglidae	35.4	0.8	8.6	55.2
Hake	*Merluccius merluccius* (L.)	69.4	3.9	2.0	24.7
Horse mackerels	*Trachurus* spp.	17.3	67.7	4.0	11.0
Jack mackerel	*Trachurus picturatus* (Bowdich, 1825)	23.4	67.7	4.4	4.5
John dory	*Zeus faber* (L.)	79.6	0.8	3.8	15.8
Large-eye dentex	*Dentex macrophthalmus* (Bloch, 1791)	51.4	2.3	4.9	41.4
Mackerel	*Scomber scombrus* (L.)	7.9	60.3	2.9	28.8
Pickerel	*Spicara smaris* (L.)	22.2	9.0	45.5	23.3
Rays	*Raja* spp.	88.0	0.2	0.4	11.3
Red mullet	*Mullus barbatus* (L.)	72.6	3.1	5.2	19.1
Red pandora	*Pagellus erythrinus* (L.)	53.0	1.9	5.3	39.8
Rockfish	*Helicolenus dactylopterus* (Delaroche, 1809)	66.6	3.1	4.7	25.7
Saddled bream	*Oblada melanura* (L.)	12.4	17.3	4.0	66.4
Salema	*Sarpa salpa* (L.)	4.9	24.5	3.1	67.5

Table 1: Common names, scientific names and percentages of mean annual total catches of the 66 species (or groups of species), recorded by the Greek National Statistical Service, fished by trawlers (T), purse seiners (P), beach seiners (S) and 'other coastal boats' (= small ring netters, liners, drifters, etc.; O) over the period 1982-1987. Species are listed in alphabetical order with respect to common name. Sum across lines is 100% (from Stergiou and Pollard, in press).

Common name	Scientific name	T	P	S	O
BONY FISH					
Scorpionfish	*Scorpaena* spp.	24.7	4.4	2.7	68.3
Shi drum	*Umbrina cirrosa* (L.)	33.5	4.7	1.5	60.3
Skipjack	*Katsuwonus pelamis* (L.)	2.4	76.4	1.9	19.4
Smoothhound	*Mustellus* spp.	38.1	36.5	0.5	24.9
Sole	*Soleidae* (mainly *Solea vulgaris* Quensel, 1806)	13.5	3.4	0.5	82.7
Sprat	*Sprattus sprattus* (L.)	9.5	68.8	4.4	17.3
Stone bass	*Polyprion americanus* (Schneider, 1801)	4.5	13.7	2.9	78.9
Striped red mullet	*Mullus surmuletus* (L.)	37.4	2.4	7.3	52.9
Swordfish	*Xiphias gladius* (L.)	4.1	5.0	1.0	89.9
Thick blotched pickerel	*Spicara maena* (L.)	9.3	22.5	10.7	57.6
Thornback ray	*Raja clavata* (L.)	89.0	1.0	0.2	9.8
Tub fish	*Trigla lucerna* (L.)	75.1	4.1	2.1	18.6
White grouper	*Epinephelus aeneus* (Geoffroy Saint-Hilaire, 1817)	27.7	2.3	2.6	67.3
White sea bream	*Diplodus sargus* (L.)	9.6	6.9	5.5	78.0
Whiting	*Merlangius merlangus euxinus* (Nordmann)	66.5	6.2	0.6	26.8
Other fishes	(numerous spp.)	28.2	10.7	4.3	56.8
CEPHALOPODS					
Common squid	*Loligo vulgaris* (Lamarck, 1798)	45.0	3.9	30.5	20.7
Cuttlefish	*Sepia officinalis* (L.)	30.4	1.0	3.1	65.5
Flying squid	*Illex coindetii* (Verany, 1839)	94.1	0.7	1.9	3.3
Octopus	*Octopus vulgaris* (Cuvier, 1797)	48.6	1.6	6.8	43.0
Poulpes	*Eledone* spp.	97.9	0.3	0.8	1.1
CRUSTACEANS					
Crabs	Brachyura	30.5	0.0	0.8	68.7
Crayfish	*Nephrops norvegicus*	92.9	0.6	1.5	4.9
Lobsters	*Homarus gammarus* (L.) and *Palinurus elephas* (Fabricius, 1787)	5.1	0.6	0.9	93.4
Common prawn	*Penaeus kerathurus* (Forsskål, 1775)	65.8	1.0	3.1	30.1
Shrimps	(no data on spp. composition)	69.8	0.4	0.5	29.3

Table 1 (continued).

The classification of the mean (1982-1989) commercial catch weight of all species for each subarea (Fig. 3) indicated that, at the 50% (Bray-Curtis) similarity level, the 16 subareas fall into three main groups: Group I (subareas 7 and 16 to 18), Group II (subareas 3 to 6, 8 to 10 and 15) and Group III (subareas 11 to 14), generally representing the southern Aegean and NW Levantine Seas, the Ionian and central Aegean Seas, and the N-NW Aegean Sea, respectively. The results of the ordination (MDS) of these subareas (Fig. 3) agree with the above pattern. The resulting stress value for the two-dimensional plot (Fig. 3) was low (=0.08), implying the adequacy of the MDS representation in these two dimensions.

The species compositions of the mean catches of the groups identified by multivariate analyses also differed considerably (Table 4). The mean catch of Group I was dominated by pickerel and bogue and, to a lesser extent, by horse mackerel, representing 21.0%, 17.6% and 8.5% of the mean total catch, respectively (Table 4). The mean catch of Group II was dominated by sardine, horse mackerel, bogue and pickerel, representing 12.1%, 12.0%, 11.3% and 10.2% of the mean

Species	Fishing subarea															
	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18
Anchovy	3	170	320	5	0	1101	96	876	265	2182	7901	4038	129	74	22	1
Bluefin tuna	1	0	7	0	0	47	0	106	0	115	418	733	33	2	245	5
Bluefish	0	1	0	4	0	5	0	8	0	2	71	102	5	1	2	2
Bogue	34	165	202	11	136	1104	48	673	13	442	522	610	1047	679	1356	542
Bonito	0	150	25	2	1	853	2	129	1	19	12	13	46	166	86	50
Chub mackerel	3	14	10	2	4	60	2	74	1	125	551	607	1020	434	129	6
European sardine	104	227	293	7	27	1369	129	650	56	646	3328	2860	716	12	111	37
Flying squid	1	1	19	0	0	51	9	36	1	8	57	41	32	1	6	19
Garfish	0	0	1	0	10	79	0	15	0	2	26	7	122	3	14	0
Gilt sardine	0	2	3	0	4	48	0	3	0	0	4	1	1	0	5	15
Horse mackerel	15	84	95	5	19	2008	57	752	12	356	1360	915	460	33	931	330
Jack mackerel	1	13	17	0	1	164	3	246	13	269	140	162	76	0	23	8
Mackerel	0	1	0	0	0	31	0	41	0	20	206	184	14	6	8	1
Skipjack	0	0	0	0	0	18	0	54	0	3	1	1	25	7	12	40
Sprat	1	5	10	0	0	10	2	7	0	0	2	0	14	1	0	0
Swordfish	21	96	69	0	14	115	5	9	0	40	5	10	20	272	138	251
Total pelagic	185	929	1072	36	218	7063	352	3679	361	4229	14606	10285	3759	1692	3087	1308
%	0.35	1.76	2.03	0.07	0.41	13.36	0.67	6.96	0.68	8.00	27.63	19.46	7.11	3.20	5.84	2.47
Anglerfish	1	1	1	0	0	23	0	63	1	1	328	54	25	0	3	2
Annular sea bream	1	0	9	2	0	11	1	28	2	9	169	44	7	2	1	1
Black sea bream	1	1	3	0	7	32	1	23	0	18	35	11	54	35	99	7
Blotched pickerel	68	19	80	0	0	7	5	111	2	30	97	71	34	1	1	8
Blue whiting	0	0	3	0	1	29	9	273	3	30	401	222	103	0	4	7
Brill	0	0	0	0	1	3	0	74	0	2	5	5	6	1	1	0
Comber	0	0	4	0	1	14	1	4	0	1	1	2	8	18	24	15
Common dentex	6	8	8	2	5	11	1	17	0	8	30	20	16	18	29	8
Common prawn	0	1	2	0	1	3	1	4	0	1	117	33	18	0	0	37
Common sea bream	2	1	4	0	5	22	1	7	0	12	14	11	72	23	47	67
Common squid	8	7	34	1	2	26	8	47	0	5	146	110	48	42	62	22
Crabs	0	0	0	0	0	2	0	14	0	0	17	4	0	0	0	0
Cuttlefish	6	3	33	2	1	15	4	40	1	7	484	280	57	4	12	38
Dogfish	3	1	15	0	3	2	2	0	0	1	4	22	77	0	1	62
Dusky grouper	2	4	9	0	2	5	1	1	0	1	4	4	5	6	2	50
European eel	0	0	0	1	0	2	0	0	0	1	6	2	0	0	0	1
European sea bass	1	0	3	2	0	3	1	49	0	2	71	9	1	2	2	1
Gilthead sea bream	5	5	4	0	0	3	1	124	0	34	23	20	1	17	1	0
Greater amberjack	1	0	1	1	2	17	2	6	0	2	4	2	3	3	4	3
Grey mullet	9	13	16	0	4	17	7	261	2	63	1366	400	29	4	7	1
Guitarfish	0	0	0	0	0	1	0	0	0	0	16	13	3	0	0	0
Gurnard	5	1	27	1	8	63	8	114	1	15	32	383	38	59	172	21
Hake	36	53	135	4	10	386	50	337	39	160	826	671	193	14	102	77

Table 2: Mean catch (in t) per species (or groups of species) and per fishing subarea, Greek waters, 1982-1989. Separation of species (or groups of species) into demersal/inshore and pelagic/semipelagic ones according to Stergiou and Pollard (in press).

Species	Fishing subarea															
	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18
John dory	1	0	1	0	0	13	0	19	0	2	10	7	8	4	5	6
Large-eye dentex	0	14	8	1	1	21	2	6	0	2	3	7	28	3	7	5
Lobster	4	1	2	0	5	25	1	13	0	19	14	9	26	2	18	6
Norway lobster	0	0	0	0	0	47	9	69	1	22	453	274	66	1	11	1
Octopus	6	3	21	2	1	30	11	21	0	9	107	278	18	11	18	24
Other fish	39	61	69	5	109	389	65	338	14	155	3653	682	284	437	1219	218
Pickerel	99	270	427	26	450	994	80	491	7	177	197	241	557	844	1334	615
Octopi	3	2	12	0	0	27	2	20	0	4	326	141	15	2	11	26
Rays	3	2	10	0	0	26	1	22	0	9	5	16	17	1	3	1
Red mullet	37	39	65	0	35	197	10	213	4	81	468	344	104	77	49	71
Red pandora	19	7	23	4	14	110	6	169	2	46	16	35	44	53	106	24
Rockfish	1	1	11	1	0	2	1	37	0	3	7	6	1	1	0	1
Saddled bream	2	5	7	15	1	64	2	40	1	57	62	371	19	38	186	6
Salema	1	8	6	0	0	24	1	8	0	2	38	83	15	1	17	1
Scorpionfish	8	3	24	2	10	72	10	44	0	11	19	84	58	98	109	81
Shi drum	0	0	1	2	0	1	0	5	0	1	15	12	0	2	1	0
Shrimps	0	1	21	0	0	43	20	3	0	10	516	100	75	2	12	126
Smoothhound	3	1	20	2	3	18	5	6	0	31	65	140	42	2	6	16
Soles	4	2	9	0	2	22	2	62	0	12	540	489	7	9	5	5
Stone bass	1	8	15	0	10	9	0	13	0	7	3	7	44	3	10	90
Striped red mullet	20	15	58	2	70	208	9	225	2	72	140	196	128	179	405	169
Thick blotched pic.	3	10	13	0	8	90	1	46	2	41	66	36	68	33	53	9
Thornback ray	1	0	7	0	0	11	2	1	0	7	144	229	8	1	3	5
Tubfish	3	1	14	0	1	17	1	68	0	10	25	7	8	13	2	2
White grouper	1	3	6	1	4	11	1	1	0	5	1	1	2	2	2	23
White sea bream	6	8	8	1	6	37	1	24	1	22	36	49	27	26	124	23
Whiting	0	2	0	0	0	5	0	0	0	0	144	77	15	1	0	0
Total demersal	420	580	1251	80	788	3207	346	3564	87	1221	11266	6314	2485	2096	4292	1983
%	1.05	1.45	3.13	0.20	1.97	8.02	0.87	8.91	0.22	3.05	28.18	15.79	6.22	5.24	10.73	4.96

Table 2 (continued).

catch, respectively (Table 4). Finally, the mean catch of Group III was dominated by anchovy and sardine, representing 29.7% and 14.3% of the mean catch, respectively (Table 4).

The mean catch density (t/km^2) per group identified by multivariate analyses is shown in Table 5, together with mean catch density values from other ecosystems of the world ocean. It is evident that the mean catch density of pelagic, demersal and all fishes combined, increase from South to North. In addition, such an increase goes along with a decrease in the relative importance of demersal species. Hence, in Group I the mean catch density of the demersal species is higher than that of the pelagic ones whereas in Group III the former is about two times less than that of the pelagic ones (Table 5).

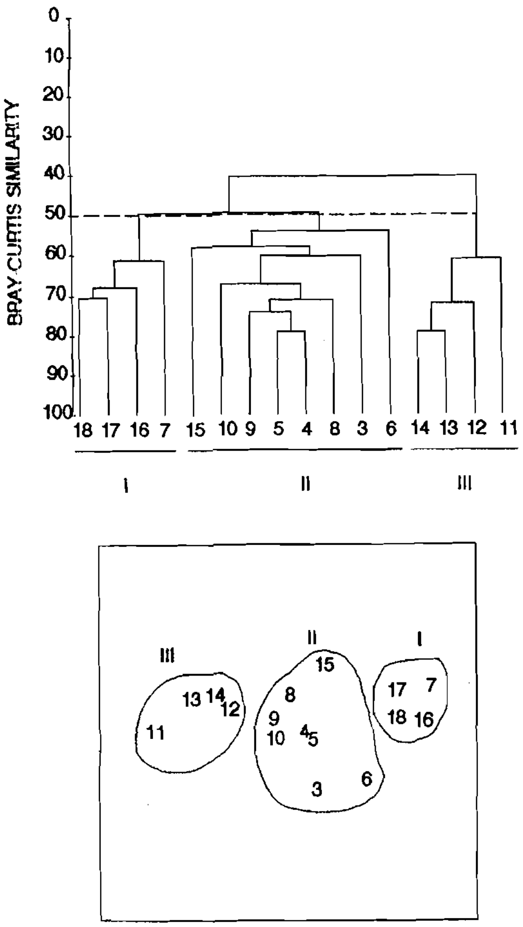

Fig. 3: Dendrogram (upper) for group-average clustering and MDS plot (lower), based on Bray-Curtis similarities between standardized mean catch weights, of all species from the 16 Greek fishing subareas, over the 1982-1989 period. For MDS plot orientation and scale are arbitrary.

3. DISCUSSION

Stergiou and Petrakis (1993) analysed the annual (standardized) commercial catch weights of the 66 species (or groups of species: Table 1) per component fishery for the years 1982-1987 (24 fisheries/year combinations). The classification and ordination of all species for each fishery/year combination indicated that the four fisheries fall into two main groups; Group A (trawlers, beach seiners and 'other coastal boats') and Group B (purse seiners), exploiting primarily demersal/inshore and primarily pelagic fisheries resources, respectively (Stergiou and Petrakis, 1993). Their results clearly reveal the multi-species and multi-gear nature of the Greek demersal/inshore and, to a lesser degree, pelagic/semi-pelagic fisheries. In addition, the results of the multivariate analyses (Fig. 3) suggested that the 16 Greek fishing subareas may be generally grouped into three geographical clusters that differ considerably from each other in terms of species composition (Table 4) and catch density (Table 5). Stergiou and Pollard (in press) did a similar analysis considering only

Fishing Subarea	C	N	D	H'	J
3	581	60	9.27	2.97	0.72
4	1480	62	8.36	2.70	0.65
5	2292	65	8.27	3.01	0.72
6	96	56	12.05	3.38	0.84
7	981	64	9.15	2.19	0.53
8	10237	66	7.04	2.77	0.66
9	667	64	9.68	2.90	0.69
10	7213	66	7.32	3.23	0.77
11	430	57	9.23	1.67	0.41
12	5422	66	7.56	2.43	0.58
13	25842	66	6.39	2.63	0.63
14	16568	66	6.69	2.91	0.69
15	6215	66	7.44	3.01	0.72
16	3757	66	7.89	2.59	0.62
17	7349	65	7.19	2.62	0.63
18	3260	64	7.79	2.93	0.71

Table 3: Mean total annual catch (C, in t), number of species (N), richness (D), Shannon-Wiener diversity (H') and evenness (J) per fishing subarea, Greek waters, 1982-1989. The highest and lowest values are underlined.

	Groups identified my multivariate analysis					
Species	Group I		Group II		Group III	
	Catch	%	Catch	%	Catch	%
Pickerel	3243	21.0	2945	10.1	—	—
Bogue	2714	17.6	3284	11.3	1586	3.2
Horse mackerel	1312	8.5	3476	12.0	2643	5.5
Striped red mullet	824	5.3	665	2.3	—	—
Swordfish	675	4.4	—	—	—	—
Chub mackerel	574	3.7	1186	4.1	1284	2.7
Bonito	303	2.0	1207	4.2	—	—
Scorpionfish	298	1.9	—	—	—	—
Gurnard	260	1.7	—	—	—	—
Bluefin tuna	253	1.6	—	—	1266	2.6
Sardine	—	—	3495	12.1	6891	14.3
Anchovy	—	—	2701	9.3	14387	29.7
Hake	—	—	1194	4.1	1696	3.5
Red mullet	—	—	664	2.3	897	1.9
Grey mullet	—	—	—	—	1831	3.8
Sole	—	—	—	—	1040	2.2
Others	5009	32.3	8190	28.2	14847	30.6

Table 4: Mean annual catches (in t) and percentages of the main species (or groups of species) per group identified by multivariate analysis (Fig. 3), Greek waters, 1982-1989. Catches and percentages for the two dominant species per group are underlined.

the ten Aegean Sea subareas for each year of the 1982-1987 period; they found that the within-subarea similarities were much more intense than the between-subarea ones (i.e., for each subarea and year of the 1982-1987 period subarea/year combinations were closely tied).

The main factors which may contribute to such a geographical differentiation most probably are the gradient in eutrophy, river runoff, temperature and salinity of the marine waters of Greece along a NNW to SSE axis. The eastern Mediterranean Sea is known to be one of the most oligotrophic marine regions of the world (Friligos, 1980, 1987; Azov, 1991). In the Aegean Sea, annual gross primary production in the outer part of subarea 8 and in the southern part of subarea 10 (see Fig. 1) was found to be 64 and 30 gC/m^2, respectively, the latter figure being among the lowest recorded for the Mediterranean Sea (Becacos-Kontos, 1968, 1977), comparable to those of the oligotrophic oceanic areas (50-70 gC/m^2: Azov, 1991) and one to two orders of magnitude lower than those in the major upwelling areas (e.g., Peru, 1100 gC/m^2: Chavez *et al.*, 1989; Cape Blanc and California, 730 and 150-720 gC/m^2, respectively: Mann and Lazier, 1991). Pavlova (1966), based on indirect estimations, suggested that secondary productivity in the Aegean Sea is 12 to 18 times lower than that in the Black Sea, four times lower than that in the Adriatic Sea, and similar to those of the Tyrrhenian and Libyan Seas. Data pertinent to secondary production in the Greek seas are only available for the Saronikos Gulf (Christou, 1991). Secondary production in the coastal area of the Saronikos Gulf (0.12-0.19 g/m^3/yr) is low when compared with those recorded in other marine areas of the world (Table 6). Hence, the generally low secondary productivity of the Greek seas is evident, especially if one takes into account that Saronikos Gulf resembles, in terms of zooplankton density and species composition, many other gulfs of Greece, and its northern part is considered one of the most eutrophic areas of the country (Christou, 1991).

The oligotrophic nature of Greek waters is clearly depicted in the Coastal Zone Colour Scanner (CZCS) image of the phytoplankton-like pigment (PLP) distribution (not shown here, but see Stergiou and Georgopoulos, 1993), and reflected also to fisheries catch densities which, on the average, are lower than those of the Mediterranean Sea as a whole and in other areas of the world ocean (Table 5). However, within this generally oligotrophic environment relatively eutrophic areas do exist. Indeed, fishing subareas 8 and 10 to 14 are all characterized by one order of magnitude higher PLP concentrations as compared with the S-SE Aegean, NW Levantine and Ionian Seas (with the exception of subareas 5 and 9), the latter areas being comparable to the most oligotrophic open ocean areas of the world. A similar distribution pattern of PLP is also indicated for the wintertime, although concentrations, because of the winter mixing, are generally higher (N-NW rim of the Aegean Sea >0.5 mg/m^3; Ionian, S-SE Aegean and NW Levantine Seas: about 0.2 mg/m^3; Georgopoulos, unpubl. data). This general pattern of PLP distribution is also true of all the 46 images examined for the period 1981-1982 (Georgopoulos, unpubl. data), and coincides also with those of nutrient distributions in Greek waters, the latter being derived from historical data and from recent cruises in open sea (during 1986-1990) and coastal waters (during early 1980s) (Stergiou and Georgopoulos, 1993). Hence, the satellite image is representative of the general pattern of the spatial differentiation in PLP distribution in the Greek seas (Stergiou and Georgopoulos, 1993).

The spatial distributions of phytoplankton and zooplankton abundance in the surface waters as well as that of fisheries catch densities generally parallel that of PLP concentration. Hence, with respect to the offshore waters, phytoplankton abundance is higher in the N Aegean Sea, especially in the area bounded by 40° and 41°N latitude (subarea 14: 9 120-586 160 cell/l; Pagou and Gotsis-Skretas, 1989). Relatively high values (up to 72 090 cells/l) of phytoplankton abundance have been also recorded in the northern part of the Greek Ionian Sea (Pagou and Gotsis-Skretas, 1989). In contrast, the lowest values of phytoplankton abundance (<29 200 cell/l) have been recorded in the central and S-SE Aegean, central Ionian and NW Levantine Seas (Pagou and Gotsis-Skretas, 1989). With respect to zooplankton, its abundance is generally higher in some enclosed or semi-enclosed bays and gulfs (enclosed gulf in subarea 4, northern part of subarea 10, part of subarea 8 close to Pireas Port, subarea 11: as high as 5 000 ind./m^3) and in the offshore waters of the North Aegean Sea (from 500 to 5 000 ind./m^3), especially in the area bounded between 40° and 41°N latitude (i.e., subareas 13 and 14), sometimes extending southward to 39.5°N (Siokou-Frangou and Pancucci-Papadopoulou, 1989; Siokou-Frangou *et al.*, 1991). The S-SE Aegean and NW Levantine Seas (southern part of subarea 16: Fig. 1) are oligotrophic areas comparable to open ocean ones, with zooplankton abundance usually ranging between 100 and 300 ind./m^3 (Siokou-Frangou *et al.*, 1991). Moreover, zooplankton abundance attains relatively higher levels (up to 900 ind./m^3: Siokou-Frangou *et al.*, 1991) in the northern part of the Greek side of the Ionian Sea (subarea 3: Fig. 1), when compared with the remaining part of the Ionian Sea (up to 500 ind./m^3: Siokou-Frangou *et al.*, 1991).

In agreement with the above mentioned patterns, the mean (1982-1989) pelagic, demersal and total fisheries catch densities all decrease from 1.3, 0.83 and 2.13 t/km^2 in N-NW Aegean Sea to 0.25, 0.37 and 1.23 t/km^2 in S-SE Aegean Sea, respectively, with the latter density being comparable to those in the Ionian Sea (Table 5). The mean pelagic catch density in the Ionian and S-SE Aegean Seas is from 3 to 150 times lower than those in other marine areas of the world ocean (Table 5). In contrast, the mean pelagic catch density in the N-NW Aegean Sea (Group III) is: (a) comparable to that in the California coast (22-38°N), (b) higher than those in the Gulf of California and Indian waters (7-25°N), and (c) 2 to 30 times

Geographic area	Catch (t)		Area in	Density (t/km^2)		
	Pelagic*	Demersal*	(km^2)	Pelagic	Demersal	Total
Greek seas (total)	52861	39979	75294	0.70	0.53	1.23
Group I	6304	9159	24998	0.25	0.37	0.62
Group II	17076	11932	27613	0.62	0.43	1.05
Group III	29481	18888	22683	1.30	0.83	2.13
Ionian Sea	2574	2677	9824	0.26	0.27	0.53
Aegean Sea	50287	37303	65470	0.77	0.57	1.34
N-NW Aegean Sea	29120	18801	22010	1.32	0.85	2.18
S-SE Aegean Sea	21166	18502	43460	0.49	0.43	0.91
Mediterranean	—	—	—	1.40	—	—
West Africa (6-36N)	—	—	—	3.14	—	—
Côte-d'Ivoire (8W-1E)	—	—	—	2.17	—	—
South Africa (6-37N)	—	—	—	3.75	—	—
California (22-38N)	—	—	—	1.75	—	—
Gulf of California (24N)	—	—	—	0.87	—	—
South America (1-43N)	—	—	—	38.40	—	—
India (7-25N)	—	—	—	0.97	—	—
Spain (36-44N)	—	—	—	3.35	—	—
North Sea	—	—	—	—	—	4.70
Cape Hateras to Nova Scotia	—	—	—	—	—	1.54
Eastern Bering Sea	—	—	—	—	—	2.10
Central Baltic Sea	—	—	—	—	—	2.75

*Separation of the 66 species (or groups of species) into pelagic/semipelagic and demersal/inshore according to Stergiou and Pollard (1994).

Table 5: Catches and densities of pelagic and demersal fishes in Greek waters and other ecosystems of the world ocean. Data for Mediterranean from Ben-Tuvia (1983), West Africa to Spain from Cury (1995), and for North Sea to Central Baltic Sea from Sparholt (1990).

lower than those in the major upwelling areas of the world (Table 5). The mean total catch density in S-SE Aegean Sea is from 2 to 7 times lower than those in the remaining areas of Greece, the Mediterranean as a whole and other areas of the world ocean (Table 5). In contrast, the mean total catch density in N-NW Aegean Sea is comparable to that in the E Bering Sea and two times higher than that of the Mediterranean as a whole (Table 5).

It must also be stressed that in the SE Mediterranean Sea the importance of picoplankton is high, a fact which presumably increases the number of trophic levels and, hence, may limit the potential production at higher trophic levels (Azov, 1991), possibly resulting in a lower biomass of small- and medium-sized pelagic fishes. This is consistent with the north-to-south decline in the mean pelagic catch density (Table 5) and with the results of echo-surveys undertaken during May 1989 - May 1992 in fishing subareas 12 to 15. The echo-surveys revealed that the echo-abundance (mm deflection per km^2) of small- and medium-sized pelagic fishes in fishing subareas 13 and 14 are higher by an order of magnitude than those in fishing subareas 12 and 15 (Stergiou *et al.*, 1993; Papaconstantinou *et al.*, 1994).

It is worthy to point out also that in the summertime (mainly from July to September) upwelling, driven by the Etesian winds (dry and cool N-NE-E winds blowing over the Aegean Sea) which very often reach gale force, takes place along the eastern Aegean coast (e.g., Metaxas, 1973). In contrast to other areas where seasonal upwelling takes place (e.g., Ivorian and Ghanaian coasts: Koranteng and Pezennec, this vol.; Venezuelan coast: Mendoza *et al.*, this vol.) seasonal upwelling along the E Aegean coast probably has no significant impact on the primary production of the area (Georgopoulos, pers. comm.) as well as on fisheries catch densities (Table 5). This could be attributed to the fact that upwelled waters reach the surface from layers immediately below the seasonal thermocline, its depth in the E Aegean Sea generally being <50 m, and, hence, are already poor in nutrients (Georgopoulos, pers. comm.). However, this issue calls for thorough studies.

Subareas 8, 12, 13 and 14 are under the influence of natural eutrophication processes. Hence the above mentioned subareas are all directly influenced by nutrient inputs from outflowing Black Sea waters. These waters enter the Aegean Sea from the Dardanelles Strait and are colder, less saline and much richer in nutrients than the waters of Levantine origin that enter the Aegean Sea mainly from the eastern straits of the Cretan Arc (Theocharis and Georgopoulos, 1992; Georgopoulos *et al.*, 1989). Freshwater runoff is also relatively important along the northern rim of the Aegean (17,657 x 106 m^3/yr) as compared to the remaining part of the Greek side of the Aegean Sea (<1,000 m^3/yr; Therianos, 1974). Other factors which contribute to the relative high eutrophy of subareas 8 and 10 to 14 may include: (a) the extended continental shelf of subareas 8, 13 and 14 (Fig. 1); (c) localized anthropogenic eutrophication (see Fig. 1; Friligos, 1980, 1987); and (d) upwelling in the northern part of subarea 10 (Balopoulos and Papageorgiou, 1991). The high values of phytoplankton pigment concentration (about 1 mg/m^3) along the northern coast of the Aegean Sea may be partly attributed to suspended material derived from river runoff.

In the Ionian Sea, catch densities (Table 5) and PLP concentrations are much higher in subareas 5 and 9. This must be attributed to the systematic wind-driven upwelling along the northern coast of these subareas (Laskaratos *et al.*, 1989), although river runoff (6,861 x 106 m^3/yr: Therianos, 1974) is also important in subarea 5.

The salinity and temperature differences in Greek waters may also be related to the geographical grouping of the 16 fishing subareas. Hence, the lower salinity prevailing along the coasts of subareas 13 and 14, which are influenced by the Black Sea waters and river runoff, may explain the predominance of the relatively euryhaline grey mullet and sole in the N-NW Aegean Sea (Group III: Table 4). In addition, the pelagic anchovy, sardine and horse mackerel and the demersal hake, which dominate the pelagic and demersal catches, respectively, are replaced by bogue and pickerel, respectively, in the S-SE Aegean and NW Levantine Seas (Group I: Table 4). Both bogue and pickerel are generally characterized by a more southern distribution (they are not found to the north of Portugal in Atlantic waters) as compared to anchovy, horse mackerel and hake (Whitehead *et al.*, 1984). It is worthy to note that the species dominating the pelagic and demersal catches (i.e., anchovy, sardine, horse mackerel hake: Table 4) of the colder, less saline and relatively more eutrophic N-NW Aegean (Group III) are known to inhabit the major upwelling areas of the world. Also, Stergiou (1992a) has suggested that seasonal upwelling, driven by the Etesian winds, may also take place along the N-NE coast of the Aegean Sea, a fact that may also explain, in a synergetic fashion with the presence of Black Sea waters, the relatively high productivity of the waters in subarea 14. However, such a wind-driven upwelling has not so far been justified from field studies.

The management implications of these results have been discussed elsewhere (Stergiou, 1992b; 1993; Stergiou and Petrakis, 1993; Stergiou and Pollard, in press; Stergiou *et al.*, 1994) and are briefly summarized below. Catch-effort studies as well as experimental trawl and echo-surveys all suggest that Greek demersal/inshore and pelagic fisheries resources are overfished (Stergiou *et al.*, 1994). Hence, the need for rational management of the Greek demersal/inshore and pelagic fisheries resources is urgent. The inadequacy of the national management regulations currently in force for the demersal and inshore fisheries has been discussed by Stergiou *et al.* (1992); despite the reinforcement of these measures, demersal and inshore fisheries resources are currently overfished (Stergiou *et al.*, 1994). The same must be true of pelagic resources. Such an inadequacy must be mainly attributed to the multi-species, multi-gear nature of the Greek and, in general, of the Mediterranean fisheries that poses certain difficulties in designing and implementing uniform protective measures, particularly so for the demersal/inshore fisheries. Recent evidence (see reviews by Davis (1989), Bohnsack (1990), Roberts and Polunin (1991) and Pollard (1993)) indicates that one of the most potentially effective management techniques to enhance the spawning success of inshore demersal and reef fishes, and particularly those contributing to multi-species fisheries, would be by the creation of marine harvest refugia that provide a refuge in space rather than a refuge in numbers, the latter being the aim of most traditional fisheries management measures. Such a measure as the creation of marine harvest refugia is potentially applicable in the case of the Greek fisheries.

Area	Period	Daily production	Annual production	Group	Reference
Baltic Sea	Y	—	1.5-4 gC m^{-2}	Z	Wulff *et al.* (1977)
Pacific Ocean (Japan)	—	10-60 mgC m^{-2}	—	Z	Ikeda and Motoda (1978)
Osaka Bay (Japan)	—	0.8-85 mgC m^{-3}	—	Z	Joh and Uno (1983)
West Coast of Sweden	Y	—	1-2 gC m^{-2}	Z	Baamsteadt (1984)
North Atlantic Ocean	Y	—	7 mg m^{-2}	Z	Razouls (1985)
St. Lawrence Gulf (Canada)	—	29 mgC m^{-2}	—	Z	Citarella (1985)
Indian Ocean	—	15-47.8 mgC m^{-2}	—	Z	Goswami (1985)
Baltic Sea	Y	—	3.1-7.8 gC m^{-2}	Z	Kankaala (1987)
Westernport Bay (Australia)	Y	—	1 gC m^{-2}	Z	Kimmerer and McKinnon (1987)
Eastern Mediterranean	Y	0.05-3.9 mg m^{-3} (0.32-18.86 mgC m^{-2})	0.12-0.19 g m^{-3} (0.58-0.93 gC m^{-2})	Z	Christou (1991)
Scotian Shelf (Canada)	Y	—	21.6 g m^{-2}	C	Tremblay and Roff (1983)
North Sea	May-Oct	—	9 g m^{-2}	C	Fransz *et al.* (1984)
Inland Sea (Japan)	Y	—	33.7 gC m^{-2}	C	Uye *et al.* (1986)
Skagerrak	Aug	3-8 mgC m^{-3}	—	C	Peterson *et al.* (1991)

Table 6: Zooplankton production in different areas of the world ocean. Y=entire year; —=no data available; dominant group: Z=zooplankton. C=copepods.

REFERENCES CITED

Azov Y. 1991. Eastern Mediterranean - a marine desert? *Mar. Pollut. Bull.* 23: 225-232.

Baamsteadt U. 1984. Secondary production. The situation in the sea area between the North Sea and the Baltic Sea. Symp. Goeteborg, 1983. Medd., Havsfiskelab, Lysekil, 292: 96-110.

Balopoulos E. and E. Papageorgiou. 1991. Water masses and flow features in the north Euboikos Gulf (eastern Mediterranean): an initial assessment. *Vie Milieu*, 41: 169-176.

Becacos-Kontos T. 1968. The annual cycle of primary production in the Saronicos Gulf (Aegean Sea) for the period Nov. 1963-Oct. 1964. *Limn. Ocean*, 13: 485-489.

Becacos-Kontos T. 1977. Primary production and environmental factors in an oligotrophic biome in the Aegean Sea. *Mar. Biol.*, 42 93-98.

Ben Tuvia A. 1983. The Mediterranean Sea - biological aspects. *In*: *Ecosystems of the world, 26: Estuaries and enclosed seas.* Elsevier Scient. Publ.: 239-251.

Bohnsack J.A. 1990. The potential of marine fishery reserves for reef fish management in the U.S. southern Atlantic. Miami, *NOAA Tech. Memo. NMFS-SFSC*, 261, 40 p.

Bray J.R. and J.T. Curtis. 1957. An ordination of the upland forest communities of southern Wisconsin. *Ecol. Monogr.*, 27: 325-349.

Chavez F.P., R.T. Barber and M.P. Sanderson. 1989. The potential primary production of the Peruvian upwelling ecosystem, 1953-1984. *In*: D. Pauly, P. Muck, J. Mendo and I. Tsukayama (eds.) The Peruvian upwelling ecosystem: dynamics and interactions. *ICLARM Conf. Proc.*, 18: 50-63.

Christou E.D. 1991. *Secondary production in the Saronikos Gulf.* Unpublished Ph.D thesis, Univ. Athens, 225p.

Citarella G. 1985. Production apparente du zooplancton. *C.r. hebd. Séances Acad. Sci.*, 301 (1): 9-12.

Clarke K.R. and R.H. Green. 1988. Statistical design and analysis for a 'biological effects' study. Mar. Ecol. Prog. Ser., 46: 213-226.

Clarke K.R. and R.M. Warwick. 1989. *Lecture notes prepared for the training workshop on the Statistical Treatment and Interpretation of Marine Community Data.* FAO/ IOC/UNEP, Athens, Hellas, Sept. 1989, Part II.

Cury P. 1995. Comparison of the Ivoiro-Ghanaian fishery with other exploited upwelling systems of the world. *In*: F.X. Bard and K. Koranteng (eds.). *Dynamics and use of sardinella resources from upwelling off Ghana and Ivory Coast.* ORSTOM, Paris. Colloques et Séminaires. 169-193.

Davis G.E. 1989. Designated harvest refugia: the next stage of marine fishery management in California. *CalCOFI Rep.*, 30: 53-58.

FAO 1989. *Yearbook of fisheries statistics - Catches and landings*, 62, Rome.

Field J.G., K.R. Clark and R.M. Warwick. 1982. A practical strategy for analysing multispecies distribution patterns. *Mar. Ecol. Prog. Ser.*, 8: 37-52.

Fransz H.G., J.C. Miquel and S.R. Gonzalez. 1984. Mesozooplankton composition biomass and vertical distribution and copepod production in the stratified central North Sea. *Neth. J. Sea Res.*, 18: 82-96.

Friligos N. 1980. Nutrients in Hellenic waters. *J. Etud. Pollut.*, 5: 1025-1034.

Friligos N. 1987. Eutrophication assessment in Greek coastal waters. *Toxicol. Env. Chem.*, 15: 185-196.

Georgopoulos D., A. Theocharis and G. Zodiatis. 1989. Intermediate water formation in the Creatan Sea (south Aegean Sea). *Oceanol. Acta.*, 12: 353-359.

Goswami S.C. 1985. Secondary production and zooplankton abundance in the coastal waters from Vergurla to Malpe West coast of India. *Indian J. Mar. Sci.*, 14(2): 85-92.

Gray J.S., M. Aschan, M.R. Carr, K.R. Clarke, R.H. Green, T.H. Pearson, R. Rosenberg and R.W. Warwick. 1988. Analysis of community attributes of the benthic macrofauna of Frierfjord/Langesundfjord and in a mesocosm experiment. *Mar. Ecol. Progr. Ser.*, 46: 151-165.

Hopkins T.S. 1978. Physical processes in the Mediterranean basin. *In*: B. Kjerfve (ed.). *Estuarine transport processes.* Bell W. Baruch Lib. in Mar. Sci. 7.

Ikeda T. and S. Motoda. 1978. Estimated zooplankton production and their ammonia excretion in the Kuroshio and adjacent seas. *Fish. Bull.* U.S., 76: 357-367.

Joh H. and S. Uno. 1983. Zooplankton standing stock and their estimated production in Osaka Bay. *Bull. Plankton. Sci. Japan*, 30 (1): 41-51.

Kankaala P. 1987. Structure, dynamics and production of mesozooplankton community in the Bothnian Bay, related to environmental factors. *Int. Revue Ges. Hydrobiol.*, 72: 121-146.

Kimmerer W.J. and A.D. McKinnon. 1987. Growth mortality and secondary production of the copepod *Acartia tranteri* in Westernport Bay, Australia. *Limn. Ocean.*, 32: 14-28.

Lascaratos A., E. Salusti and G. Papageorgaki. 1989. Wind-induced upwellings and currents in the gulfs of Patras, Nafpaktos and Korinthos, western Hellas. *Oceanol. Acta*, 12: 159-164.

Mann K.H. and J.R.N. Lazier. 1991. *Dynamics of marine ecosystems, biological-physical interactions in the oceans*. Blackwell Scient. Publ. Boston, 466 p.

Maguran A.E. 1988. *Ecological diversity and its measurement*. Groom Helm, London, 179p.

Metaxas D.A. 1973. *Air-sea interaction in the Greek seas and resulted etesian wind characteristics*. Univ. Ioannina, Greece, School of Physics and Mathematics Techn. Rep., 5: 1-32.

NSSH (National Statistical Service of Hellas). 1965-1990. *Statistical Year-Book*. 26 issues (for the years 1964-1989), Athens, Greece.

Pagou K. and O. Gotsis-Skretas. 1989. Phytoplankton. *In*: A. Boussoulengas and A.V. Catsiki (eds.). *Pollution research and monitoring programme in the Aegean and Ionian Seas. Rep.* 2 (1986-1987), NCMR, Athens, 128-156.

Papaconstantinou C., K.I. Stergiou, S. Christianides, P. Chatzinikolaou, S. Kavadas, M. Kleanthous and A. Fourtouni. 1994. Hydro-acoustic assessment of the distribution and relative abundance of small pelagic fishes in the north Aegean Sea. *NCMR, Athens, Final Techn. Rep.*, 5, 120 p.

Pavlova E.V. 1966. Composition et repartition du zooplancton en mer Egée. *In*: *Recherches sur le plancton des mers du Sud*. Nauka. (in Russian).

Peterson W.T., P. Tiselius and T. Kjørboe.1991. Copepod egg production, moulting and growth rates, and secondary production in the Skagerrak in August 1988. *J. Plankton Res.*, 13: 131-154.

Pollard D. 1993. Maximizing the potential for both sustainable fisheries and alternative uses of fish habitat through marine harvest refugia. *Proc. Austr. Soc. for Fish Biology Workshop on Sustainable Fisheries through Sustaining Fish Habitat*. Bur. of Res. Sci., Canberra, 156-158.

Razouls S. 1985. Adaptations des êtres marins aux eaux froides: Aspects physiologiques et écophysiologiques: Séminaire animé par P. Mayzaud, 6-13 Novembre 1984. *Oceanis*, 11 (1): 53-71.

Roberts C.M. and N.V.C. Polunin. 1991. Are marine reserves effective in management of reef fisheries? *Rev. Fish Biol. Fish.*, 1: 65-91.

Siokou-Frangou, I. and A. Pancucci-Papadopoulou. 1989. Zooplankton. *In*: A. Boussoulengas and A.V. Catsiki (eds.). *Pollution research and monitoring programme in the Aegean and Ionian Seas*. Rep. 2 (1986-1987), NCMR, Athens. 157-173.

Siokou-Frangou I., E. Christou and A. Pancucci-Papadopoulou. 1991. Zooplankton data. *In*: *Pollution research and monitoring program in the Aegean and Ionian seas*. Data Report 1988-1989, NCMR 1991 (Katsiki).

Sparholt H. 1990. An estimate of the total biomass of fish in the North Sea. *J. Cons.*, Cons. int. Exp. Mer, 46: 200-210.

Stergiou K.I. 1992a. Variability of the monthly catches of anchovy, *Engraulis encrasicolus*, in the Aegean Sea. *Fish. Bull.* U.S., 90: 211-215.

Stergiou K.I. 1992b. Geographic variations in biological parameters of red bandfish, *Cepola macrophthalma*, in the western Aegean Sea: implications for fisheries management in the eastern Mediterranean. *FAO Fish. Rep.*, 477: 35-42.

Stergiou K.I. 1993. Nutrient-dependent variation in growth and longevity of the red bandfish, *Cepola macrophthalma* (L.), in the Aegean Sea. *J. Fish. Biol.*, 42: 633-644.

Stergiou K.I., C. Papaconstantinou and G. Petrakis. 1989. Fisheries production in the Patraikos and Korinthiakos Gulfs and the Ionian Sea, 1980-1985. *Proceedings of the 2nd Hellenic Symposium on Oceanography and Fisheries*, 2: 571-576 (in Greek, with English abstract).

Stergiou K.I., C. Papaconstantinou and G. Petrakis. 1992. The Mullidae (*Mullus barbatus*, *M. surmuletus*) fishery in Greek waters, 1964-1986. *FAO Fish. Rep.*, 477: 97-113.

Stergiou K.I. and D. Georgopoulos. 1993. The distribution of phytoplankton pigments and the fishery of anchovy (*Engraulis encrasicolus*) in the Greek seas. *ICLARM*, Naga, Quarterly 16(2): 34-37.

Stergiou K.I. and G. Petrakis. 1993. Description, assessment of the state and management of the demersal and inshore fisheries resources in the Hellenic Seas. *Fresenius Envir. Bull.*, 2: 312-319.

Stergiou K.I., C. Papaconstantinou, M. Kleanthous and A. Fourtouni. 1993. The relative abundance and distribution of small pelagic fishes in the Aegean Sea. *Fresenius Envir. Bull.*, 2: 357-362.

Stergiou K.I., E.D. Christou and G. Petrakis. 1994. *Operational forecasting of Hellenic fisheries catches*. Final Rep. (Contract number MED92/019) to the Commission of the European Union, Directorate General for Fisheries, Unit XIV-1., Stergiou & Co., Athens, Hellas, July 1994. 1-98. (+83p. Appendix).

Stergiou K.I. and D. Pollard. (in press). A spatial analysis of the commercial fisheries catches from the Hellenic Aegean Sea. *Fish. Res.*

Theocharis A. and D. Georgopoulos. In press. Deep water formation over the Samothraki and Limnos plateaux in the north Aegean Sea (eastern Mediterranean Sea). *Cont. Shelf Res.*

Therianos A.D. 1974. The geographic distribution of river water supply in Hellas. *Bull. Hell. Geol. Soc.* 11: 28-58 (in Greek).

Tremblay M.J. and J.C. Roff. 1983. Production estimates for Scotian Shelf copepods based on mass-specific P/B ratios. *Can. J. Fish. Aquat. Sci.*, 40: 749-753.

Uye S., Y.H. Kuwata and T. Endo. 1986. Standing stocks and production rates of phytoplankton and planktonic copepods in the Inland Sea of Japan. *J. Oceanogr. Soc. Japan*, 42: 421-434.

Whitehead P.J.P., M.L. Bauchot, J.C. Hureau, J. Nielsen and E. Tortonese. (eds.) 1984. *Fishes of the north-eastern Atlantic and the Mediterranean*. Unesco, Vol. II.

Wulff F. 1977. *Ekologiska undersokningar i Lulea skargard 1976.* Slutrapport till Statens Naturvardsverk. Askolaboratoriet Stockholms Universitet och Ecologisk Zoologi Umea Universitet.

Pelagic Fisheries and Environmental Constraints in Upwelling Areas: How much is Possible?

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ABSTRACT

The relations among fish productivity and five environmental variables are analyzed for eleven upwelling areas of the world. Three 'fish catch productivity' indices, calculated from fish catch statistics, are used as surrogates for fish productivity in the ecosystems. Five environmental parameters are considered in each upwelling areas: coastal upwelling and turbulence indices, sea surface temperature, continental shelf surface and length. On its own, the size of the ecosystem does not explain the observed differences of the pelagic fish productivity indices. Using non-parametric regression methods, it is shown that a combination of several environmental factors is required for high fish productivity. These optimal conditions are a high upwelling index (around 1.3 $m^3/s/m$), a moderate turbulence (around 200-250 m^3/s^3), a medium sea surface temperature (15-16°C) and a relatively large continental shelf (around 100 000 km^2). The Peruvian ecosystem is the only system which combines all of these environmental conditions. The environmental factors which limit fish productivity are identified in each upwelling zones; they can help to predict changes under future climatic events. The limits of the analysis as well as some possibly circular aspects of the analysis are emphasized.

RÉSUMÉ

La productivité halieutique est analysée en relation avec cinq variables environnementales pour onze zones d'upwelling mondiales. Trois indices de productivité sont estimés à partir des statistiques de captures disponibles ; ils sont assimilés à la productivité en poisson d'un écosystème. Cinq variables environnementales sont considérées pour chaque zone d'upwelling : indices d'upwelling côtier et de turbulence, température de surface de la mer, surface et longueur du plateau continental. La taille d'un écosystème en elle-même n'explique pas la disparité observée entre les différentes productivités en poissons pélagiques des zones d'upwelling. Des méthodes régressives non paramétriques révèlent qu'une combinaison de plusieurs facteurs environnementaux est en effet nécessaire pour qu'une forte productivité en poisson soit réalisable. Les conditions optimales sont les suivantes : un fort indice d'upwelling (proche de 1.28 $m^3/s^1/m^1$), une turbulence modérée (proche de 200-250 m^3/s^3), une température de surface moyenne (15-16 °C) associés à un plateau continental relativement vaste (d'environ 100 000 km^2). L'écosystème péruvien s'avère être le seul qui regroupe l'ensemble des conditions environnementales optimales. Le ou les facteurs environnementaux qui sont supposés limiter la productivité en poisson sont identifiés pour chacune des zones d'upwelling ; ils peuvent aider à prédire les éventuels changements consécutifs aux futurs événements climatiques. Les limites ainsi que les aspects tautologiques de cette analyse sont soulignés.

INTRODUCTION

Approximately one hundred million tonnes of fish and shellfish are extracted every year from the sea and the inland waters since 1989 (Fig. 1). The total marine fish catch represents 75% and around one third of it is composed of pelagic fish (Fig. 1).

Pelagic fisheries are mainly located in the four main upwelling areas which are located in the eastern boundary currents, i.e., the Canary, the Benguela, the California and the Humbolt currents. Two fisheries contribute most to the world pelagic fish catch: the Peruvian and the Chilean fisheries. Annually they land millions of tonnes whereas countries like Morocco, the USA (California) or South Africa contribute hundred thousand of tonnes, while the catches in Côte-d'Ivoire or Ghana remain in the order of a few thousand tonnes. It is natural to think that large upwelling systems are able to produce more than small ones. However is it correct to say that a large upwelling system will always produce as much as a medium one? This is not obvious: the size of an ecosystem is an important factor when considering productivity, however it may not be

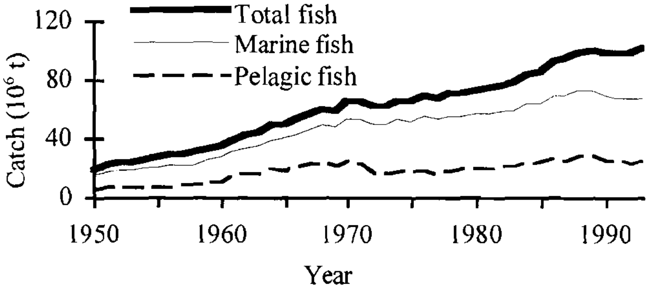

Fig. 1: Marine and pelagic fish contributions to world catches (FAO, 1995).

the only factor affecting pelagic fish productivity. Pelagic fish stocks are known for their instability and numerous authors have examined the causes of catch variations (Sharp and Csirke, 1983; Lluch-Belda *et al.*, 1991; Kawasaki, 1992; Bakun, 1994; Cury *et al.*, 1995). Environmental factors such as turbulence, upwelling intensity, offshore Ekman transport were found to be responsible for recruitment successes or failures. Do environmental factors involved in fish population fluctuations also explain the observed difference in pelagic fish productivity among upwelling systems? The comparative approach constitutes a powerful tool in ecological science as it allows to establish the generality of phenomena (Bakun, 1985). However, as stated by Maynard Smith and Holliday (1979) "we must learn to treat comparative data with the same respect as we would treat experimental results". Whereas it is a currently adopted method in evolutionary biology (Harvey and Pagel, 1991), it is not so frequently used in ecology. A comparative approach could lead to an empirical understanding of the disparity between fish productivity among upwelling systems by identifying the responsible environmental factor(s) which contribute to a low or high productivity. In this paper, the productivity of pelagic fish in eleven upwelling systems is therefore compared and its relationship with the environment examined, using variables such as the area and extent of continental shelves, upwelling intensity, turbulence, and sea surface temperature.

1. IS SYSTEM SIZE ENOUGH?

Numerous variables can be used to estimate the biological production of an ecosystem, for example planktonic production, fish biomass, turn-over of living matter, etc. However, such measurements are not available in most upwelling systems, making their comparison impossible. Fish catch statistics are the only data that have been collected in most upwelling systems during long time periods (Table 1). These data are biased for multiple reasons: changes in the availability of fish, in the fishing effort, in the target species, in the markets, etc. However used as a surrogate, fishery data can give an approximate value for biological productivity which can be considered adequate when comparing extreme range of values (from several thousand to millions of tonnes).

'Fish catch productivity' indices can be derived in several ways from catch data (Table 2):

- a 'mean fish catch productivity' index can be calculated by averaging the catch data for the period during which the fishery was sustained;
- a 'maximum fish catch productivity' index can be estimated from the observed maximum catch value; and
- a 'maximum fish catch productivity per unit of surface' index can be calculated by dividing the maximum fish catch productivity index by the surface of the continental shelf.

All of these three options were used here.

Upwelling areas	Pelagic fish species	Time period	Data sources
California	*Sardinops sagax*	1879-1990	NMFS (National Marine Fishery Service)
	Engraulis ringens	1928-1991	
	Scomber japonicus	1926-1991	
Peru	*Sardinops sagax*	1950-1993	IMARPE (Instituto del Mar del Perù)
	Engraulis ringens	1950-1993	
	Scomber japonicus	1964-1993	
Chile	*Sardinops sagax*	1964-1993	IFOP (Instituto de Fomento Pesquero)
	Engraulis ringens	1952-1993	
	Scomber japonicus	1964-1993	
Spain and Portugal	*Sardina pilchardus*	1940-1988	FAO (Food and Agriculture Organization of the United Nations) 1995
	Engraulis encrasicolus	1968-1988	
Morocco	*Sardina pilchardus*	1925-1991	FAO (1995) and ISPM (Institut Scientifique des Pêches Maritimes)
	Engraulis encrasicolus	1964-1991	
	Scomber japonicus	1964-1991	
Senegal	*Sardinella aurita*	1966-1991	CRODT (Centre de Recherches Océanographiques de Dakar-Thiaroye)
	Sardinella maderensis	1966-1991	
Côte-d'Ivoire - Ghana	*Sardinella aurita*	1966-1991	CROA (Centre de Recherches Océanologiques d'Abidjan) and FRUB (Fisheries Department Research and Utilisation Branch)
	Sardinella maderensis	1966-1991	
	Scomber japonicus	1966-1993	
Namibia	*Sardinops ocellatus*	1949-1992	Crawford *et al.* (1987) and Crawford (pers. comm.)
	Engraulis japonicus	1964-1992	
South Africa	*Sardinops ocellatus*	1950-1991	Crawford *et al.* (1987) and Crawford (pers. comm.)
	Scomber japonicus	1963-1991	
Venezuela	*Sardinella aurita*	1957-1989	Guzman *et al.* (in press)
India	*Sardinella longiceps*	1896-1989	Longhurst and Wooster (1990) and FAO (1995)
	Rasterlliger kanagurta	1925-1989	
	Anchovy nei	1963-1989	

Table 1: Fishery data from eleven upwelling areas and for three main pelagic species (sardine, anchovy and mackerel) collected during different time period.

These productivity indices are calculated for two main pelagic species (sardine and anchovy), and for the pelagic species total (sardine, anchovy and mackerel) (Table 2).

Important differences are observed among pelagic fisheries (Table 2). Three fisheries catch more than one million tonnes: Peru, Chile and Namibia. The Peruvian ecosystem has a maximum total pelagic catch productivity well above that for other systems. Species productivity is also different from one geographic zone to another. For Venezuela maximum catch for sardine is around 80 000 t whereas more than 2 million t are caught in Chile. The anchovy in Morocco never reached more than 19 000 t and more than 12 million t were landed in Peru.

Large ecosystems should a priori be able to produce more fish than small ones. In order to quantify the size of the ecosystems, the length and the surface of the continental shelf were measured. The surfaces of the continental shelves vary from 17 000 km^2 for Venezuela to 178 300 km^2 for South Africa (Table 3). South Africa, Morocco and California have large continental shelves (higher than 100 000 km^2) while Spain-Portugal, Senegal, Côte-d'Ivoire-Ghana or Venezuela have medium to small ones (lower than 60 000 km^2).

The Peruvian and Chilean total pelagic catch productivity are the highest among the others whereas their continental shelf surfaces are of medium sizes (Fig. 2a). On the other hand, the South African and the Moroccan ecosystems have a wide continental shelf and a poor fish productivity compared to the others (Fig. 2b). Thus, areas with a large continental shelf

	Sardine 'catch productivity' index				Anchovy 'catch productivity' index				Total pelagic 'catch productivity' index			
Upwelling areas	Time period considered	Mean (t/year)	Maximum (t/year)	Maximum per unit of surface (t/km^2/year)	Time period considered	Mean (t/year)	Maximum (t/year)	Maximum per unit of surface (t/km^2/year)	Time period considered	Mean (t/year)	Maximum (t/year)	Maximum per unit of surface (t/km^2/year)
1 California	1924-1990	130919	572661	15.6	1970-1991	141316	310811	141.9	1924-1991	200901	609979	6.0
2 Peru	1978-1993	2068449	3470422	43.4	1960-1993	4486294	12277022	21.6	1958-1993	5299183	12286264	142.0
3 Chile	1978-1993	1528795	2709926	15.5	1962-1993	571572	1350626	4.2	1966-1993	1540109	3708071	59.3
4 Spain-Portugal	1927-1988	161752	241000	5.7	1968-1988	30988	66700	3.1	1937-1989	331839	368893	6.1
5 Morocco	1950-1991	169858	338100	3.9	1965-1991	3552	19124	1.1	1950-1991	192885	362023	3.1
6 Senegal	1974-1991	101008	194693	5.9	—	—	—	—	1964-1991	77234	194693	5.9
7 Côte-d'Ivoire - Ghana	1966-1993	74809	172977	3.2	1966-1993	52007	92988	1.7	1966-1993	7188405	270570	5.0
8 Namibia	1963-1992	371720	1400100	4.0	1963-1990	161996	376000	1.1	1966-1992	507663	1561300	17.3
9 South-Africa	1960-1991	113916	410200	2.9	1969-1992	234752	596000	0.2	1950-1992	274312	623200	3.5
10 Venezuela	1957-1989	38032	80079	4.7	—	—	—	—	1957-1989	38032	80079	4.7
11 India	1956-1989	190523	274772	2.3	1963-1989	35529	79655	3.3	1948-1988	249382	448206	6.4

Table. 2: Fish catch productivity indices of eleven upwelling ecosystems.

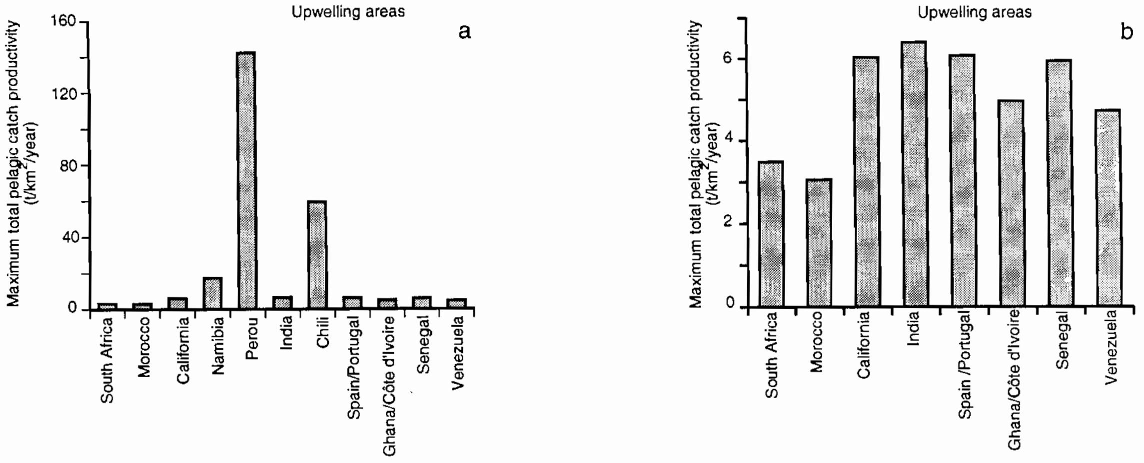

Fig. 2: a) Maximum total pelagic catch productivity per unit of surface (t/km^2) for the studied upwelling areas; b) the same as Fig. 2a, but without the Chilean and Peruvian values.

are not necessarily among the most productive. Other environmental variables than surface area undoubtedly play a role in the intrinsic production of upwelling ecosystems.

2. HOW MANY ENVIRONMENTAL FACTORS?

Environmental parameters cause fish population fluctuations mainly through their role in the recruitment process (Parrish and MacCall, 1978; Bakun and Parrish, 1982; Cury and Roy, 1989; Lluch-Belda *et al.*, 1989; Cushing, 1990; Cushing, 1995). Five environmental parameters were selected for the analysis: coastal upwelling index (CUI in m^3/s/m) using standard assumptions[1], turbulence index (V^3 in m^3/s^3), sea surface temperature (SST in °C) and continental shelf length or surface (CSl in km and CSs in km^2). The turbulence index was calculated by averaging all the cubed wind measurements. The COADS data (Comprehensive Ocean Atmosphere Data Set) collected by merchant ships of opportunity all around the world oceans were used (Roy and Mendelssohn, this vol.). As they are obtained in a similar fashion in all areas, they are strictly comparable and they also provide a data base which is compatible in time with the fishery data. Mean environmental values were calculated for the different upwelling areas (Table 3). Upwelling index varies from 0.36 m^3/s/m for Spain-Portugal to 1.28 m^3/s/m for Namibia. Three areas exhibit strong upwelling indices: Namibia, Peru and Côte-d'Ivoire-Ghana. Turbulence index varies from 103 m^3/s^3 for Côte-d'Ivoire-Ghana to 723 m^3/s^3 for South Africa. A high

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[1] *$CUI = rCdV^2 / 2\Omega \sin \phi$ with V^2 wind component perpendicular to coast , r air density (0.0012 g.cm^3), Ω angular velocity of earth rotation, ϕ latitude, Cd roughness coefficient at interface air/sea.*

		Geographic characteristics				Environmental parameters (mean from 1946 to 1990)		
	Upwellings areas	Latitude	Longitude	Continental shelf		Upw. index	Turbulence	Sea surface
				surface (km^2)	length (km)	($m^3/s/m$)	(m^3/s^3)	temperature (°C)
1	California	22°-38°N	—	101167	1778	0,54	654	15,6
2	Peru	5°-18°N	—	86523	1444	1,20	225	19,1
3	Chile	18°N-43°S	—	62516	2778	0,93	346	16,5
4	Spain and Portugal	2°-44°N	5°-9°	59864	1667	0,36	628	16,3
5	Morocco	21°-36°N	2°-0°	118539	1667	0,66	306	19,6
6	Senegal	12°-16°N	—	32887	445	0,59	150	23,7
7	Côte-d'Ivoire - Ghana	2°-8°N	0°-8°	54647	667	1,04	103	27,1
8	Namibia	16°-28°S	—	90508	1334	1,28	517	16,8
9	South-Africa	28°-36°S	—	178315	1778	0,65	723	16,9
10	Venezuela	8°-11°N	62°-65.5°	17000	389	—	332	27,1
11	India	8°-15°N	—	70135	778	0,40	240	28.1

Table 3: Environmental characteristics of the eleven upwelling areas compared in this study.

upwelling intensity is classically associated with a high turbulence intensity (in Namibia and Chile), but sometimes, it corresponds to a moderate turbulence index (in Peru and Côte d'Ivoire-Ghana). In the same way, moderate upwelling indices may be associated with strong turbulence indices (in California, Spain-Portugal, South-Africa). The mean sea surface temperature ranges between 15.6°C for California and 28.1°C for India.

The relationship between fish catch productivity and environmental factors is explored using non-parametric regressive models. Iterative algorithms that extend linear multiple regression analysis to generalized additive models provide a method to explore the relationship between the response and the predictor variables when the form of these relationships are a priori unknown. The non-linearity of the relationships as well as the multiplicity of factors can be considered. The ACE (Alternating Conditional Expectation) and the GAIM (Generalized Additive Interactive Modeling) statistical methods estimate optimal transformations for multiple regressions (Hastie and Tibshirani, 1990).

The usual linear multiple regression model for predicting a response variable Y from p predictor variables X_i, i =1,..., p and for n observations, j = 1,...,n, is given by :

$$Y(j) = \Sigma b_i X_i(j) + e(j) \qquad e(j) \text{ are independent}$$

The response variable Y and the predictor variables X1.....Xp in the nonparametric model are replaced by functions $T_1(Y)$ and $T_2(X_1)....T_{p-1}(X_p)$:

$$S(Y(j)) = \Sigma b_i T_i(X_i(j)) + w(j)$$

S(Y) and $T_i(X)$ are unknown and estimated by minimizing: $E((T_1(Y) - \Sigma T_{i+1}(X_i))^2) / \mathrm{var}(T_1(Y))$

Several approaches exist to estimate the last equation. ACE includes the b_i in the function $T_i()$, while GAIM estimates the b_i's in order to perform analysis of deviance tests on the parameters. GAIM produces an analysis of deviance as well as coordinates for plotting the function estimates and their standard errors. The algorithms converge to optimal solutions for a given criterion as they have their own smoothers and convergence criterion (See Cury *et al.*, 1995 for a detailed application).

A regressive analysis is done using the fish catch productivity index as the response variable and five environmental parameters as predictor variables. The transformation shape is found by plotting the transformed values of a variable versus the original values. Results using the ACE algorithm are presented.

2.1. Maximum total pelagic catch productivity as a response variable

The relationships between fish catch productivity index and every environmental variable are first explored. Optimal transformations (T1,T2) for the multiple regression were calculated using maximum total pelagic catch productivity index as the response variable and the upwelling index, the turbulence index, sea surface temperature and/or continental shelf surface as the predictor.

T1 (maximum total pelagic catch productivity) = T2 (CUI) $R^2 : 0.34$ (1)

T1 (maximum total pelagic catch productivity) = T2 (V3) $R^2 : 0.11$ (2)

T1 (maximum total pelagic catch productivity) = T2 (SST) $R^2 : 0.49$ (3)

T1 (maximum total pelagic catch productivity) = T2 (CSs) $R^2 : 0.93$ (4)

The transformations for the maximum total pelagic catch productivity are positive and linear in models (1) and (2) (Fig. 3a and 3b) and are close to a log transformation in models (3) and (4) (fig. 3c and 3d). On the whole, the upwelling transformation is linear and positive (fig. 3a). The turbulence is transformed to a nearly dome shaped curve. It first increases to a value around 200 m^3/s^3 then decreases strongly (Fig. 3b). The transformation for the sea surface temperature decreases strongly and linearly (Fig. 3c). The estimated transformation of continental shelf surface is close to logarithmic in form, with a breaking point around 100 000 km^2 (Fig. 3d). The R^2 value for model (4) is very high; however when the response variable is forced to be linear, its value decreases to 0.17.

Multivariate analyses are realized by considering several environmental variables simultaneously in the model. Results which combine three environmental predictors are presented on figures 4 and 5.

Optimal transformations (T1, T2, T3, T4) for multiple regression were calculated using first maximum total pelagic catch productivity index as the response variable and turbulence, sea surface temperature and upwelling index as predictors in model (5) (Fig. 4) or the upwelling index, the turbulence and the continental shelf surface as the predictors in model (6) (Fig. 5). Thus, we have

T1(maximum total pelagic catch productivity) = T2 (V3) + T3 (SST) + T4 (CUI) $R^2 : 0.59$ (5)
T1(maximum total pelagic catch productivity) = T2 (CUI) + T3 (V3) + T4 (CSs) $R^2 : 0.44$ (6)

The response variable transformation is forced to be linear (Fig. 4a). Both transformations of turbulence and of sea surface temperature are linear and negative (Fig. 4b and 4c). On the whole, the upwelling transformation is linear and positive, particularly above a value around 0.7 $m^3/s/m$ (Fig.4d).

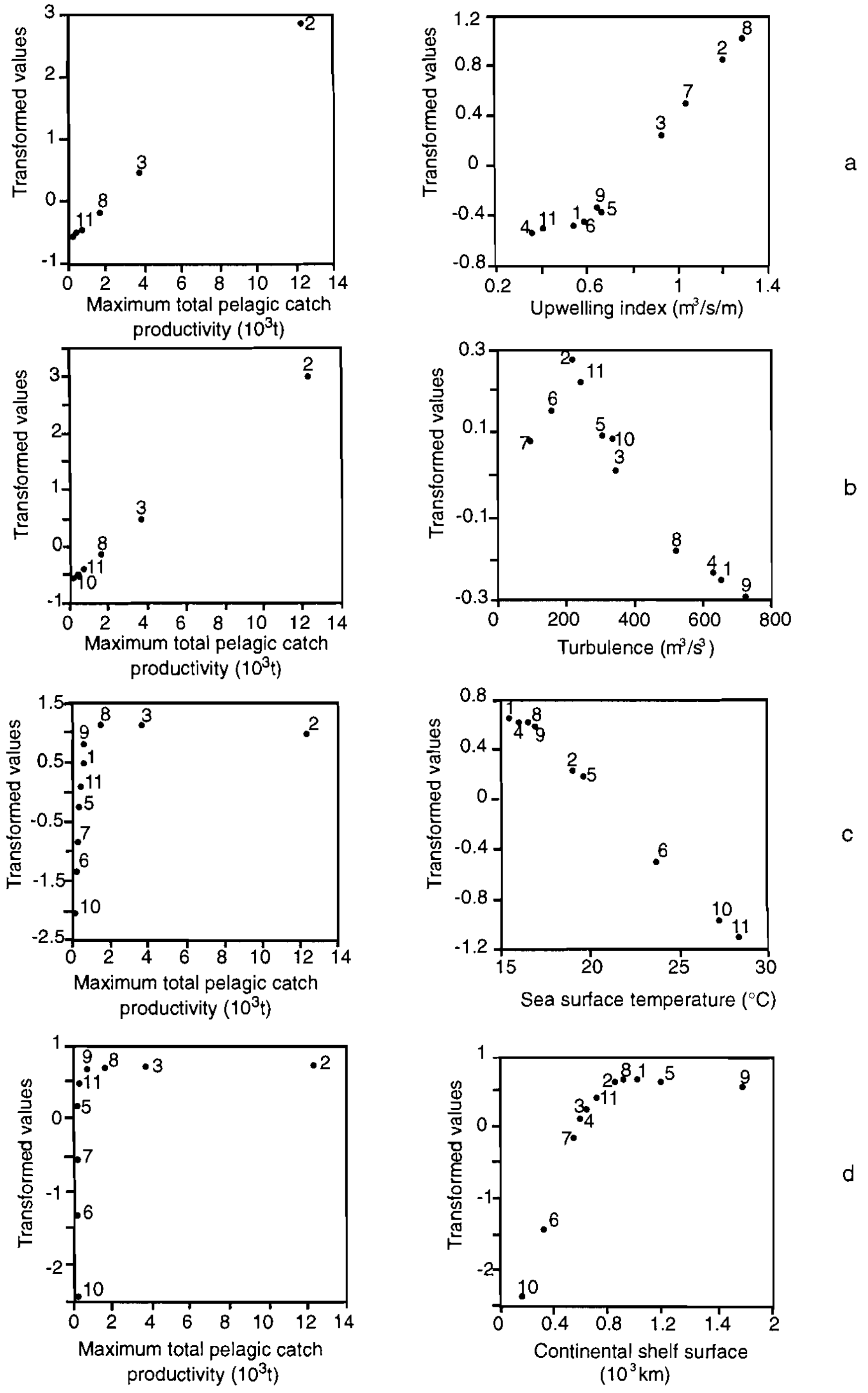

Fig. 3: Optimal empirical transformations from the ACE algorithm using maximum total pelagic catch productivity as the dependent variable and upwelling index, turbulence, sea surface temperature and continental shelf surface as the predictor variables. R² values are for figure a: 0.34; b: 0.11; c: 0.49; and d: 0.93. Numbers identify ecosystems (see Tab. 2 and 3).

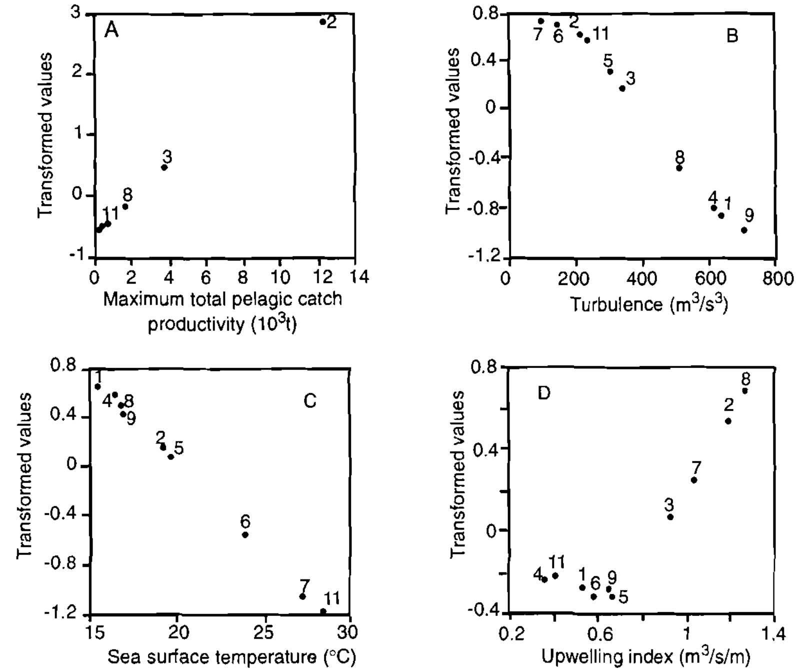

Fig. 4: Optimal empirical transformations from the ACE algorithm using maximum total pelagic catch productivity as the dependent variable and turbulence, upwelling index and sea surface temperature as predictor variables. The transformation of the response variable is forced to be linear. R^2= 0.59. Numbers identify ecosystems (see Tab. 2 and 3).

The productivity index transformation can be forced to be linear (Fig. 5a). Generally, a linear and positive relationship appears between upwelling intensity index and the productivity index (Fig. 5b), particulary above a value around 0.7 $m^3/s/m$. The transformation of the turbulence is dome-shaped with a breaking point around 250 m^3/s^3 (Fig. 5c). The transformation of the continental shelf surface is close to a log transformation Fig. 5d). It first increases, then stabilizes beyond a value around 100 000 km^2.

The transformed value scale gives indication of the relative contributions of the environmental variables to the variance. It indicates a higher contribution either of turbulence and sea surface temperature for model (5) or of upwelling intensity for model (6). The percentage of the observed variance in the total pelagic catch productivity (R^2) are: 59% and 44% for models (5) and (6), respectively.

2.2. Maximum sardine catch productivity as response variable

Optimal transformations (T1, T2, T3, T4) for multiple regression were calculated using the maximum sardine catch productivity versus upwelling index, turbulence index and sea surface temperature, i.e.,

T1 (maximum sardine catch productivity) = T2 (CUI) + T3 (V3) + T4 (SST) R^2: 0.74 (7)

The estimated transformation of maximum sardine catch productivity as well as the transformation of the upwelling index are linear and positive (Figs. 6a and 6b). The turbulence transformation has a flat top then decreases linearly beyond 200 m^3/s^3 (Fig. 6c). The sea surface temperature transformation is strongly negative and linear (Fig. 6d). The resulting model explains 74% of the observed variance of maximum sardine catch productivity.

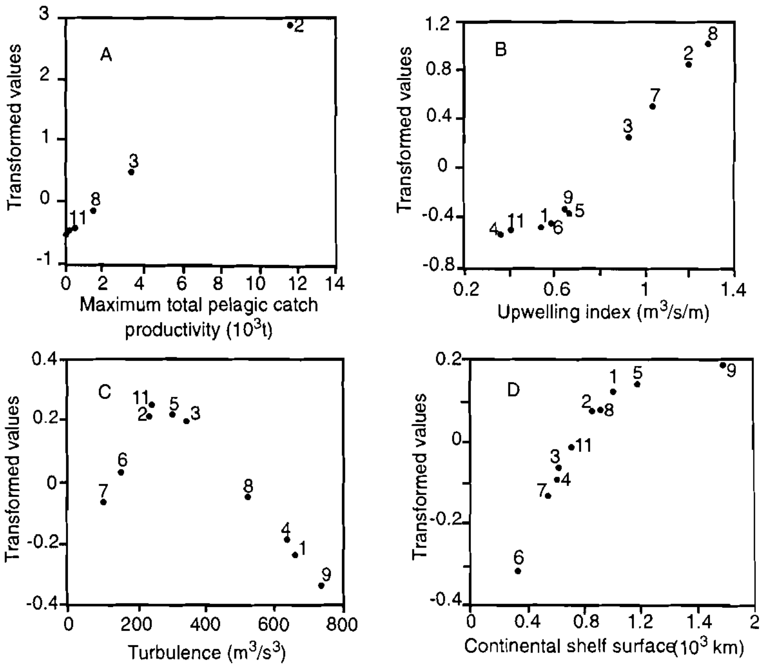

Fig. 5: Optimal empirical transformations from the ACE algorithm using maximum total pelagic catch productivity as the dependent variable and upwelling index, turbulence and continental shelf surface as predictor variables. The transformation of the response variable is forced to be linear. $R^2 = 0.44$. Numbers identify ecosystems (see Tab. 2 and 3).

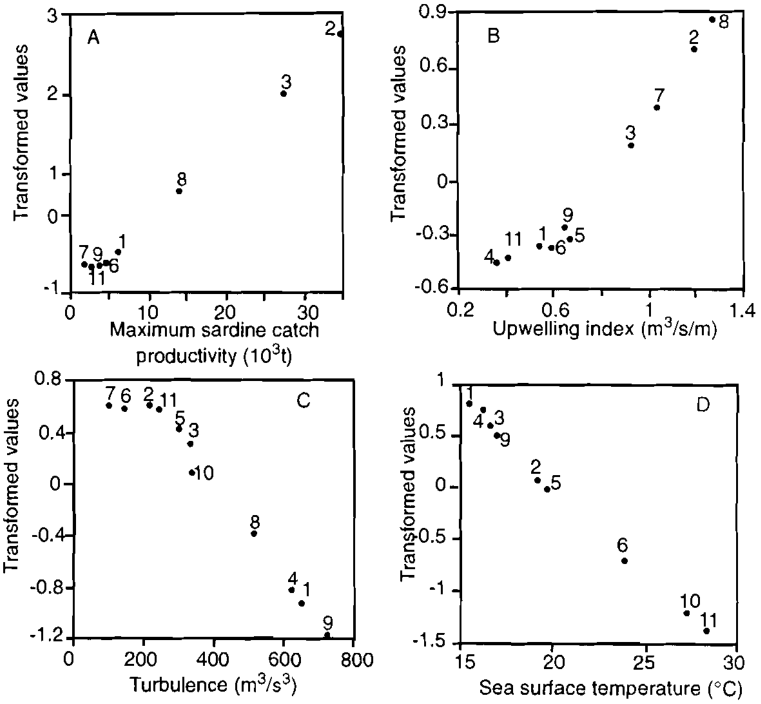

Fig. 6: Optimal empirical transformations from the ACE algorithm using maximum sardine catch productivity as dependent variable and upwelling index, turbulence and sea surface temperature as predictor variables. $R^2 = 0.74$. Numbers identify ecosystems (see Tab. 2 and 3).

2.3. Maximum anchovy catch productivity as response variable

Optimal transformations (T1, T2, T3, T4) for the multiple regressive model (8) were calculated using the maximum anchovy catch productivity index versus upwelling index, continental shelf surface and turbulence index, i.e.,

$$\text{T1 (maximum anchovy catch productivity)} = \text{T2 (CUI)} + \text{T3 (CSs)} + \text{T4 (V3)} \quad R^2 : 0.40 \qquad (8)$$

The transformation of maximum anchovy catch productivity is forced to be linear (Fig. 7a). The upwelling index transformation is on the whole linear and positive, particularily beyond a value around 0.7 m³/s/m (Fig. 7b). Continental shelf surface is transformed to a nearly log shaped curve with a breaking point around 100 000 km² (Fig. 7c). Turbulence is transformed to a linear and negative transformation (Fig. 7d). The model explains 40% of the observed variance of maximum anchovy catch productivity.

Similar results are found when using continental shelf length instead of its surface. Also, using mean fish catch productivity instead of maximum fish catch productivity indices provide similar results (not shown). Results using the GAIM algorithm instead of the ACE algorithm are similar as well (Fig. 8).

Both monovariate and multivariate analyses suggest similar patterns for the relations among fish catch productivity and environmental variables :

-the transformation of the upwelling index is mostly linear and positive;

-the transformation of the turbulence index is close to be linear and negative particulary after a value around 200-250 m³/s³;

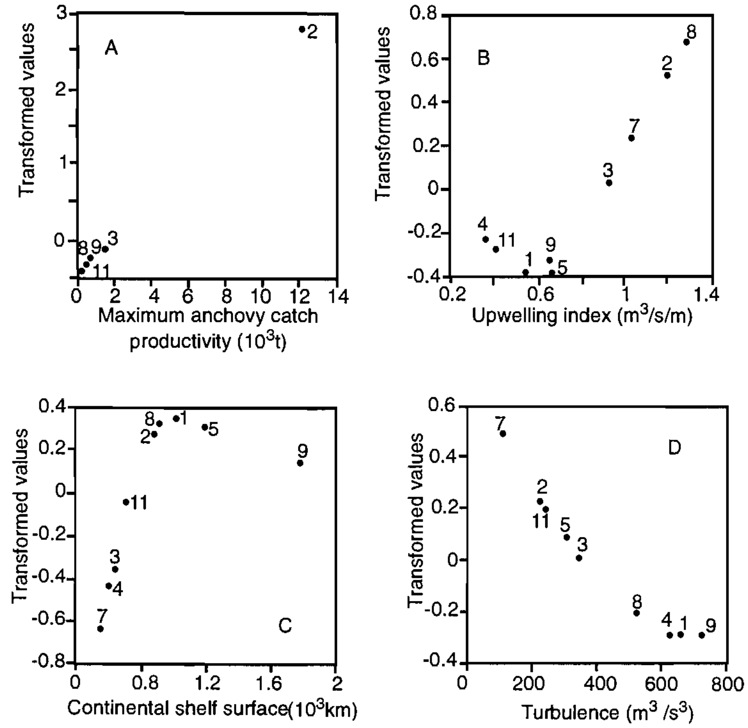

Fig. 7: Optimal empirical transformations from the ACE algorithm using maximum anchovy catch productivity as dependent variable and upwelling index, continental shelf surface and turbulence as predictor variables. The transformation of the response variable is forced to be linear. R^2 value is 0.4. Numbers identify ecosystems (see Tab. 2 and 3).

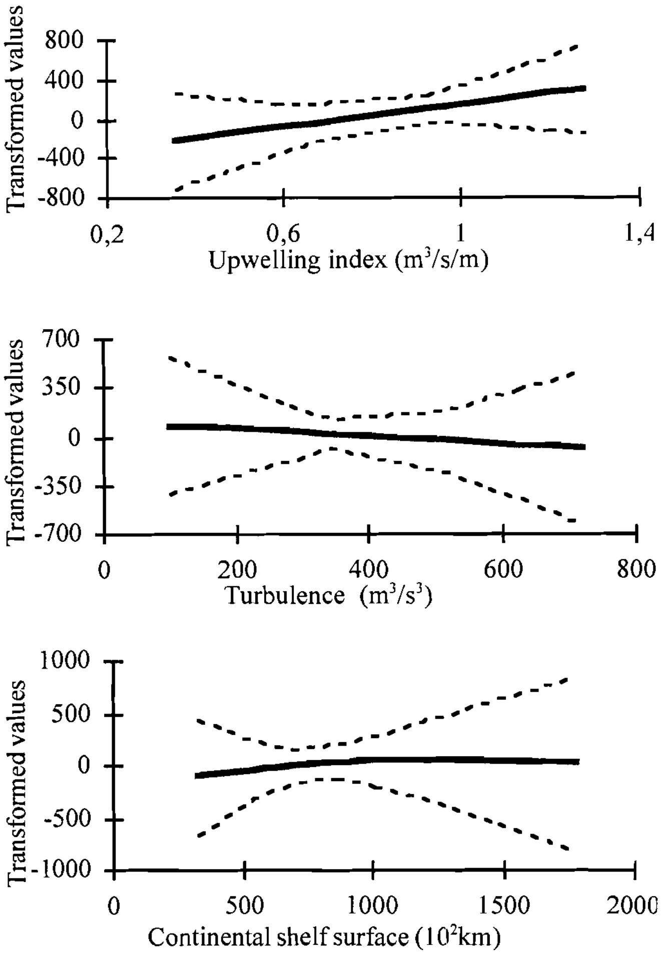

Fig. 8: Optimal empirical transformations from the GAIM algorithm using maximum total pelagic catch productivity as the dependent variable and upwelling index, turbulence and continental shelf surface as the predictor variables. The dashed lines indicates the lower and the upper standard error curves. R2= 0.36.

- the transformation of sea surface temperature is linear and negative; and
- the transformation of continental shelf surface is close to a log transformation with a breaking point around 100 000 km^2.

The comparative and exploratory analysis of the relationship among estimates of fish productivity and environmental features of upwelling systems reveals that a combination of several factors is necessary for high productivity:

- a high upwelling intensity (near to 1.28 m^3/s/m);
- a moderate turbulence (around 200-250 m^3/s^3);
- a medium sea surface temperature (15-16°C);
- a relatively large continental shelf (approximately 100 000 km^2).

The results of our statistical analysis must be considered with caution, however, as important limitations do exist:

- the comparisons are based on only eleven data points, and consequently, the statistical validity of the results is questionable due to the low number of degrees of freedom;
- one system with extreme values (Peru) plays an important role in all analyses.

This represents important limitation in our comparative analysis. However, it is also true that:

- the number of ecosystems with a documented pelagic fisheries and for which environmental data exist are limited; and
- the number of environmental factors which have been hypothesized impact on productivity is large compared to the number of ecosystems that can be compared.

Nevertheless, the present analysis gives some valuable information and cues. First, it appears that the size of the ecosystem is not the only parameter that influences its fish catches. Upwelling strength, turbulence, and sea surface temperature also play an important role. Only a combination of several environmental factors ensure a high fish productivity. The relationships between fish catch productivity and environmental variables appears to be in agreement with independent ecological knowledge on ecosystem functioning. High upwelling intensities as source of food availability (Wroblewski and Richman, 1987; Cushing, 1990) and small-scale turbulences that increase the encounter rate between food particles and larvae (Rothschild and Osborn, 1988; MacKenzie and Leggett, 1991) are thought to be beneficial to larval survival. The positive relationship between upwelling intensity and fish catch productivity could be related to these combined effects. In contrast, intense wind-driven turbulent mixing that mixes up patches of larval food appears to be detrimental (Lasker, 1975; Peterman and Bradford, 1987; Cury and Roy, 1989). Bakun (this vol.) identified a 'fundamental triad' of three major processes that combine to yield favorable environmental conditions for fishes: an enrichment process (upwelling, mixing...), a concentration process (water column stability, convergence...) and processes favoring retention within appropriate habitat. In some degree, the environmental parameters we selected may be considered as proxy variables that account for some of the processes involved in such triad. For example, the size of the ecosystem combined with upwelling intensity determines global enrichment of the ecosystem while turbulence is involved in processes that concentrate and retain food and larvae.

A comparison of the environmental values of the upwelling areas with the 'optimal environmental values' is presented on Figure 9 and the limiting factor(s) to productivity are identified (Table 4).

First, it is apparent that the Peruvian ecosystem is the only one which combines all the optimal environmental conditions (Fig. 9). In Chile and Namibia, the upwelling index is favorable; however, it is associated with an excessively high turbulence index. The same high upwelling index is found off Côte d'Ivoire-Ghana, but is associated with low turbulence. In South Africa, Spain and California, the turbulence index is high and associated with a low upwelling intensity, therefore limiting productivity.

In every upwelling areas, except Peru, at least one environmental condition differs from the 'optimal conditions' and consequently tends to limit productivity. But what will happen under changes of one or several environmental factors?

The effect of a gradual or a rapid climatic change on living marine resources is a challenge as numerous parameters are involved. There is no reliable computer-generated climate impact scenario about the next several decade, but generalizations derived from case-to-case assessments of past and present experiences can be used (Glantz, 1992). Such assessments can indeed provide first approximations on how fisheries might respond to environmental changes. Comparative analysis constitutes a good base of information to begin such assessment of possible impacts of environmental changes on fish productivity. Some scenarios for fish productivity under climatic changes derived from previous studies (Fig. 9) can thus be considered for forecast by analogy (Glantz, 1992). How and how much will productivity evolve if one or several environmental parameters change? Let's assume for example two simple scenarios. First, a drastic increase of upwelling intensity that provides more nutrients would probably improve the fish productivity in major ecosystems. The consequences may be stronger in areas where low upwelling intensity is the main limiting factor: Morocco, Senegal and Venezuela (Table 4). Secondly, under a decrease of the intensity of turbulence, a higher fish productivity may be expected in areas where high turbulence is limiting factor: California, Chile, Spain-Portugal, Morocco, Namibia, South-Africa and Venezuela (Table 4).

The reality is obviously more complex as environmental factors change simultaneously. A scenario involving one environmental parameter is thus only a very simplified view of what might occur under climatic changes. However, a qualitative approach allows to predict the increase or the decrease of the fish productivity and can give some preliminary answers.

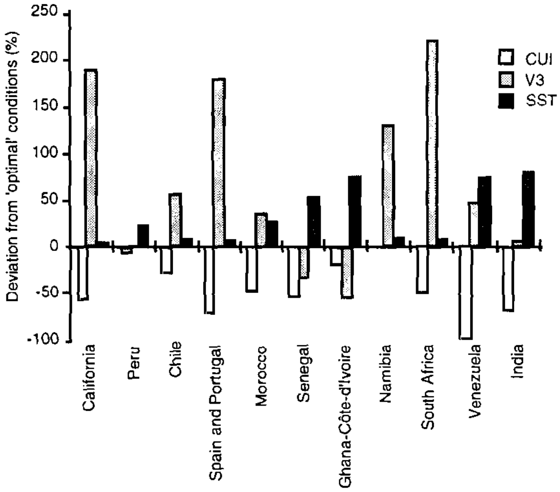

Fig. 9: Relative deviation of the environmental values (%) from the 'optimal environmental values' as defined in the comparative analysis.

Tab. 4: The limiting factor(s) to productivity in upwelling areas. The signs (+ and -) indicate negative or positive deviation from the 'optimal environmental values'. The limiting factors are noted in decreasing order of deviation.

Upwelling areas		Limiting factors		
1	California	V3 +	CUI -	SST -
2	Peru	SST +	-	-
3	Chile	V3 +	CUI -	-
4	Spain-Portugal	V3 +	CUI -	
5	Morocco	CUI -	V3 +	SST +
6	Senegal	CUI -	SST +	V3 -
7	Côte d'Ivoire - Ghana	SST +	V3 -	CUI -
8	Namibia	V3 +	CUI +	-
9	South Africa	V3 +	CUI -	SST +
10	Venezuela	CUI -	SST +	V3 +
11	India	SST +	CUI -	V3 +

3. OPTIMAL ENVIRONMENTAL CONDITIONS IN THE PERUVIAN ECOSYSTEM: REALITY OR TAUTOLOGY?

It is possible to compare environmental variables in a given upwelling area to what appears to be the optimal environmental conditions. These, however, were largely derived from the Peruvian ecosystem's values. Peters (1991) defines a tautology as "purely logical constructs that describe the implication of given premises and never reveal more than those premises contain". As Peru is known to be the most productive upwelling area, it is clear that using our approach it will define the optimal environmental combination of factors. Thus, our results may be regarded as a tautology of poor scientific value. However, our comparative analysis did provide a framework for considering the relative impact of several environmental factors on fish productivity. It emphasized the importance of limiting factors such as turbulence, upwelling intensity or size of the ecosystem. This should promote new insights of how to relate environmental variables to fish productivity in a multivariate context. Paleoecological studies reveal that pelagic fish populations experienced large natural fluctuations which were clearly unrelated to fishing pressure and that past abundances in California or in Peru were sometimes much higher than during the last century (Soutar and Isaacs, 1974; De Vries and Pearcy, 1982; Baumgartner *et al.*, 1992). For California, we identified factors that limit fish productivity but whithout any reference point; this was not possible for Peru. This stresses the limit of our approach as it may be that the Peruvian ecosystem is able to produce even more under other, but still undefined, environmental conditions.

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REFERENCES CITED

Bakun A. 1985. Comparative studies and the recruitment problem: searching for generalizations. *CalCOFI Rep.*, 26: 30-40.

Bakun A. 1994. *Climate change and marine populations: interactions of physical and biological dynamics.* Paper presented at Greenpeace/University of Rhode Island Workshop on the Scope, Significance, and Policy Implications of Global Change and the Marine Environment, 16 p.

Bakun A. et R.H. Parrish. 1982. Turbulence, transport, and pelagic fish in the California and Peru Current systems. *CalCOFI Rep.*, 23: 99-112.

Baumgartner T.R., A. Soutar et V. Ferreira-Bartrina. 1992. Reconstitution of the history of Pacific sardine and northern anchovy populations over the past two millennia from sediments of the Santa Barbara basin, California. *CalCOFI Rep.*, 33: 24-40.

Crawford R.J.M., L.V. Shannon and D.E. Pollock. 1987. The Benguela ecosystem. Part IV. The major fish and invertebrate resources. *Oceanogr. Mar. Biol. Ann. Rev.*, 25: 353-505.

Cury P., C. Roy, R. Mendelssohn, A. Bakun, D.M. Husby and R.H. Parrish. 1995. Moderate is better: exploring nonlinear climatic effect on Californian anchovy (*Engraulis mordax*). Climate change and fish population. R.J. Beamish (ed.). *Can. Spec. Publ. Fish. Aquat. Sci.*, 121: 417-424.

Cury P. and C. Roy, 1989. Optimal environmental window and pelagic fish recruitment success in upwelling areas. *Can. J. Fish. Aquat. Sci.*, 46 (4): 670-680.

Cushing D.H. 1995. *Population production and regulation in the sea. A fisheries perspective.* Cambridge University Press, 354 p.

Cushing D.H. 1990. Plankton production and year-class strength in fish populations: an update of the match/mismatch hypothesis. *Advances in Marine Biology*, Academic Press, 26: 249-293.

De Vries T. J. and W.G. Pearcy. 1982. Fish debris in sediments of the upwelling zone off central Peru: a late Quaternary record. *Deep. Sea. Res.*, 29: 87-109.

FAO. 1995. *Production halieutique mondiale. 1950-1993.* Supplément au volume 76 de l'annuaire statistique des pêches 1993. Captures et quantités débarquées de la FAO. Rome.

Guzman R., P. Fréon and J. Mendoza. In press. La pesquerià de sardina *Sardinella aurita* en el oriente de Venezuela, su evolucion en el période 1973-1989. *Bol. Inst. Oceanogr. Univ. Oriente.*

Glantz M.H. 1992. Introduction. *In*: M.H. Glantz (ed.). *Climate variability, climate change and fisheries.* Cambridge University Press: 1-14.

Harvey P. H. and M. D. Pagel. 1991. The comparative method in evolutionary biology. *In*: R.M. May and P.H. Harvey (eds.). *Oxford series in ecology and evolution.* Oxford University Press. 239 p.

Hastie T.J et R.J. Tibshirani. 1990. *Generalized additive models.* Chapman et Hall, London, 335 p.

Kawasaki T. 1992. Climate-dependent fluctuations in the far eastern sardine population and their impacts in the fisheries and society. *In*: M.H. Glantz (ed.). *Climate variability, climate change and fisheries.* Cambridge University Press: 325-354.

Lasker R. 1975. Field criteria for survival of anchovy larvae: the relationship between inshore chlorophyll maximum layers and successful first feeding. *U.S. Fish. Bull.*, 73: 453-462.

Lluch-Belda D., R.J.M. Crawford, T. Kawasaki, A.D. MacCall, R.H. Parrish, R.H. Schwartzlose and P.E. Smith. 1989. World-wide fluctuations of sardine and anchovy stocks: the regime problem. *S. Afr. J. Mar. Sci.*, 8: 195-205.

Lluch-Belda D., D.B. Lluch-Cota, S. Hernadez-Vasquez and C.A. Salinas-Zavala. 1991. Sardine and anchovy spawning as related to temperature and upwelling in the California Current system. *CalCOFI Rep.*, 32: 105-111.

Longhurst A.R. and W.S. Wooster. 1990. Abundance of oil sardine (*Sardinella longiceps*) and upwelling on the southwest coast of India. *Can. J. Fish. Aquat. Sci.*, 47 (2): 2407-2419.

MacKenzie B.R. and W.C. Leggett. 1991. Quantifying the contribution of small scale turbulence to the encounter rates between larval fish and their zooplankton prey: effects of wind and tide. *Mar. Ecol. Prog. Ser.*, 73: 149-160.

Maynard Smith J. and R. Holliday. 1979. Preface. *In*: J. Maynard and R. Holliday (eds.). *The evolution of adaptation by natural selection.* The Royal Society, London: 5-7.

Parrish R.H. et A.D. MacCall. 1978. Climatic variation and exploitation in the Pacific mackerel fishery. *Calif. Dept. Fish. Game Fish. Bull.*, 167: 1-110.

Peterman M.R. and M.J. Bradford. 1987. Wind speed and mortality rate of a marine fish, the northern anchovy (*Engraulis mordax*). *Science* (Wash., DC), 235: 354-356.

Peters R.H. 1991. Tautology. *In*: R.H. Peters (ed.). *A critique for ecology.* Cambridge University Press. 38-73.

Rothschild B.J. and T.R. Osborn. 1988. The effects of turbulence on planktonic contact rates. *J. Plankton Res.*, 10 (3): 465-474.

Sharp G.D. and J. Csirke. 1983. Proceedings of the Expert Consultation to Examine Changes in Abundance and Species Composition of Neretic Fish Resources. *FAO Fish. Rep.*, 291(3).

Soutar A. and J.D. Isaacs. 1974. Abundance of pelagic fish during the 19th and 20th centuries as recorded in anaerobic sediment of the Californias. *Fish. Bull.*, 72: 257-274.

Wroblewski J.S. and J.G. Richman. 1987. The non-linear response of plankton to wind mixing events. Implications for survival of larval northern anchovy. *J. Plankton Res.*, 9 (1): 103-123.

Clupeoids Reproductive Strategies in Upwelling Areas: a Tentative Generalization

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ABSTRACT

Using a comparative approach, the reproductive strategies of sardines, anchovies and sardinellas in twelve upwelling areas over the Atlantic, Indian and Pacific Oceans are investigated in relation with major environmental processes affecting recruitment success. The main reproductive habits are identified, in each area and for each species, based on an extensive survey of the literature. From this, the main spawning grounds and the months corresponding to the peaks of the spawning season are identified. The monthly mean values of upwelling intensity and of wind speed are calculated in each spawning grounds using data from the Comprehensive Ocean Atmosphere Dataset (COADS). A comparison, between areas, of the value of these environmental parameters during the peaks of the spawning season is performed. Off Peru, spawning occurs when the intensity of upwelling is maximum (1.8 $m^3/s/m$). Off Morocco, reproduction is out of phase with the upwelling process (upwelling intensity is in the range of 0.2-0.3 $m^3/s/m$). Off Namibia, Chile and California, spawning occurs at intermediate values. It appears that the timing of the reproduction of sardines, sardinella or anchovies occurs over a wide range of upwelling intensity. There is no apparent link between the timing or the intensity of upwelling and the occurrence of the seasonal spawning peaks. A similar analysis is performed using the monthly values of wind speed during the seasonal spawning peaks. It turns out that for sardine and sardinella, reproduction occurs when the monthly values of wind speed are within a narrow window, bounded by 5.3 and 6.1 m/s for ten of the twelve upwelling ecosystems. The two outliers are the sardine populations from the southern Benguela and the Iberian Peninsula. For anchovy, there is apparently little correspondence between the timing of reproduction and wind speed values. These results are discussed in the light of the 'optimal environmental window' concept of P. Cury and C. Roy, and a generalization of the spawning strategies of small pelagic fishes in upwelling areas is presented.

RÉSUMÉ

A travers une approche comparative incluant douze régions d'upwelling des océans Atlantique, Indien et Pacifique, les stratégies de reproduction des sardines, anchois et sardinelles sont étudiées en relation avec les processus environnementaux majeurs affectant le succès du recrutement. Dans chaque région et pour chaque espèce considérée, une revue exhaustive de la littérature permet d'identifier les principales caractéristiques de la dynamique de reproduction. Les principales zones de ponte et les mois correspondant aux pics de la saison de reproduction sont ainsi identifiés. Les moyennes mensuelles de l'intensité de l'upwelling et de la vitesse du vent sont calculées dans chaque zone de ponte à partir de la base de données COADS (Comprehensive Ocean Atmosphere Dataset). Une comparaison des valeurs de ces paramètres environnementaux durant les pics de la saison de reproduction est effectuée entre les différentes zones d'upwelling étudiées. Au large du Pérou, la reproduction a lieu lorsque l'intensité de l'upwelling est maximale (1,8 $m^3/s/m$). Au large du Maroc, la reproduction est décalée par rapport au processus d'upwelling (l'intensité de l'upwelling se situe dans l'intervalle 0,2-0,3 $m^3/s/m$). Le long des côtes de la Namibie, du Chili et de la Californie, la ponte a lieu à des valeurs intermédiaires d'upwelling. Il apparaît que le calendrier de la reproduction des sardines, anchois et sardinelles, s'étale sur une large gamme d'intensité d'upwelling. Il n'y a pas de lien apparent entre l'occurrence du processus d'upwelling et celle des pics saisonniers de reproduction. Une analyse similaire est effectuée en utilisant les valeurs moyennes de la vitesse du vent durant les pics saisonniers de reproduction. Il en résulte que pour les sardines et sardinelles, la reproduction a lieu lorsque les moyennes mensuelles de la vitesse du vent sont comprises dans une étroite fourchette de valeurs de 5,3 à 6,1 $m^3/s/m$ pour dix des douze écosystèmes d'upwelling étudiés. Les deux exceptions sont les populations de sardine du sud du Benguela et de la péninsule ibérienne.

Pour l'anchois, il y a apparemment peu de correspondance entre le calendrier de la reproduction et les valeurs de la vitesse du vent. Les résultats sont discutés à la lumière du concept de la « Fenêtre Environnementale Optimale » de P. Cury et C. Roy, et une généralisation des stratégies de reproduction des petits poissons pélagiques dans les zones d'upwelling est présentée.

INTRODUCTION

Located in the tropical or subtropical zones, coastal upwelling ecosystems represent less than 0,1% of the entire oceanic surface but are part of the most productive oceanic regions and are able to produce between 20 and 30% of the worldwide annual fish catches (Cushing, 1969; Ryther, 1969; Pauly and Tsukayama, 1987). Coastal upwelling ecosystems are mainly colonized by small pelagic fishes such as anchovies, sardines or sardinellas. These fish populations are characterized by important annual fluctuations of their abundance. For instance, after a peak of production in 1970, the Peruvian anchoveta stock collapsed in 1972-1973 (Valvidia, 1978; Pauly and Tsukayama, 1987); similarly, Pacific sardine suddenly disappeared from the fishery in the 1950s (Lasker and MacCall, 1983). Although these populations are usually submitted to strong fishing pressure, these variations of abundance appear mainly due to recruitment failure related to changes in the marine environment (Kawasaki, 1983; Shepherd *et al.*, 1984). Upwelling ecosystems are characterized by a very high rate of primary production. An upwelling ecosystem is also a dispersive environment where particles tend to be swept away from the coastal environment by the wind-induced offshore drift. Persistent equatorward winds also induce a strong and continuous mixing of the surface water column. These are some of the major characteristic of coastal upwelling ecosystems; they can have strong ecological implications.

In a recent synthesis of the major environmental processes affecting fish reproduction, Bakun (1996) identified three major classes of processes that combine to yield favorable reproductive fish habitat. They are: 1) enrichment processes (upwelling or mixing); 2) concentration processes (convergence, fronts, stratification) and 3) retention processes that maintain eggs and larvae in the suitable habitat. Despite the high rate of production, the triad indicates that the offshore flow and the intense wind mixing that characterize upwelling ecosystems can create adverse conditions for larval survival and subsequent recruitment success. The migrations that some of the major small pelagic fish population undertake in order to find suitable reproductive habitat confirm that an upwelling ecosystem can be an adverse habitat for fish to reproduce (Hutchings, 1992; Bakun, 1996). However, small pelagic fish populations are quite successful: they are well known for being able to develop very important biomass in eastern boundary ecosystems. Comparative studies, in several upwelling ecosystems, of the reproductive strategy of fishes helped identify common key environmental processes for small pelagic fish reproductive strategy: sardine, sardinella and anchovy tend to avoid spawning in areas dominated by strong offshore transport and strong wind mixing (Parrish *et al.*, 1983; Roy *et al.*, 1989). Reproductive strategies of small pelagics appear to be tuned to minimize the detrimental effects of the environment on larval survival (Bakun, 1996).

The Optimal Environmental Window concept (OEW; Cury and Roy, 1989) provides a simple model for relating the upwelling process to larval survival and recruitment success. Roy *et al.* (1992) used the OEW to account for the difference between reproductive strategies of small pelagic fishes observed in several areas within the Canary Current upwelling ecosystem. These authors showed that off West Africa, there is no apparent relationship between the upwelling process and reproduction, but rather a striking correspondence between the timing of reproduction and the occurrence of wind speed of about 5-6 m/s. This range of wind speed corresponds to the optimal wind conditions defined by the OEW. We present here an attempt to generalize the results of Roy *et al.* (1992) to other upwelling areas such as the Benguela Current system, the California Current system, the Humboldt Current system and the Malabar coastal upwelling ecosystem off India. These upwelling areas constitute a unique opportunity to develop a comparative approach. They share fundamental characteristics: wind is the driving force of the upwelling process in these areas; they are colonized by closely related species, such as anchovies, sardines and sardinellas (Table 1), which are all small-sized, and have fast growth, a short life span, an early maturation and very high fecundity.

System	Dominant clupeoids
Canary Current	*Sardina pilchardus* *Sardinella aurita* *Sardinella maderensis* *Engraulis encrasicolus*
Benguela Current	*Sardinops ocellatus* *Engraulis capensis*
California Current	*Sardinops caeruleus* *Engraulis mordax*
Humboldt Current	*Sardinops sagax* *Engraulis ringens*
India, Malabar Coast	*Sardinella longiceps* *Sardinella fimbriata*

Table 1: Species of coastal pelagic fishes studied in each upwelling area.

1. BIOLOGICAL AND ENVIRONMENTAL DATA

A review of the literature provides information on the reproductive seasons and locations for each spawning area and each species. Table 2 summarizes the information gained through this review. The identification of the spawning seasons results from a compromise between the information collected. It can be considered as being, in average, valid for the period covering the 1950s to the 1990s. In some cases, data do not extend on a sufficiently long time interval. Then, some particular years are chosen to compare biological information and environmental data (Table 3).

Environmental data are derived from the Comprehensive Ocean Atmosphere Dataset (COADS; Woodruff *et al.*, 1987) using the software and CD-Rom produced for CEOS (Mendelssohn and Roy, 1996; Roy and Mendelssohn, this vol.).

ECOSYSTEMS **Spawning grounds**	**Spawning seasons**												**References**
SARDINES													
CALIFORNIA CURRENT ***Sardinops caeruleus***													
Southern California Bight (30-34°N)			M	A̲	M̲	J̲							Ahlstrom (1960), Rosa and Laevastu (1960), Ahlstrom (1967), Parrish *et al.* (1981, 1983).
Baja California (26-30°N)								A̲	S̲				Ahlstrom (1967).
CANARY CURRENT ***Sardina pilchardus***													
Spain, Bay of Biscay			M̲	A	M̲								Wyatt and Pérez-Gandaras (1989), Sola (1987), Lago de Lanzos *et al.* (1988), Sola *et al.* (1992).
Portugal (37-41°N)	J̲	F̲	M̲								N	D̲	Ré (1981), Ré *et al.* (1982), Figueiredo and Miguel Santos (1988), Cunha and Figueiredo (1988), Ré *et al.* (1990).
Morocco (28-30°N and 32-34°N)	J̲	F̲										D̲	Furnestin and Furnestin (1959), Parrish *et al.* (1983). Domanevsky and Barkova (1976), FAO (1985).
Western Sahara (22-26°N)			M	A	M					O̲	N̲	D̲	
HUMBOLDT CURRENT ***Sardinops sagax***													
Peru (6-14°S)	J	F					J̲	A̲	S̲	O			Sharp (1980), Parrish *et al.* (1983), Muck *et al.* (1987). Parrish *et al.* (1983).
Chile, Arica (18-24°S)							J̲	A̲	S̲	O			
BENGUELA CURRENT ***Sardinops ocellatus***													
Walvis Bay (20-24°S)	J̲	F̲	M̲						S	O	N		Matthews (1960), Parrish *et al.* (1983), Le Clus (1990), Hutchings (1992).
Western Agulhas Bank (34-36°S, 18-20°S)	J̲	F̲							S̲	O	N	D	De Jager (1960), Rosa and Laevastu (1960). Parrish *et al.* (1983).
SARDINELLAS													
CANARY CURRENT ***Sardinella aurita***													
Mauritania, Banc d'Arguin (18-22°N)							J̲	A̲	S̲				Conand (1977), Boëly *et al.* (1982), Fréon (1988).
Southern Senegal (12-15°N)					M̲	J̲				O	N		Conand (1977), Boëly *et al.* (1982), Fréon (1988).
INDIA ***Sardinella longiceps***													
Malabar Coast (8-16°N)						J	J̲	A̲	S				Nair (1959, 1960), Rosa and Laevastu (1960), Antony Raja (1964), Longhurst and Wooster (1990).
ANCHOVIES													
CALIFORNIA CURRENT ***Engraulis mordax***													
Southern California Bight (30-34°N)		F̲	M̲	A̲									Hunter (1977), Lasker and Smith (1977), Smith and Richardson (1977), Smith and Lasker (1978), Parrish *et al.* (1981, 1983, 1986).
Baja California (26-30°N)		F	M̲	A	M								Sharp (1980).
Southern Baja California (22-26°N)	J	F	M	A									Parrish *et al.* (1983).
CANARY CURRENT ***Engraulis encrasicolus***													
Morocco (28-30°N and 32-34°N)						J̲	J̲	A̲					Furnestin and Furnestin (1959).
HUMBOLDT CURRENT ***Engraulis ringens***													
Peru (6-14°S)		F	M					A̲	S̲	O̲			Valvidia (1978), Sharp (1980), Cushing (1982), Parrish *et al.* (1983), Alheit *et al.* (1984), Pauly and Soriano (1987), Muck (1989), Senocak *et al.* (1989).
Chile, Arica (18-24°S)							J	A̲	S	O			Parrish *et al.* (1983).
BENGUELA CURRENT ***Engraulis capensis***													
Walvis Bay (20-24°S)	J̲	F̲	M̲									D̲	Parrish *et al.* (1983), Le Clus (1990), Hutchings (1992).
Western Agulhas Bank (34-36°S, 18-20°E)	J̲	F							S	O̲	N̲	D̲	Shelton and Hutchings (1982), Parrish *et al.* (1983), Hutchings (1992), Waldron *et al.* (1992).

Table 2: Spawning seasons of sardines, sardinellas and anchovies in upwelling areas. The months corresponding to the peaks of reproduction are underlined.

SARDINES		ANCHOVIES	
Baja California	1952-1959	Southern Baja California	1970-1990
Spain	1980-1990	Walvis Bay	1970-1990
Portugal	1970-1990	Agulhas Bank	1970-1990
Chile, Arica	1970-1990	—	—

Table 3: Years considered in the study of biological and climatological data, by species.

Monthly time series of scalar wind speed and wind-stress, from 1950 to 1990, were constructed in each spawning areas (Table 2). A Coastal Upwelling Index (CUI) was calculated from the wind stress data following Bakun (1973). This index of the strength of the upwelling process is the offshore component of the wind induced Ekman transport. From the monthly time-series of scalar wind speed and CUI, a mean monthly cycle was calculated.

In most cases spawning grounds and nursery grounds have a similar location. This is not the case for the spawning areas located on the Agulhas Bank (Benguela) and in the Bay of Biscay (Spain). In these two areas, spawning occurs outside the upwelling area and eggs, once spawned, are removed from the spawning grounds and carried by coastal jets to the nursery grounds located in the upwelling (Shelton and Hutchings, 1982; Cabanas *et al.*, 1989). Consequently, for these two examples, environmental data corresponding to the nursery grounds are considered: the Galician Coast (Spain: 42-44°N) and the area surrounding St Helena Bay (Benguela: 30-34°S).

2. RESULTS

The duration of the upwelling season varies from one ecosystem to the other (Fig. 1): it is a year-round process off Peru and South Africa but limited to spring and summer off California and Morocco. There is no apparent relationship between the timing of reproduction and the upwelling process (Fig. 2): for instance, off Morocco, sardine reproduces outside the upwelling season; on the contrary, in the California Bight or off Peru, spawning occurs when the upwelling is active.

Following Bakun and Parrish (1982) and Parrish *et al.* (1983), we try to characterize the environmental conditions prevailing during the spawning season by using CUI and wind speed. These two environmental parameters are used as proxy-variables to estimate the strength of several environmental processes such as mixing by the wind, enrichment by the upwelling and offshore drift by the wind induced Ekman transport. These wind related processes are thought to be the key environmental processes to be considered when addressing the effect of the environment on fish population in upwelling areas (Lasker, 1975; Parrish *et al.*, 1981; Cury and Roy, 1989; Bakun, 1996). Since the observed spawning habits reflect the net adaptive response to a history of annual successes or failure in reproduction, one may expect that spawning habits would be seasonally and geographically tuned in order to provide a compromise between the environmental processes affecting recruitment success (Bakun *et al.*, 1991).

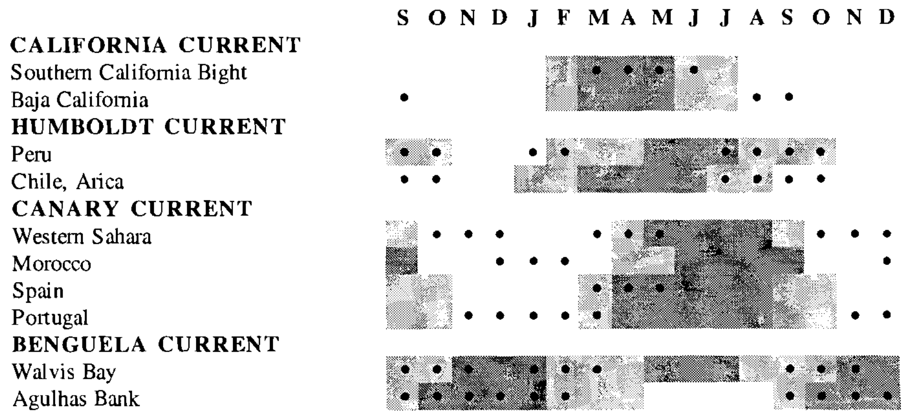

Fig. 1: Temporal relationships between sardines reproduction seasons and upwelling seasons. Spawning periods are represented by black points, upwelling seasons are in light grey, and upwelling peaks in dark grey (references for upwelling seasons : Cushing, 1971; Chesney and Alonso-Noval, 1989).

The mean monthly values of the two parameters during the sardine peak spawning season in each ecosystem are selected and plotted against each other (Fig. 2). Each ecosystem is characterized by different CUI values, either high or low. Two groups can be clearly distinguished. A first one corresponding to the sardine population off California, Morocco, Western Sahara, Peru, Chile and Namibia; for this group the wind speed values reported during the spawning seasons are clustered within a narrow band of wind speed, between 5 and 6 m/s. The second group corresponds to the Iberian Peninsula (Spain, Portugal) and the Agulhas Bank; in these ecosystems, the sardine populations do not follow the same pattern, wind values reported during the spawning season reach 7 to 9 m/s.

We follow the same procedure for the anchovy and sardinella populations. For anchovy, there is no clear pattern of correspondence between spawning and wind speed. Reproduction occurs within a wide wind range: data points are scattered between wind speed values of 5 and 8 m/s (Fig. 3). For the West African and Indian sardinella populations, spawning appears to be restricted to a range of wind speed between 5 and 6.8 m/s (Fig. 4). However, one should note that the number of data points for sardinella is rather limited.

3. DISCUSSION

Through the study of clupeoid reproductive strategies, two categories of ecosystems can be identified:

- Ecosystems of low latitudes: the main upwelling ecosystems of the world are part of this group: California, West Africa (Morocco, Sahara, Mauritania, Senegal), Peru, northern Chile, Namibia and India (Malabar Coast).
- Ecosystems of mid latitudes: the southern Benguela (South Africa) and the Iberian Peninsula (Spain and Portugal).

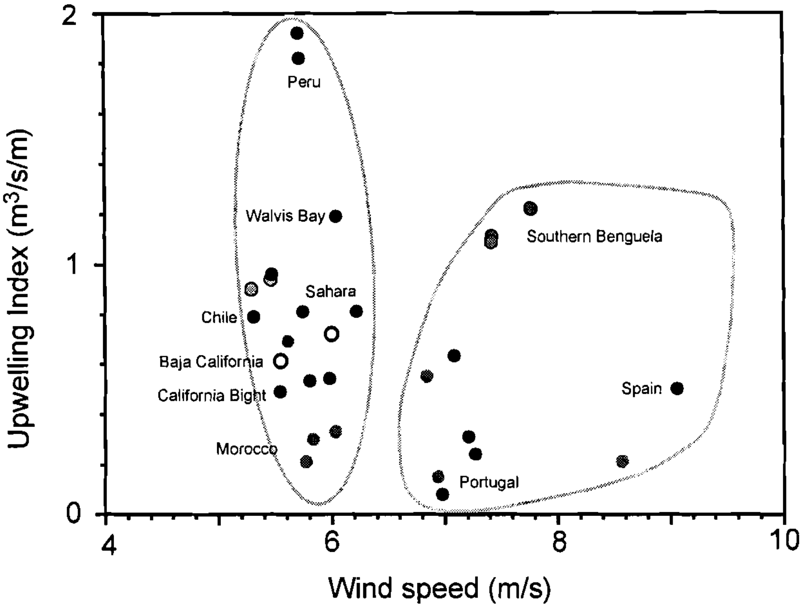

Fig. 2: Plots of spawning peaks of sardines against monthly means of wind speed and of coastal upwelling index (CUI), by ecosystem.

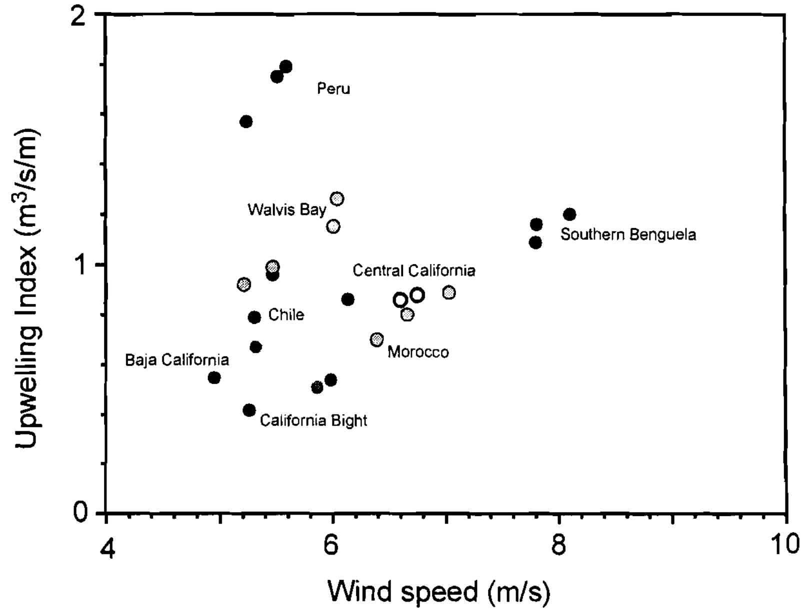

Fig. 3: Plots of spawning peaks of anchovies against monthly means of wind speed and of coastal upwelling index (CUI), by ecosystem.

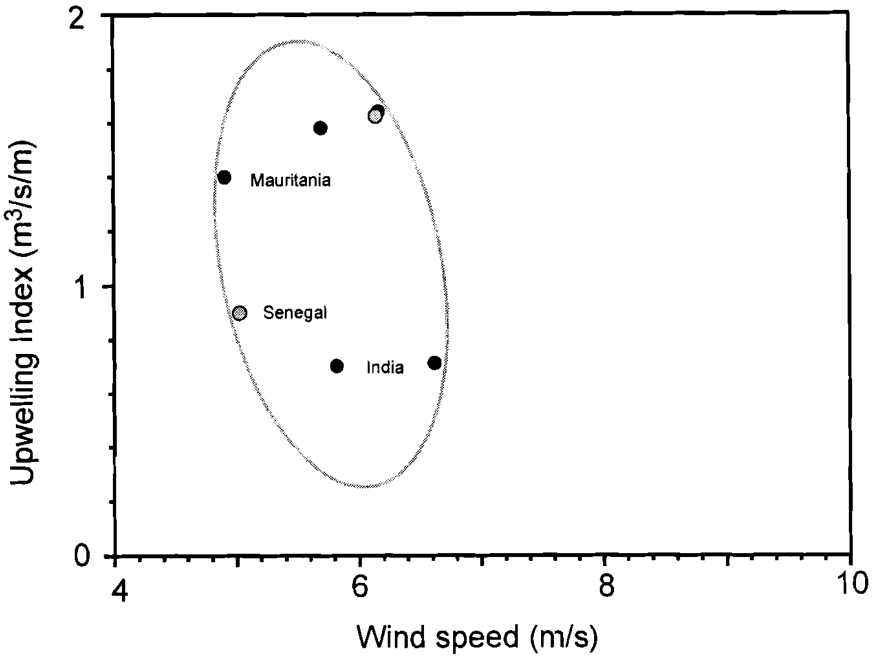

Fig. 4: Plot of spawning peaks of sardinella against monthly means of wind speed and of coastal upwelling index (CUI), by ecosystem.

3.1. Low latitude ecosystems

In these ecosystems, a generalization of Roy *et al.'s* (1992) results is possible for the sardines and sardinella population. The timing of reproduction for these two species coincides with the occurrence of 5-6 m/s winds. This range of wind speed values is in accordance with the 'Optimal Environmental Window' defined by Cury and Roy (1989). There is no apparent relationship between spawning and upwelling intensity. Spawning occurs sometimes during the upwelling season and sometimes outside the upwelling season.

The coincidence between spawning and the optimal wind range defined by the OEW suggests that reproductive strategies are strongly influenced by the seasonal fluctuations of the wind regime. Reproductive strategies appear to be seasonally tuned in order to coincide with the wind value that maximizes recruitment success. The wind value corresponding to the seasonal occurrence of the spawning peaks is constant over a wide range of latitude: from 5°N for Peru to 33°N for Morocco. This apparent constancy of the 'ideal' wind intensity around which the spawning activity of sardines and sardinella is maximum and is remarkable in view of the strong latitudinal dependence of some of the key environmental processes and scales that can be expected to be involved (Bakun *et al.*, 1991; Bakun, 1996). The magnitude of the enrichment by the upwelling and of the offshore drift by the wind-induced Ekman transport are both related to the intensity of the wind, but are also latitude-dependent processes. Wind generated turbulent mixing is estimated to be proportional to the third power of the wind speed, and is a process independent of latitude. The apparent constancy of the optimal wind intensity over several ecosystems located at different latitudes, can therefore be interpreted as an indication of the dominance of wind mixing in the seasonal adjustment of small pelagic fish reproductive strategy in upwelling areas. This may leave the choice of an adequate spawning location as an available means for dealing with limiting factors such as offshore transport and enrichment.

The duration and the intensity of the upwelling process appears to have a limited effect on the timing of the reproduction. However, offshore Ekman transport can be detrimental for larval survival and the fate of a fish population. Fish may have to select an adequate location for spawning in order to avoid the detrimental effect of wind-induced offshore drift. In these mid-latitude ecosystems, the spawning grounds are located in bays or in coastal indentations, downstream of intense upwelling centres (Parrish *et al.*, 1983; Roy *et al.*, 1989). Off Walvis Bay, the upwelled waters coming from the Lüderitz upwelling centre, are carried away by the main current, diffuse in the bay and supply the nursery with nutrients. The advection of cold waters in the bay induces at the same time the formation of convection cells, reducing larval offshore drift (Bakun, 1996). Furthermore, the larvae are sheltered from strong mixing by the wind. The width of the continental shelf is also an important characteristic. A wide continental shelf enables the formation of retention eddies (Brink, 1983; Nelson and Hutchings, 1987). As the retention process applies also to plankton, a wide continental shelf may allow a better coupling between primary and secondary productions. The inshore side of upwelling plumes also provide adequate locations for larvae retention (Graham and Largier, 1997; Roy, in press).

3.2. Mid-latitudes ecosystems

There are two ecosystems for which the seasonal spawning is not related to the occurrence of the optimal wind value defined by the OEW (Fig. 2). These ecosystems are the Iberian Peninsula and the southern Benguela. In these ecosystems, reproduction occurs during time period characterized by an intense wind regime. One also notes that the spawning grounds and nursery grounds are spatially distinct. In these two areas, the configuration of the coastline is quite similar with a North-South coast where the upwelling develops and an East-West coast located poleward and up-wind of the upwelling area. This configuration of the coast provides a unique opportunity for the fish populations to avoid the reproductive difficulties inherent in an exposed upwelling coast (Bakun, 1996). In both cases, the spawning grounds are located outside the upwelling coast and rather concentrate poleward along the East-West oriented coast (the Agulhas Bank off South Africa and the Bay of Biscay off Spain).

Eggs laid in the Bay of Biscay are carried by a coastal jet towards the Galician Coast, in the North-West of Spain (Cabanas *et al.*, 1989). Unlike most cases, eggs are thus laid upward the upwelling centres as regards to the main surface circulation. As spawning occurs outside the upwelling zone (Garcia *et al.*, 1991), early larval stages are not subjected to the detrimental effects of dispersion linked to Ekman transport. Furthermore, they probably take advantage of the spring bloom. This seasonal primary production peak indeed favors larval survival. After being transported along the Galician Coast, they can take advantage of the upper layers enrichment by the upwelling process. Moreover, at this stage of development, larvae are more mobile; therefore, their survival is supposed to depend less on concentration (pursuit and attack behavior) and retention processes (horizontal and vertical displacement).

The reproductive strategies of sardine and anchovy in the southern Benguela follow a similar pattern. Sardine and anchovy eggs are laid on the Agulhas Bank, upward the upwelling centre, and are then carried by a coastal jet toward the west coast upwelling area, North of Cape Columbine (Largier *et al.*, 1992). Shelton and Hutchings (1982) have estimated that the time for the eggs to be transported to west coast upwelling is in order of days. Along the west coast, St Helena Bay is thought to be an important nursery ground. It is a place where biological production can benefit from the input of nutrient by the upwelling. The upwelling plume that develops down-wind Cape Colombine creates a physical barrier allowing retention to occur within St Helena Bay (Graham and Largier, 1997). This area constitutes a place a priori favorable for a nursery ground.

In these two ecosystems, the question of the evolutionary advantage of developing such a strategy, i.e. to spawn outside the upwelling area during time period characterized by intense wind induced mixing remains an open question. In both places, the spawning grounds seem to be characterized by a strong vertical stratification which may counteract the detrimental effect of wind mixing. Over the Agulhas Bank, warm waters advected from the Indian Ocean by the Agulhas Current overlie cooler and dense water from the Atlantic (Shannon, 1985). This allows to form a protected stable layer where fish can successfully reproduce under energetic wind conditions (Parrish *et al.*, 1983). Egg development is also strongly affected by temperature. The cold temperature encountered along the west coast upwelling may also be an important element in favor of spawning in the warm waters off the Agulhas Bank. In the Bay of Biscay, spawning occurred in spring and is in phase with the annual planktonic bloom, this might be an important element favoring larvae survival within the Bay.

CONCLUSION

The timing of sardine and sardinella spawning in low latitude upwelling ecosystems appears to be linked with the occurrence of wind speed within a range of 5 to 6 m/s. There is no apparent relationship between spawning and upwelling intensity. Thus, it was possible to extend Roy *et al.'s* (1992) results to the major low latitude upwelling ecosystems of the world. This optimal wind range is in accordance with the OEW (Cury and Roy, 1989) which defines 5-6 m/s wind as being the optimal condition for small pelagic fish recruitment success in upwelling areas. The constancy over a wide range of latitude of the optimal wind range is an indication of the dominance of wind mixing in the adjustment of small pelagic fish reproductive strategy to seasonal upwellings. This may leave the choice of an adequate spawning location as an available means for dealing with limiting factors such as offshore transport and enrichment.

There are two outliers for which the spawning is not related to the occurrence of the optimal wind value. These ecosystems are the Iberian Peninsula and the southern Benguela. In these areas, spawning grounds and nursery grounds are also spatially distinct. They both share similar topographical characteristics with a North-South oriented coast where the upwelling develops (the nursery grounds) and an East-West oriented coast located poleward and up-wind of the upwelling area (the spawning grounds). This configuration of the coast provides a unique opportunity for fish population to avoid the reproductive difficulties inherent in an exposed upwelling coast.

Anchovy reproductive strategy appears to be quite distinct from sardine and sardinella strategies. There is no apparent relationship between the upwelling indices or the wind intensity and the timing of anchovy spawning. This remains an open question.

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REFERENCES CITED

Ahlstrom E.H. 1960. Synopsis on the biology of the Pacific sardine (*Sardinops caerulea*). *In*: *Proceedings of the World Scientific Meeting on the Biology of Sardines and Related Species, Rome. FAO, II, Species Synopses*: 415-451.

Ahlstrom E.H. 1967. Co-occurences of sardine and anchovy larvae in the California Current region off California and Baja California. *CalCOFI Rep.*, XI: 117-135.

Alheit J., V.H. Alarcon and B.J. Macewicz. 1984. Spawning frequency and sex ratio in the Peruvian anchovy, *Engraulis ringens*. *CalCOFI Rep.*, XXV: 43-52.

Antony Raja B.T. 1964. Some aspects of spawning biology of indian oil sardine *Sardinella longiceps* Val. *Indian J. Fish.*, 11(1): 45-120.

Bakun A. 1973. Daily and weekly upwelling indices, west coast of North America 1946-71. *U.S. Dep. Comm., NOAA Tech. Rep. NMFS SSRF*, 671, 103p.

Bakun A. 1996. *Patterns in the ocean: ocean processes and marine population dynamics.* University of California Sea Grant, San Diego, California, USA, in cooperation with Centro de Investigaciones Biologicas de Noroeste, La Paz, Baja California Sur, Mexico, 323 p.

Bakun A. and R.H. Parrish 1982. Turbulence, transport, and pelagic fish in the California and Peru Current systems. *CalCOFI Rep.*, 23: 99-112.

Bakun A., C. Roy and P. Cury. 1991. *The comparative approach: latitude-dependence and effects of wind forcing on reproductive success.* ICES CM 1991/H45, 12 p.

Boëly T., J. Chabanne, P. Fréon and B. Stéquert. 1982. Cycle sexuel et migrations de *Sardinella aurita* sur le plateau continental ouest-africain, des Iles Bissagos à la Mauritanie. *Rapp. P.-v. Réun. Cons. int. Explor. Mer*, 180: 350-355.

Brink K.H. 1983. The near-surface dynamics of coastal upwelling. *Prog. Oceanogr.*, 12: 223-257.

Cabanas J.M., C. Porteiro and M. Valera. 1989. *A possible relation between sardine fisheries and oceanographic conditions in NW Spanish coastal waters.* ICES CM 1989/H 18, 12 p.

Chesney E.J. and M. Alonso-Noval. 1989. Coastal upwelling and the early life history of sardines (*Sardina pilchardus*) along the Galician coast of Spain. *Rapp. P.-v. Réun. Cons. int. Explor. Mer*, 191: 63-69.

Conand F. 1977. Oeufs et larves de la sardinelle ronde (*Sardinella aurita*) au Sénégal: distribution, croissance, mortalité, variations d'abondance de 1971 à 1976. *Cah. ORSTOM, sér. Océanogr.*, 15(3): 201-214.

Cunha M.E. and I. Figueiredo 1988. *Reproductive cycle of Sardina pilchardus in the central region off the Portuguese coast (1971/1987).* ICES CM 1988/H61, 9 p.

Cury P. and C. Roy. 1989. Optimal environmental window and pelagic fish recruitment success in upwelling areas. *Can. J. Fish. aquat. Sci.*, 46(4): 670-680.

Cushing D.H. 1969. Upwelling and fish production. *FAO Fish. Tech. Pap.*, 84, 40 p.

Cushing D.H. 1971. The regularity of the spawning season of some fishes. *J. Cons.*, Cons. int. Explor. Mer, 33(1): 81-92.

Cushing D.H. 1982. *Climate and fisheries.* London. Academic Press. 373 p.

De Jager B.D. 1960. Synopsis on the biology of the South African pilchard *Sardinops ocellata* (Pappé). *In*: *Proceedings of the World Scientific Meeting on the Biology of Sardines and Related Species, Rome. FAO, II, Species Synopses*: 97-114.

Domanevsky L.N. and N.A. Barkova. 1976. *Some peculiarities of sardine (Sardina pilchardus Walb.) distribution and spawning along the northwest Africa.* ICES. CM 1976/56, 6, 15p.

FAO. 1985. Rapport de la troisième réunion du groupe de travail ad hoc sur la sardine *Sardina pilchardus* (Walb.). *COPACE/PACE Series*, 85/39, 157 p.

Figueiredo I.M. and A. Miguel Santos. 1988. *On sexual maturation, condition factor and gonadosomatic index of Sardina pilchardus Walb., off Portugal (1986/1987).* ICES CM 1988/H70, 4p.

Fréon P. 1988. *Réponses et adaptations des stocks de clupéidés d'Afrique de l'Ouest à la variabilité du milieu et de l'exploitation. Analyse et réflexion à partir de l'exemple du Sénégal.* Etudes et Thèses ORSTOM. 287 p.

Furnestin J. and M.L. Furnestin. 1959. La reproduction de la sardine et de l'anchois des côtes atlantiques du Maroc. *Rev. Trav. Inst. Pêches marit.*, 23(1): 79-104.

Garcia A., C. Franco, A. Sola and A. Lago de Lanzos. 1991. *Sardine (Sardina pilchardus Walb.) daily egg production off the Galician, Cantabrian and Bay of Biscay waters in April-May 1990.* ICES C.M. 1991/H37.

Graham W.M. and J. L. Largier. 1997. Upwelling shadows as nearshore retention sites: the example of northern Monterey Bay. *Continental Shelf Research*, 17 (5): 509-532.

Hunter J.R. 1977. Behavior and survival of northern anchovy *Engraulis mordax* larvae. *CalCOFI Rep.*, XIX: 138-146.

Hutchings L. 1992. Fish harvesting in a variable, productive environment. Searching for rules or searching for exceptions ? *In*: A.I.L. Payne, K.H. Brink, K.H. Mann, and R. Hilborn (eds). Benguela trophic functioning. *S. Afr. J. mar. Sci.*, 12: 297-318.

Kawasaki T. 1983. Why do some pelagic fishes have wide fluctuations in their numbers? Biological basis of fluctuation from the viewpoint of evolutionary ecology. *In*: G.D. Sharp and J. Csirke (eds.). Proceedings of the Expert Consultation to Examine Changes in Abundance and Species Composition of Neritic Fish Resources, San José, Costa Rica, 18-29 April 1983. *FAO Fish. Rep.*, 291(3): 1065-1080.

Lago de Lanzos A., C. Franco and A. Sola. 1988. *Comparative study of the annual variation in the spawning intensity or sardine Sardina pilchardus (Walb. 1792) of the Cantabric and NW Spain.* ICES CM 1988/H73, 5 p.

Largier J.L., P. Chapman, W.T. Peterson and V.P. Swart. 1992. The western Agulhas Bank: circulation, stratification and ecology. *In*: A.I.L. Payne, K.H. Brink, K.H. Mann and R. Hilborn (eds.). Benguela trophic functioning. *S. Afr. J. mar. Sci.*, 12: 319-339.

Lasker R. 1975. Field criteria for survival of anchovy larvae : the relation between inshore chlorophyll maximum layers and successful first feeding. *Fish. Bull.*, 73(3): 453-462.

Lasker R. and P.E. Smith. 1977. Estimation of the effects of environmental variations on the eggs and larvae of the northern anchovy. *CalCOFI Rep.*, XIX: 128-137.

Lasker R. and A. MacCall. 1983. New ideas on the fluctuations of the clupeoid stocks off California. *In*: *Proceedings of the Joint Oceanographic Assembly 1982*, General Symposia, Can. National Committee, Sc. Committee on Oceanic Research, Ottawa: 110-120.

Le Clus F. 1990. Impact and implications of large-scale environmental anomalies on the spatial distribution of spawning of the Namibian pilchard and anchovy populations. *S. Afr. J. mar. Sci.*, 9: 141-159.

Longhurst A.R. and W.S. Wooster. 1990. Abundance of oil sardine (*Sardinella longiceps*) and upwelling on the Southwest coast of India. *Can. J. Fish. aquat. sci.*, 47: 2407-2419.

Matthews J.P. 1960. Synopsis on the biology of the south west African pilchard (*Sardinops ocellata* Pappé). *In*: *Proceedings of the World Scientific Meeting on the Biology of Sardines and Related Species. Rome FAO, II, Species Synopses*: 115-135.

Mendelssohn R. and C. Roy. 1996. Comprehensive Ocean Data Extraction Users Guide. *U.S. Dep. Comm., NOAA Tech. Memo. NOAA-Tech. Rep. NMFS SWFSC*, La Jolla, CA., 228, 67p.

Muck P. 1989. Relationships between anchoveta spawning strategies and the spatial variability of sea surface temperature off Peru. *In*: D. Pauly, P. Muck, J. Mendo and I. Tsukayama (eds.). The Peruvian upwelling ecosystem: dynamics and interactions. *ICLARM Conf. Proc.*, 18: 168-173.

Muck P., O. Sandoval de Castillo and S. Carrasco. 1987. Abundance of sardine, mackerel and horse mackerel eggs and larvae and their relationship to temperature, turbulence and anchoveta biomass off Peru. *In*: D. Pauly and I. Tsukayama (eds.).The Peruvian anchoveta and its upwelling ecosystem : three decades of change. *ICLARM Stud. Rev.*, 15: 268-275.

Nair R.V. 1959. Notes on the spawning habits and early life-history of the oil sardine *Sardinella longiceps* Cuv. et Val. *Indian J. Fish.*, 6(2): 342-359.

Nair R.V. 1960. Synopsis on the biology and fishery of the Indian sardines. *In*: *Proceedings of the World Scientific Meeting on the Biology of Sardines and Related Species. Rome. FAO Vol. II, Species Synopses*: 329-414.

Nelson G. and L. Hutchings. 1987. Passive transportation of pelagic system components in the southern Benguela area. *In*: A.I.L. Payne, J.A. Gulland and K.H. Brink (eds.). The Benguela and comparative ecosystems. *S. Afr. J. mar. Sci.*, 5: 223-234.

Parrish R.H., C.S. Nelson and A. Bakun. 1981. Transport mechanisms and reproductive success of fishes in the California Current. *Biological Oceanography*, 1(2): 175-203.

Parrish R.H., A. Bakun, D.M. Husby and C.S. Nelson. 1983. Comparative climatology of selected environmental processes in relation to eastern boundary current pelagic fish reproduction. *In*: G.D. Sharp and J. Csirke (eds.). Proceedings of the Expert Consultation to Examine Changes in Abundance and Species Composition of Neritic Fish Resources,San José, Costa Rica, April 1983. *FAO Fish. Rep.*, 291(3): 731-777.

Parrish R.H., D.L. Mallicoate and R.A. Klingbeil. 1986. Age dependent fecundity, number of spawning per year, sex ratio, and maturation stages in northern anchovy, *Engraulis mordax*. *Fish. Bull.*, 84(3): 503-517.

Pauly D. and M. Soriano. 1987. Monthly spawning stock and egg production of peruvian anchoveta (*Engraulis ringens*), 1953 to 1982. *In*: D. Pauly and I. Tsukayama (eds.). The Peruvian anchoveta and its upwelling ecosystem: three decades of change. *ICLARM Stud. Rev.*, 15: 167-178.

Pauly D. and I. Tsukayama (eds.). 1987. *The Peruvian anchoveta and its upwelling ecosystem : three decades of change*. ICLARM Stud. Rev.,15, 351p.

Ré P. 1981. Seasonal occurrence, mortality and dimensions of sardine eggs (*Sardina pilchardus* Walb.) off Portugal. *Cybium*, 5(4): 41-48.

Ré P., A. Farinha and I. Meneses. 1982. Ichthyoplankton from the coast of Peniche (Portugal) (1979/1980). *Arquivos do Museu Bocage*, série A, 1(16): 369-401.

Ré P., R. Cabral, E. Silva, E. Cunha, A. Farinha, I. Meneses and T. Moita. 1990. Sardine spawning off Portugal. *Bol. Inst. Nac. Invest. Pescas*, 15: 31-44.

Rosa H. and T. Laevastu. 1960. Comparison of biological and ecological characteristics of sardines and related species - A preliminary study. *In*: *Proceedings of the World Scientific Meeting on the Biology of Sardines and Related Species. Rome. FAO Vol. II, Species Synopses*: 523-552.

Roy C. In press. Upwelling-induced retention area: a mechanism to link upwelling and retention processes. *In*: S. C. Pillar, C. Moloney, A.I.L. Payne and F. A. Shillington (eds.). Benguela dynamics. *S. Afr. J. Mar. Sci.*, 19.

Roy C., P. Cury, A. Fontana and H. Belvèze. 1989. Stratégies spatio-temporelles de la reproduction des clupéidés des zones d'upwelling d'Afrique de l'Ouest. *Aquat. Living Resour.*, 2: 21-29.

Roy C., P. Cury and S. Kifani. 1992. Pelagic fish recruitment success and reproductive strategy in upwelling areas: environmental compromises. *In*: A.I.L. Payne, K.H. Brink, K.H. Mann and R. Hilborn (eds). Benguela Trophic Functioning. *S. Afr. J. mar. Sci.*, 12: 135-146.

Ryther J.H. 1969. Photosynthesis and fish production in the sea. *Science* ,166: 72-76.

Senocak T., D. Schnak and D. Pauly. 1989. Mean monthly distribution, abundance and production of anchoveta eggs off Peru (4-14°S), 1964-1971 and 1972-1986. *In*: D. Pauly, P. Muck., J. Mendo and I. Tsukayama (eds.).The Peruvian upwelling ecosystem: dynamics and interactions. *ICLARM Conf. Proc.*, 18: 143-154.

Shannon L.V. 1985. The Benguela ecosystem. Part 1, Evolution of the Benguela physical features and processes. *Oceanogr. Mar. Biol. Ann. Rev*, 23: 105-182.

Sharp G.D. 1980. Report of the workshop on effects of environmental variation on survival of larval pelagic fishes. *In*: Workshop on the Effects of Environmental Variation on the Survival of Larval Pelagic Fishes, Lima, 20 April-5 May 1980. *IOC Workshop Report*, 28: 15-66.

Shelton P.A. and L. Hutchings. 1982. Transport of anchovy, *Engraulis capensis* Gilchrist, eggs and early larvae by a frontal jet current. *J. Cons.*, Cons. int. Explor. Mer, 40: 185-198.

Shepherd J.G., J.G. Pope and R.D. Cousens. 1984. Variations in fish stocks and hypotheses concerning their links with climate. *Rapp. P.-v. Réun. Cons. int. Explor. Mer*, 185: 255-267.

Smith P.E. and S.L. Richardson (eds.). 1977. Standard techniques for pelagic egg and larva surveys. *FAO Fish. Tech. Pap.*, 175, 100p.

Smith P.E. and R. Lasker. 1978. Position of larval fish in an ecosystem. *Rapp. P.-v. Réun. int. Explor. Mer*, 173: 77-84.

Sola A. 1987. *Yearly variation of the ichthyoplankton of commercial interest species in the Santander coast (north of Spain)*. ICES CM 1987/L32, 6p.

Sola A., C. Franco, A. Lago de Lanzos and L. Motos. 1992. Temporal evolution of *Sardina pilchardus* (Walb.) spawning on the N-NW coast of the Iberian Peninsula. *Bol. Inst. Esp. Oceanogr.*, 8(1): 97-114.

Valvidia J.E. 1978. The anchoveta and El Niño. *Rapp. P.-v. Réun. int. Explor. Mer*, 173: 196-202.

Waldron M.E., M.J. Amstrong and B.A. Roel. 1992. Birthdate distribution of juvenile anchovy *Engraulis capensis* caught in the southern Benguela ecosystem. *In*: A.I.L. Payne, K.H. Brink, K.H. Mann and R. Hilborn (eds.). Benguela trophic functioning. *S. Afr. J. mar. Sci.*, 12: 865-871.

Woodruff S.D., R.J. Slutz, R.L. Jenne and P.M. Steurer. 1987. A Comprehensive Ocean-Atmosphere Data Set. *Bull. Amer. Meteor. Soc.*, 68: 1239-1250.

Wyatt T. and G. Pérez-Gandaras. 1989. Ekman transport and sardine yields in western Iberia. *In*: *Int. Symp. Long-term Changes Mar. Fish Pop.*, Vigo: 125-138.

Comparative Modelling of Trophic Flows in four Large Upwelling Ecosystems: Global versus Local Effects

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ABSTRACT

Trophic flow models of productive subsystems of the four large eastern boundary current ecosystems, i.e., the Humboldt Current off northern and central Peru (4-14°S), the northern Benguela Current off Namibia (15-35°S), the Canary Current (12-25°N) off Senegal and Mauritania, and the California Current (28-43°N) were constructed to represent different regimes in these systems during the mid-1960s to the early 1980s. The models were then analysed and compared by means of flow network analysis. The present contribution summarizes the results of a more detailed study with emphasis on the five dominant fish species: anchovy, sardine, horse-mackerel, mackerel and hake, and on the distinction between local and global effects. Whereas the general structure of the systems is very similar, characteristics pertaining to their size are system specific. The systems are all rather inefficient in terms of energy transfer up the food web. Total catch is correlated with primary production, as well as with the trophic level of the fishery. Productivities of small pelagics, as well as favorable conditions for them, appear of global nature, whereas properties pertaining to the medium-sized fish, as well as the inhibition of all dominant fish groups, appear more similar within the systems. Properties related to the fishing regime, e.g., fishing mortality, or the fraction of available primary production required to sustain fishery catches, are highly variable among systems and regimes. A closer focus on time-series of flows in the plankton compartments is required to obtain a more detailed understanding of regime-specific properties at the ecosystem level.

RÉSUMÉ

Des modèles de flux trophiques de sous-systèmes productifs des quatre grands écosystèmes du bord est des océans, c'est-à-dire le courant de Humboldt devant le nord et le centre du Pérou (4-14 °S), le courant nord du Benguela devant la Namibie (15-35 °S), le courant des Canaries (12-25 °N) devant le Sénégal et la Mauritanie, et le courant de Californie (28-43 °N), sont construits afin de représenter les différents régimes de ces systèmes du milieu des années 60 au début des années 80. Les modèles sont analysés et comparés au moyen de l'analyse des réseaux de flux. La présente contribution synthétise les résultats d'une étude plus détaillée focalisée sur les cinq espèces dominantes : l'anchois, la sardine, le chinchard, le maquereau et le merlu, et sur la distinction entre effets locaux et globaux. Tandis que la structure générale des systèmes est similaire, les caractéristiques propres à la taille des systèmes sont spécifiques. Les systèmes sont presque tous inefficaces en termes de transfert d'énergie au travers du réseau trophique. Les productivités en petits pélagiques, de même que les conditions favorables pour elles, apparaissent de nature globale, tandis que les propriétés relatives aux poissons de taille moyenne ainsi que les effets d'inhibition de tous les autres groupes dominants de poisson apparaissent plus semblables à l'intérieur des systèmes. Les propriétés relatives au régime de pêche, c'est-à-dire à la mortalité par pêche, ou à la fraction de production primaire disponible et nécessaire pour maintenir les pêcheries, sont très fluctuantes d'un système ou d'un régime à l'autre. Une attention particulière est nécessaire pour analyser les séries temporelles de flux dans les compartiments planctoniques afin d'obtenir une compréhension plus détaillée des propriétés spécifiques de l'écosystème.

INTRODUCTION

Eastern boundary current systems, or upwelling ecosystems, are among the most productive marine areas of the world. The four largest of these are the Humboldt Current off South America, the Benguela Current off southern Africa, the Canary Current of northwest Africa and the California Current off North America. They support large fish stocks of a similar species composition (Table 1) and important fisheries, accounting for more than 25% of the world catch of marine fish (FAO, 1990). Major scientific attention has been devoted towards the management of these fisheries, but to date no tool exists which would be capable of dealing with the considerable interannual fluctuations, notably of the anchovies and sardines stocks. Recent approaches emphasize the necessity of managing fisheries a multispecies context (see, e.g., contributions in Daan and Sissenwine, 1991), giving expression to the need of understanding the ecology of the systems components and their interactions.

The productivity of the upwelling systems depends strongly on the oceanographic conditions (Parrish *et al.*, 1983; Cury and Roy, 1989), which are likely to change along with intensifying coastal winds due to global warming (Bakun, 1990, 1993). Additionally, upwelling systems are carbon sinks (Walsh, 1989; Siegenthaler and Sarmiento, 1993), which is relevant to our understanding of the global carbon cycle.

In line with the CEOS concept (Bakun *et al.*, 1993; Cury *et al.*, this vol.), and based on published results of research relevant to models of upwelling ecosystems and earlier modelling studies on the Peruvian upwelling system (Jarre *et al.*, 1991; Jarre-Teichmann, 1992), trophic flow models of subsystems of the four upwelling regions (Fig. 1) were constructed and analyzed, aiming at a comparison of energy flows and systems characteristics under different climatic and/or fishing regimes (Jarre-Teichmann and Christensen, in press). This contribution contrasts the results of this study relevant to global versus those relevant to local properties of the four upwelling ecosystems, with emphasis on the five commercially most important fish anchovy, sardine, horse mackerel, mackerel and hake.

Common name	Genus	Species			
		Peru	California	Benguela	Northwest Africa
Anchovy	*Engraulis*	*ringens*	*mordax*	*capensis*	*encrasicolus*
Sardine	*Sardinops*	*sagax*	*caeruleus*	*ocellatus*	*Sardina pilchardus*
Horse mackerel	*Trachurus*	*murphyi*	*symmetricus*	*capensis*	*trachurus*, *trecae*
Mackerel	*Scomber*	*japonicus*	*japonicus*	*japonicus*	*japonicus*
Hake	*Merluccius*	*gayi*	*productus*	*capensis*, *paradoxus*	*pollis*, *senegalensis*

Table 1: Dominant fish species in the four large upwelling systems (modified from Bakun and Parrish, 1980).

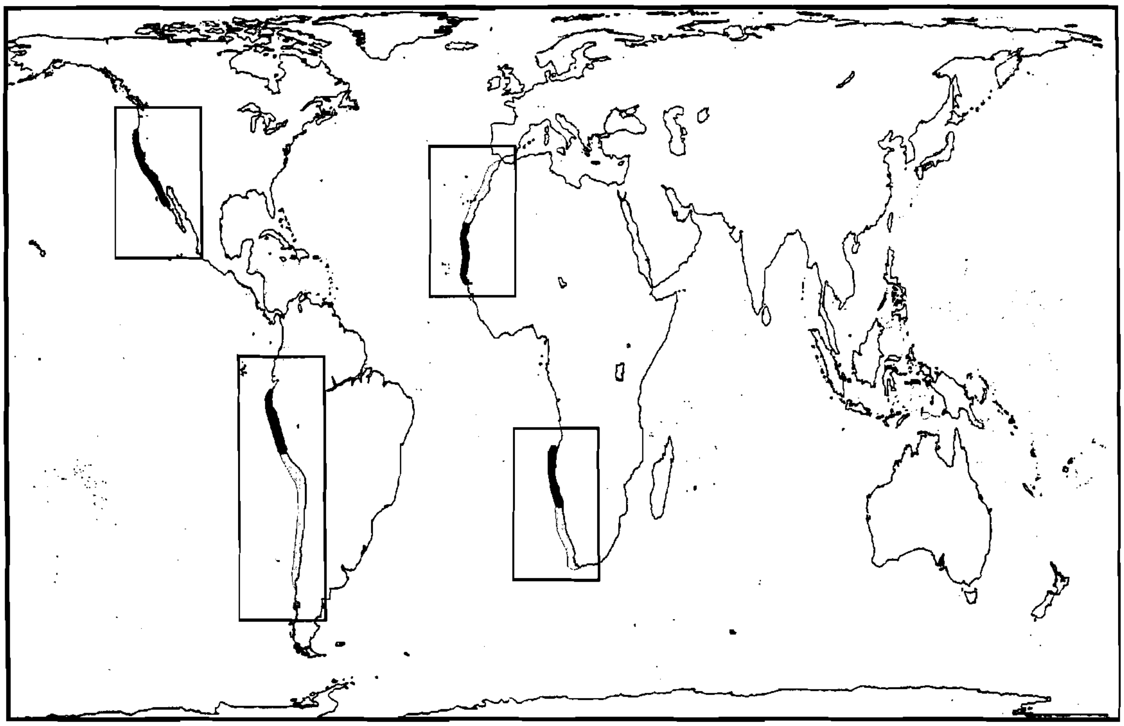


Fig. 1: The four large eastern boundary currents of the world (shaded) and the subsystems modelled for the present contribution (solid black). The subsystems were chosen such that they comprise the areas occupied by the dominant stocks of small pelagics.

1. MATERIAL AND METHODS

1.1. Model construction

A set of seven models was constructed of the four large upwelling ecosystems, averaging two periods each for the systems off Peru, Namibia and California, and one period for the upwelling system off Northwest Africa (Table 2). As the models are described in detail in Jarre-Teichmann and Christensen (in press), we confine ourselves here to a brief overview of their approach.

We used the Ecopath software (Christensen and Pauly, 1992), which based on the work of Polovina and associates (Polovina and Ow, 1983; Polovina, 1984, 1985). Assuming mass-balance over an appropriate period of time, trophic interactions between the components of an ecosystem (species or species groups) are described by a set of linear equations, wherein the production of each component equals its withdrawals by other components in the system (predation mortality), its export from the system (fishing mortality and other exports), and the baseline mortality, i.e.:

Production by (i) = All predation on (i) + nonpredatory biomass losses of (i) + fishery catches of (i) + other exports of (i)

The terms in this equation may be replaced by:

Production by (i) = B_i (P/B_i)

Predatory losses of (i) = $M_2 = \Sigma_j (B_j\ (Q/B_j)\ DC_{j,i})$

Other losses of (i) = $(1 - EE_i)\ B_i\ (P/B_i)$

and this leads, for any component in the system, to:

$$B_i\ (P/B_i)\ (EE_i - S_j)\ (B_j\ (Q/B_j)\ DC_{j,i}) - Ex_i = 0$$

where:

i indicates a component (stock, species, species group) of the model;
j any of its predators;
B_i its biomass;
P/B_i the production of a component per unit biomass (= total mortality under steady-state conditions);
Q/B_i the consumption of a component per unit biomass;
$DC_{j,i}$ the average fraction of i in the diet of j (in terms of weight);
EE_i its ecotrophic efficiency (the fraction of the total production consumed by predators or exported from the system);
Ex_i its export from the system (e.g., by emigration or advection, or fishery catch).

The energy balance of each component is given by:
Consumption = Production + Respiration + Non-assimilated food

wherein consumption is composed of consumption within the system and consumption of imports (i.e., consumption 'outside the system'), and production may be consumed by predators, exported from the system, or be a contribution to detritus.

This structure defines the necessary inputs to the model. These are, for each component, an estimate of its

- biomass;
- production per unit biomass;
- total food consumption per unit biomass;
- assimilation efficiency;
- diet composition;
- exports from the system;
- ecotrophic efficiency.

For each component, one of above parameters B, P/B, Q/B, or EE may be unknown and is estimated when solving the system, along with the respiration of that component. If an acceptable result for each of the unknowns is achieved from the inputs, the model is mass-balanced and may be analysed further.

In this study, the ecotrophic efficiencies were computed for most of the components (Table 3) and used to balance the models, where, for obvious reasons $0 \leq EE < 1$ served as a constraint. For components for which the biomasses were not available or proved erroneous during the modelling process, EEs were set and the biomasses estimated.

System (Latitude)	Period	Dominant[a] pelagic fish species	Regime characteristics, remarks
Peru, (4-14 °S)	1964-1971	Anchovy	Overwhelming anchovy biomass with world's largest single-species fishery; prior to collapse of anchovy
	1973-1981	Anchovy	Slow increase of anchovy stock
Northern Benguela, (15-35 °S)	1971-1977	Sardine	Sardine biomass lower than in the late 1960s, but still high. Strong fishery on sardine and hake.
	1978-1983	Horse mackerel	Sardine and hake biomasses strongly decreased, nevertheless heavily fished.
NorthWest Africa, (12-25 °N)	1970-1979	Sardine	System with least published information. Sardinella hold ecological niche occupied by anchovies in the other upwelling systems. Strong fishery for sardine and horse mackerel. Seasonal upwelling, system comprises several tropical fish species.
California, (28-43 °N)	1965-1972	Anchovy	Highly seasonal upwelling. Very low fish biomasses after breakdown of sardine and mackerel stocks. Fishing moratoria effective for both species.
	1978-1985	Anchovy	Fish biomasses recovering, end of fishing moratoria.

[a] in terms of production

Table 2: Major characteristics of the four large upwelling systems and the periods modeled.

1.2. Analysis of the models

After a model has been balanced, it is assured that the various estimates of biomass and turnover rates are mutually compatible, and hence represent a possible and consistent picture of energy flows in the system. Only then is it meaningful to perform further analyses of the model, e.g., for interactions between its components, or towards a holistic assessment of the system's structure based on the theories of Odum (1969) or Ulanowicz (1986). If shifts in biomass or catches in an ecosystem reflect transitions between alternative states of that system (Steele and Henderson, 1984; Lluch-Belda *et al.*, 1989), these changes should be reflected in such ecological properties.

Various types of favorable or inhibitive interactions are commonly described in ecology (see, e.g., Odum, 1971). Direct trophic interactions can be assessed by analysing partial mortality coefficients of the prey groups. In order to also consider indirect interactions between the components in an ecosystem, such as competition, we used the mixed trophic impact routine suggested by Ulanowicz and Puccia (1990). This approach assesses the relative impact that infinitissimally small changes in the biomass of a given group would have on the biomass of other groups, provided that the trophic structure in the system does not change. The latter is the reason why it cannot be used for predictive purposes; however, it can well be used as a sensitivity analysis for interspecific interactions.

Component	Estimated paramater Peru	 Northern Benguela	 Northwest Africa	 California
Phytoplankton	EE	EE	B	B
Benthic producers	B	B	B	B
Zooplankton	EE	B[a], EE[b]	EE	EE
Anchovy	EE	EE	EE	EE
Sardinella	—	—	EE	—
Sardine	EE	EE	EE	EE
Mackerel	EE	EE	EE	EE
Horse mackerel	EE	EE	EE	EE
Large scombrids	EE	EE	EE	EE
Other pelagics	B	B	B	B
Meiobenthos	B	B	B	B
Macrobenthos	EE	B	EE	EE
Hake	EE	EE	EE	EE
Demersals	B	B	B	B
Marine birds	EE	EE	EE	EE
Marine mammals	EE	EE	EE	EE
Mesopelagics	—	EE	EE	EE
Detritus	EE	EE	EE	EE

[a] Period 1971-1977

[b] Period 1978-1983

Table 3: Estimated parameters in the models of the four large upwelling ecosystems constructed. B: biomass, EE: ecotrophic efficiency; -: component not included in model. List refers to all time periods modeled if not stated otherwise.

Fractional trophic levels may also be reexpressed into discrete trophic levels sensu Lindemann (1942) (Ulanowicz, 1995). Thus, a given consumer is not placed on a single (fractional) trophic level according to its diet composition, but is perceived as finding on various (discrete) trophic levels simultaneously. The ratio between trophic flows consumed or exported from one trophic level and the flows entering it is defined as transfer efficiency.

Fisheries in different areas may have catches of similar size, but their species composition can be rather different, based, of course, on the availability of fish and on the fishing regime. The exploitation of fish on higher trophic levels in the food web is more costly in ecological terms than the exploitation of groups on lower trophic levels, because the energy transfer efficiency up the food web is far below unity. Hence, the maintenance cost of a fishery (or, generally, any system component) can only be compared across systems by using a common currency, e.g., primary production equivalents as implemented by Christensen & Pauly (1993). Following their approach, cycles in the system are removed first. The end flow of each path in the system (e.g., fishery catch) is then traced backwards to the primary producers, using, for each step, the ratio between consumption and production as a raising factor. Consequently, the sum of the primary production required at the basis of each path is the total primary production needed to sustain the system component in question, or the fishery.

2. RESULTS AND DISCUSSION

2.1. Trophic flow diagrams

Examples of trophic flow diagrams are given for the Peruvian upwelling ecosystem for the periods 1964-1971 and 1973-1981 (Fig. 2). The general structure of the trophic flow diagrams looks similar for all four upwelling systems. With the primary producers and detritus situated on trophic level 1 (by definition), the planktonic and benthic invertebrate groups are located at trophic levels 2.0 - 2.5. Small pelagics and other pelagics ranged next, with trophic levels between 2.5 and 3.0, while the predatory fish, as well as marine birds and mammals, were operate at trophic levels 3 and 4. Large scombrids and birds are the top predators in the system.

The major flows in all systems occurred in the plankton. Other important flows in the Peruvian ecosystem comprised anchovy and the benthic invertebrates, as well as sardine during the later period. Flows towards anchovy were reduced by a factor of more than four between the two periods, while those to sardine increased by a factor of seven, towards values similar to those for anchovy. Flows toward macrobenthos and hake also increased with the higher abundance of these groups. Due to the overall shortage of small pelagics in the system, the trophic level of predatory fish decreased (as they switched to a larger fraction of zooplankton) while that of hake, mammals and birds increased. Feeding of marine mammals 'outside' the system (i.e., on oceanic squid and mesopelagics) was important during both periods. In spite of the considerable changes in the ecosystem, the general structure of the pathways in the system was not altered.

2.2. Systems characteristics

The four upwelling systems ranked rather distinctly after the 'size' of their primary production, total biomass sustained in the system, catches and, consequently, total system throughput (Fig. 3). The Peruvian upwelling ecosystem was the largest of these four systems. It was also the system in which the most pronounced changes of system size occurred during the periods analysed. After the collapse of the anchovy stock, it became more similar to the northern Benguela system. The latter decreased in size from the mid-70s to the early 80s, due to the strong decrease of small pelagics (notably sardine), not compensated by the increased abundance of horse mackerel. The upwelling system off northwest Africa was similar in size to the northern Benguela system, despite the seasonality of its upwelling. The California system, whose upwelling is also highly seasonal, was the smallest of these four systems.

2.3. Productivity of small pelagics

The productivity (or P/B ratio, equivalent to total mortality) of small pelagics ranged between 1.1 year^{-1} and 2.7 year^{-1} for anchovy, and between 0.4 year^{-1} and 1.2 year^{-1} for sardine in the balanced models (Fig. 4). The productivity of anchovy was highest off Peru, followed by Namibia, northwest Africa and California. Their natural mortality (1.1 - 2.1 year^{-1}) was

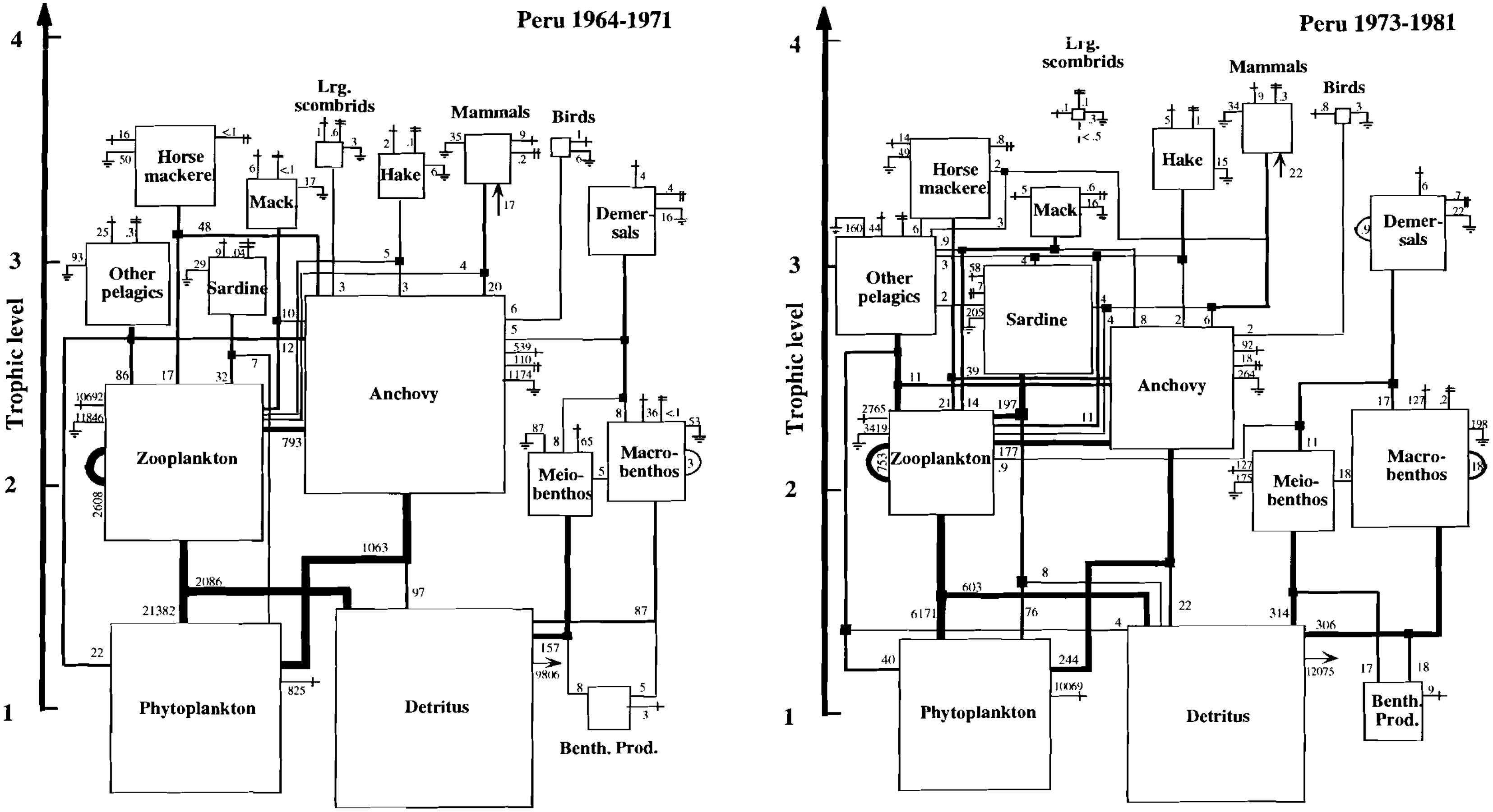


Fig. 2: Trophic flows in the Peruvian ecosystem, averaging the period 1964-1971, and the period 1973-1981. The size of the boxes is proportional to the biomass of the corresponding components in the models, if the boxes are imagined as cubes instead of squares. Boxes are arranged along the vertical axis according to their trophic level, defined as one for primary producers and detritus, and for consumers as one plus the mean trophic level of the prey items, weighted according to their fraction in the consumer's total diet. Flows are in units of t wet mass km^{-2} year^{-1}. Flows leave boxes on the upper half and enter them on the lower half, the width of the line indicates the order of magnitude of trophic flows. Flows of at least 1 t km^{-2} year^{-1} were rounded to integers, those below to one digit. Trophic flows of less than 0.1 ppt of the total consumption in the system, corresponding to about 3 t km^{-2} year^{-1} during 1964-1971 and to about 0.9 t km^{-2} year^{-1} during 1973-1981, were ommitted for clarity. Biomass of detritus is a rough guess only.

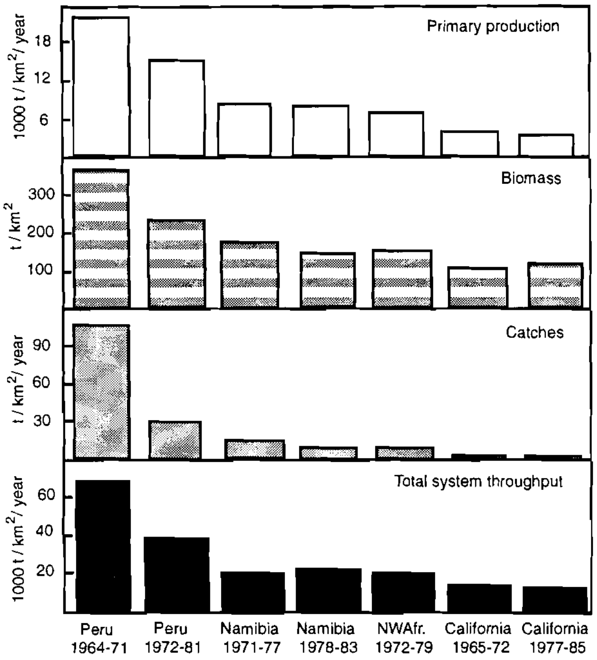


Fig. 3: Summary statistics of the seven balanced models constructed, referring to system size. Systems are arranged after decreasing primary production. Note that systems are set apart in geographic rather than in regime-specific order. Also note similar trend, in all four parameters, of primary production, total biomass (excl. detritus), total catches and total system throughput.

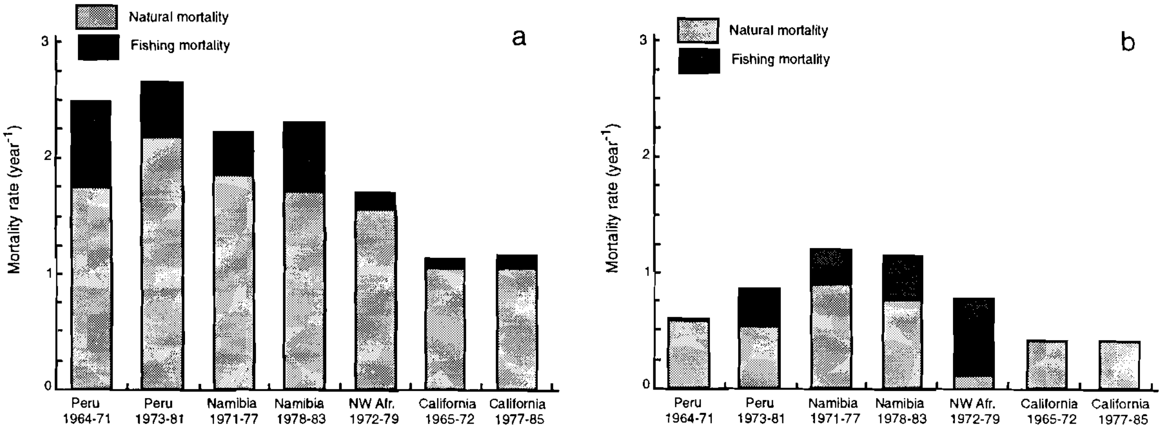


Fig. 4: Breakdown of total mortality rates for anchovy (a) and sardine (b). Note consistent scale of vertical axes. Systems are arranged after decreasing primary production.

always considerably higher than their fishing mortality (0.1 to 0.7 year^{-1}), indicating their importance as a food resource for other system components. Fishing mortality of anchovy was highest off Peru during the late 1960s, followed by Namibia in the early 1980s. The latter is remarkable as anchovy were not dominant off Namibia, neither in the system, nor in the landings. Anchovy fishing mortality was still high in the Peruvian and Namibian systems during the other periods, while it was lower in the northwest African and Californian systems, due to a lack of directed fishery in the former, and a more restrictive fishery management in the latter.

Sardine were subjected to the highest fishing mortality off Northwest Africa, followed by the northern Benguela system and Peruvian system during the 1970s. Due to the closure of the sardine fishery off California, fishing mortality of sardine off California was negligible. The natural mortality of sardine was highest off Namibia during both periods, followed by the Peruvian and the Californian systems.

2.4. Productivity of mackerel, horse mackerel and hake

Mackerel tended to be more productive than horse mackerel, with productivities ranging from 0.5 year^{-1} to 0.9 year^{-1}, and 0.3 year^{-1} to 1.1 year^{-1}, respectively (Fig. 5). Total mortality of mackerel was lowest off California due to the closure of its fishery, and similar in the other systems. Total productivity of horse mackerel was rather low in the Peruvian upwelling system, where they grew relatively large. It was more than three times as high off Northwest Africa, were also the highest fishing mortalities were observed. Apart from the Namibian system in the early 1980s, fishing mortalities were generally low reflecting the lack of major directed fisheries.

The productivity of hake ranged from 0.4 year^{-1} to 0.9 year^{-1} (Fig. 5). It was lowest off Peru in the 1960s, reflecting the focus of the fishery on small pelagics. During the 1970s, hake were more strongly exploited off Peru.

The natural mortality of horse mackerel was similar in all systems except off Northwest Africa, where it was twice as high as in the other systems. For mackerel and hake, both components were approximately equal off Peru during the 1970s, as well as in the Namibian and Northwest African systems, reflecting their strong exploitation.

In general, the results from our balanced ecosystem models confirm that the rates of natural mortality are not system-specific (see also Beverton and Holt, 1959; Pauly, 1980). The fishing mortalities, however, showed marked differences among systems and regimes. In consequence, a fishing regime should be regarded as a local property of a system, whereas the productivities of each of the major fish components are probably more similar on the global scale.

2.5. Interactions between ecosystem components

Recruitment success is largely determined by the dynamics of primary production (Cushing, 1982; Parrish *et al.*, 1983), and moderate upwelling conditions are most favorable for small pelagics in upwelling regions (Cury and Roy, 1989; Cury *et al.*, 1995). Cushing (1982) also linked recruitment success to competition and stressed the need for information on how recruitment is affected by predation, although he considered the latter a minor process.

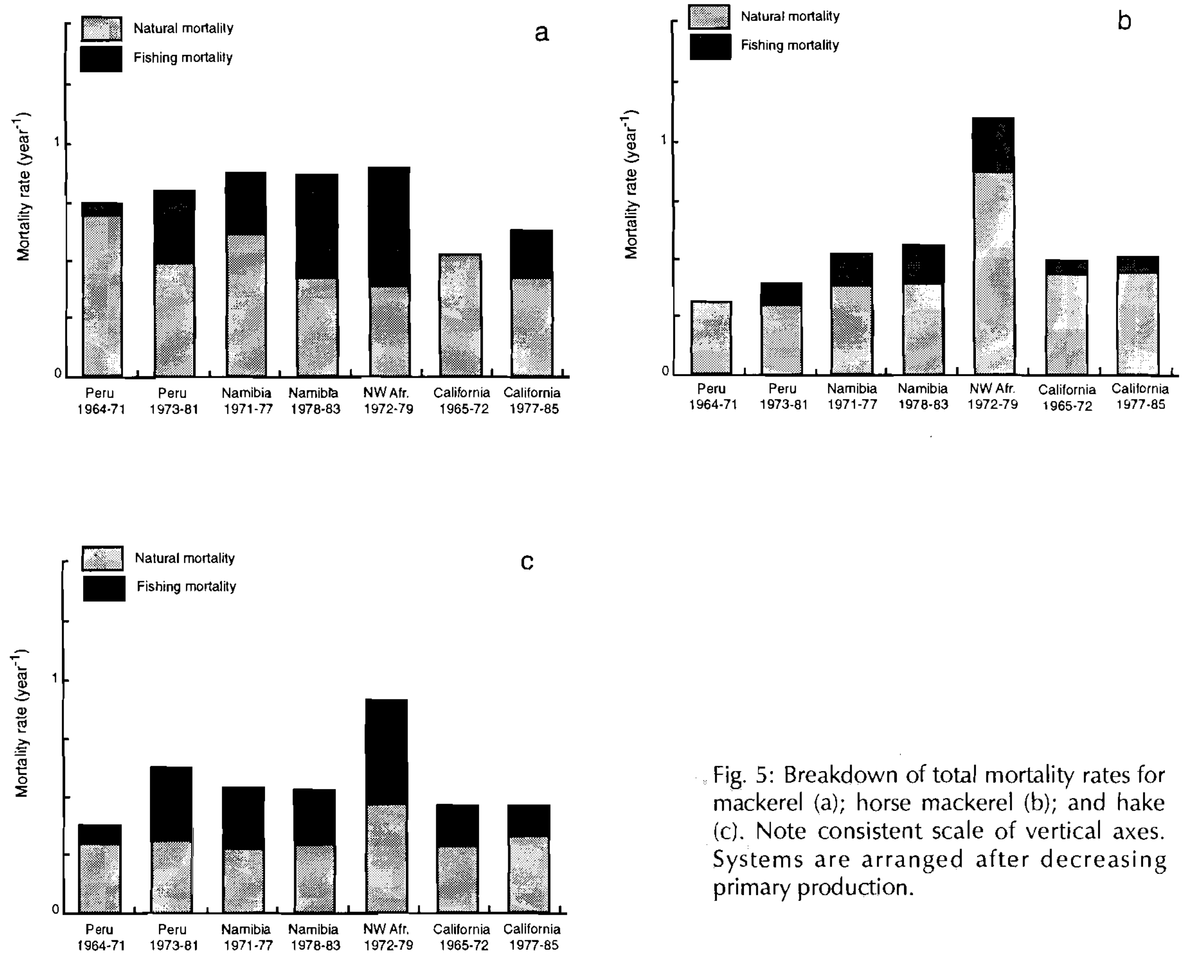


Fig. 5: Breakdown of total mortality rates for mackerel (a); horse mackerel (b); and hake (c). Note consistent scale of vertical axes. Systems are arranged after decreasing primary production.

The dominant food items in the diet of the five commercially most important fish are given in Table 4. All of them were essentially planktivores. Anchovy fed largely on phytoplankton, except off California, where they ingested a larger fraction of zooplankton. Sardine were predominantly phytoplanktivores in the Atlantic, and zooplanktivores in the Pacific. However, due to the well-known ambiguities in assessing the diet composition (see, e.g., James, 1988 for a review), this geographic division should be viewed with caution. Mackerel and hake fed predominantly on zooplankton throughout, and horse mackerel fed mostly on zooplankton except off Peru, where they fed mainly on anchovy.

Although the dominance of planktivores suggests a food web of rather simple structure, mixed trophic impact analysis suggested some indirect effects, as some of the groups most strongly favoring those five fish species differed from the most important food items. For anchovy, sardine and mackerel off California, primary production was the most enhancing factor. This also held true for the Peruvian system after the collapse of anchovy, where phytoplankon became the dominant factor for all fish groups. Hake off Namibia were also favored most strongly by primary production.

System / Group	Anchovy	Sardine	Mackerel	Horse mackerel	Hake
Peru 1964-1971	Phytoplankton	Zooplankton	Zooplankton	Anchovy	Zooplankton
Peru 1973-1981	Phytoplankton	Zooplankton	Zooplankton	Anchovy	Zooplankton
Namibia 1971-1977	Phytoplankton	Phytoplankton	Zooplankton	Zooplankton	Zooplankton
Namibia 1978-1983	Phytoplankton	Phytoplankton	Zooplankton	Zooplankton	Zooplankton
NW Africa 1972-1979	Phytoplankton	Phytoplankton	Zooplankton	Zooplankton	Zooplankton
California 1965-1972	Zooplankton	Zooplankton	Zooplankton	Zooplankton	Zooplankton
California 1978-1985	Zooplankton	Zooplankton	Zooplankton	Zooplankton	Zooplankton

Table 4a: Dominant food item (by weight) in the diet of the five commercially most important fish species by system and regime.

System / Group	Anchovy	Sardine	Mackerel	Horse mackerel	Hake
Peru 1964-1971	Phytoplankton	Zooplankton	Zooplankton	Anchovy	Zooplankton
Peru 1973-1981	Phytoplankton	Phytoplankton	Phytoplankton	Phytoplankton Anchovy	Phytoplankton
Namibia 1971-1977	Phytoplankton	Phytoplankton	Zooplankton	Zooplankton	Phytoplankton
Namibia 1978-1983	Phytoplankton	Phytoplankton	Zooplankton	Zooplankton	Phytoplankton
NW Africa 1972-1979	Phytoplankton	Phytoplankton	Zooplankton	Zooplankton	Zooplankton
California 1965-1972	Phytoplankton	Phytoplankton	Phytoplankton	Zooplankton	Zooplankton
California 1978-1985	Phytoplankton	Phytoplankton	Phytoplankton	Zooplankton	Zooplankton

Table 4b: Strongest trophic enhancement of the five commercially most important fish species by system and regime, based on mixed trophic impact analysis. Components that differ from the most important diet components, and thus point at indirect effects in the system, are shaded.

In general, the small pelagics appeared to be similarly favored in all systems, whereas the enhancement of mackerel, horse mackerel and hake was more system-specific. Within a system, the positive impacts were generally similar between regimes, except for pronounced changes in ecosystem structure, such occurred off Peru in the early 1970s.

The groups causing the highest mortality of the five most important commercial fish species differed more strongly among systems and regimes. Anchovy were heavily exploited by the fishery in the late 1960s off Peru, while horse mackerel caused most of its mortality during the 1970s. Hake was the dominant predator on anchovy off Namibia, other pelagics off Northwest Africa, and horse mackerel and mackerel off California. Sardine were preyed upon intensively by mammals and heavily fished off Peru; they were preyed upon most strongly by hake off Namibia, and by other pelagics off Northwest Africa. Mackerel were more strongly exploited by the fisheries off Peru, Namibia, and (after its reopening) off California than subjected to predation by any single group. Horse mackerel were preyed upon by mammals and other pelagics, except off Namibia, where predation by hake and exploitation by the fishery were the most important causes of mortality in the first and second periods, respectively. Hake was either influenced by cannibalism or by the fishery, except off California, where cannibalism was less important because the hake population consisted mainly of juveniles, preyed upon by the abundant marine mammals.

Whereas anchovy was inhibited rather directly, indirect effects of trophic interactions were more pronounced for the other groups. It is worth noting, though, that intraspecific competition apparently had a larger effect on anchovy during the 1960s than food limitation. Competition with anchovy was more important for sardine off Peru than predation by mammals. Inhibition by mackerel, exclusively based on indirect effects, was more important for sardine off Namibia in the 1970s than predation by hake. Competition for food could also have been limiting for sardine off northwest Africa. All in all, our results are thus supported by the competition model of Silvert and Crawford (1988).

Mackerel were subjected to more direct effects rather than indirect ones, except off California during the early 1980s, where intraspecific competition for food inhibited its population growth more than any other group. Horse mackerel competed with the fishery during the period of high anchovy abundance off Peru, and with each other after the collapse of its major food resource. Off Namibia, horse mackerel were inhibited by hake to the same extent as by the fishery. Inhibition by other pelagics was more important to horse mackerel than direct predation by mammals off California during the late 1960s. Hake were generally predator-controlled, either by each other, by the fishery, or (off California) by marine mammals. Indirect interaction with anchovy turned out to be strongly inhibiting for hake off California during the early 1980s.

These results supplement earlier work by Korrubel (1992), who suggested that fisheries may induce species dominance shifts while emphasizing the need for further assessment of the role of other ecosystem components, based on improved knowledge of their interactions. In general, the components the Peruvian system were indeed most strongly inhibited by the fishery, but those in the northern Benguela system most strongly by hake. The cross-impacts included more groups in the two systems with seasonal upwelling, off California and Northwest Africa. However, all in all, the inhibition of these five groups appeared to be a highly local property.

2.6. Transfer efficiency

Restructuring of the fractional trophic levels (as used for the trophic flow diagrams) yielded six discrete trophic levels, i.e., producers, herbivores, and first- to fourth-order carnivores, for all of the models except Northwest Africa which had seven trophic levels. As the absolute flows on the topmost level were negligible, we computed the average transfer efficiency of the consumer levels II to V (i.e., herbivores to third-order carnivores) (Fig. 6). The grand mean of all models yielded a transfer efficiency of slightly above 5% (range 3.6 - 7.4%), much lower than the general mean of about 10% computed for a cross-section of aquatic ecosystems (Christensen and Pauly, 1993; Pauly and Christensen, 1995). Hence, upwelling systems are all relatively inefficient systems regardless of the prevailing fishing regime. Moreover, despite relatively large changes of the transfer efficiencies between different regimes in a given system, there is some suggestion that the systems might be slightly different from each other, the California system being the least, and the two Atlantic systems the most efficient ones.

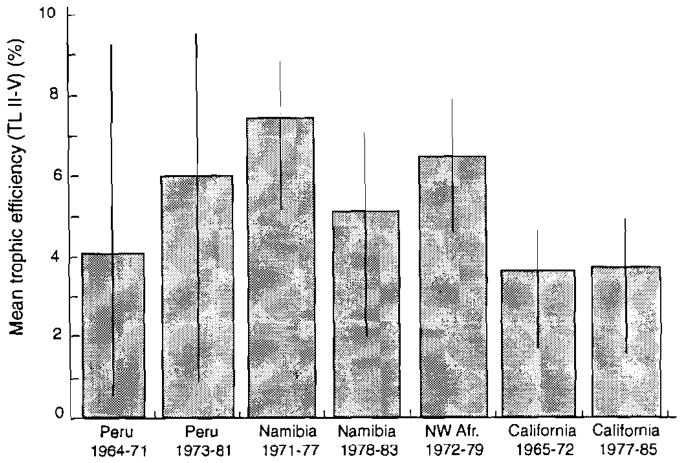


Fig. 6: Mean transfer efficiencies between discrete trophic levels II to V, i.e., herbivores to third-order carnivores, in seven models of the four major upwelling ecosystems. Thin lines indicate ranges. Systems are arranged after decreasing primary production.

2.7. Primary production required to sustain the fishery

Figure 7 gives the primary production required to sustain the fishery in the seven models constructed both in absolute terms, and relative to the primary production available in the corresponding system. In absolute terms, the flows from the primary producers required to sustain the fishery reflected the size of the catches, with high catches implying high primary production requirements. The systems could thus be ranked in the same way as after the 'size' parameters (Fig. 3). However, changes in the fishing regime must be considered as well: although the magnitude of the catches off Peru was reduced by a factor of more than three between the two periods analysed, the primary production required to sustain the fishery in the 1970s decreased only by about 10%, as sardine and hake, both situated on higher trophic levels, accounted for a considerable fraction of total catches.

The fraction of the available primary production used to sustain the catches, however, showed a rather different picture. Although the catches decreased significantly between the two periods analysed in the Peruvian system, a larger fraction of the available primary production was used in the later period. The fishery off Namibia during the early 1970s required the largest share of the available primary production, whereas the fishery off California took only a minor share. Comparing the 1970s as a period modelled for all four upwelling areas, we conclude that the primary production required to sustain the fishery is a local characteristic of the system, depending on the intensity of fishing and the trophic levels of its target species. It cannot straightforwardly be linked to species dominance, as the differences between sardine-dominated systems, such as the Northwest African and the northern Benguela systems during the 1970s, were larger than the differences between an anchovy-dominated system (off Peru during the late 1960s) and a horse-mackerel dominated one (off Namibia, during 1978-83).

The grand mean of the primary production used to sustain the fishery amounted to 9.5% of the available primary production in our models. This figure is higher than the global average of 8% estimated by Pauly and Christensen (1995), but seems strikingly low if compared with their results for upwelling regions of 25%. This apparent discrepancy is

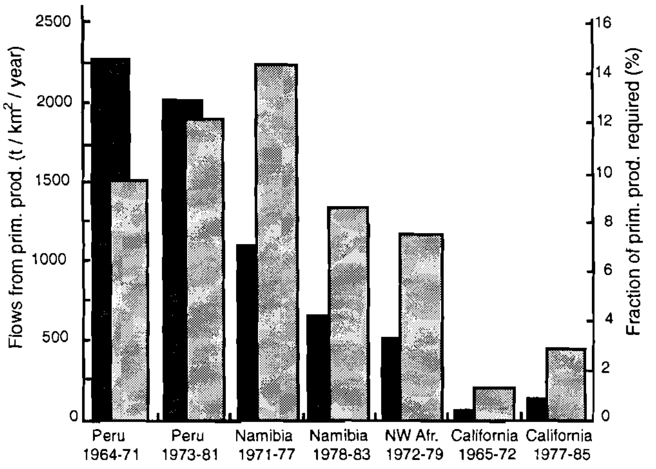


Fig. 7: Flows from the producers's level to the fishery, both in absolute (light shading) as well as in relative (dark shading) terms. Systems are arranged after decreasing primary production.

explained as follows: Pauly and Christensen (1995) used primary production estimates similar to the 1970s conditions in our models, but (i) catches of small pelagics were considerably higher in 1990 than they were during the 1970s; (ii) we used, except for Peruvian anchovy, nominal catches in our models, whereas Pauly and Christensen (1995) accounted for additional 15% of discards for each group; and (iii) catches of horse mackerel were disproportionally large in the southern part of the Humboldt Current, not included in the present comparisons. We have, thus, been looking at very productive subsystems in the four upwelling regions, but not necessarily at those parts of the systems and/or periods subjected to the highest rate of exploitation by the fishery. Using the respective raising factors for the catches, we would, too, arrive at relative requirements of 6-8% to sustain the fishery of anchovy and sardine, 15-17% for the fishery of horse mackerel and mackerel, and <1% for other pelagic groups, indicating the considerable degree of present exploitation of these systems. Additionally, it should be kept in mind that another 3-4% of the primary production are required to sustain the fishery of hake, not explicitly attributed to upwelling regions in the above study.

2.8. Primary production required to sustain the five major fish groups

About 20% - 35% of the available flows from the producers' level were generally used to sustain the five dominant fish groups in the system (Fig. 8 and Table 5), with the exception of the Namibian system during the 1970s, where almost half of the available flow was required. The latter seemed particularly high at first glance, but went along with a slightly elevated mean trophic efficiency in the system, and was also consistent with the high fraction of primary production required to sustain the fishery. The shift in species dominance in the Peruvian system between the late 1960s and the 1970s was clearly reflected, and it is worth noting that — in spite of the considerably smaller total biomass in the system — a similar fraction of primary production was required to sustain the dominant fish species.

It was also striking that the fraction of primary production used to sustain the fish in the Californian system was not much lower than in the other systems, indicating that the structure of the Californian system was indeed very similar to the other systems, despite their large differences in size. We should thus moderate the statement of Ware (1992) on the particular inefficiency of the Californian ecosystem with respect to fish production.

Within the systems where anchovy were the dominant fish by production (i.e., off Peru and California, see Table 2), it was also anchovy which required the largest single fraction of primary production among the fish groups. The same held true for horse mackerel off Namibia in the early 1980s. Strikingly, within the two systems dominated by sardine (the Namibian and northwest African systems during the 1970s), hake and horse mackerel required the single largest share of primary production, respectively, but not sardine. It would be premature to draw any conclusion from this inconsistency with respect to the persistence of species dominance or the diversity of flows in the systems (see also Shannon *et al.* (1988), and LeClus (1991)).

System / Group	Anchovy	Sardine	Mackerel	Horse mackerel	Hake
Peru 1964-1971	Fishery	Mammals	Fishery	Mammals	Hake
Peru 1973-1981	Horse mackerel	Fishery	Fishery	Mammals	Fishery
Namibia 1971-1977	Hake	Hake	Hake	Hake	Fishery
Namibia 1978-1983	Hake	Hake	Fishery	Fishery	Hake
NW Africa 1972-1979	Other pelagics	Other pelagics	Lrg. scombrids	Other pelagics	Fishery
California 1965-1972	Horse mackerel	—[a]	Marine birds	Mammals	Mammals
California 1978-1985	Mackerel	—[a]	Fishery	Other pelagics	Mammals

[a] The biomass of sardine was so low that it could only be a marginal component in the diet of its predators. It was hence impossible to determine the main predator on sardine.

Table 5a: Strongest predator group of the five commercially most important fish species by system and regime.

System / Group	Anchovy	Sardine	Mackerel	Horse mackerel	Hake
Peru 1964-1971	Anchovy	Anchovy	Fishery	Fishery	Hake
Peru 1973-1981	Horse mackerel	Anchovy / Fishery	Fishery	Horse mackerel	Fishery
Namibia 1971-1977	Hake	Horse mackerel	Hake	Hake	Hake
Namibia 1978-1983	Hake	Hake	Fishery	Hake / Fishery	Hake
NW Africa 1972-1979	Other pelagics	Zooplankton	Lrg. scombrids	Other pelagics	Demersals
California 1965-1972	Horse mackerel	—[a]	Marine birds	Other pelagics	Mammals
California 1978-1985	Mackerel	—[a]	Mackerel	Other pelagics	Anchovy/Mammals

[a] The biomass of sardine was so low that it could only be a marginal component in the diet of its predators. It was hence impossible to account for its proper role in the mixed trophic impacts routine.

Table 5b: Strongest inhibition of the five commercially most important fish species by system and regime, based on mixed trophic impact analysis. Components that differ from the strongest predator, and thus point at food limitation or competitive inhibition of the respective fish group, are shaded.

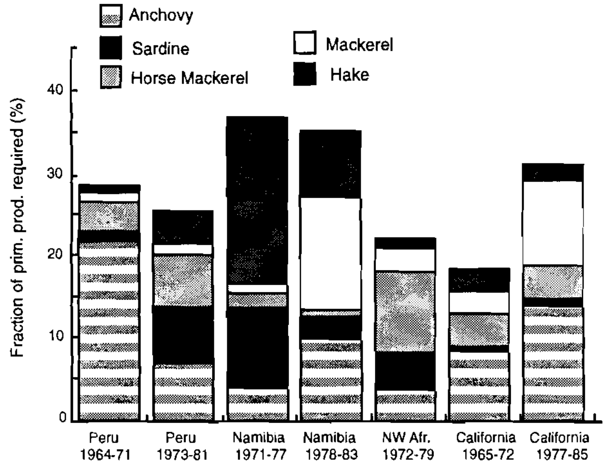


Fig. 8: Fraction of flows from the producers' level required to sustain the five dominant groups in the system. For the Northwest Africa system, the requirements of anchovy and sardinella have been combined, as sardinella occupies, in part, the ecological niche of anchovy. Systems are arranged after decreasing primary production.

CONCLUSION

The different aspects of our analysis with respect to global versus local properties are summarized in Table 6. The consistent set of species dominating the flow on the higher trophic levels is one of the obvious global characteristics of upwelling ecosystems. Also, the distribution of the major flows in the models is also quite similar among systems.

However, it is necessary to keep in mind that all flows among the fish groups and toward the warm-blooded top predators are small in comparison to those in the plankton. Hence, for improved comparison of the systems with respect to system-level properties (maturity, ascendency, etc.) under different environmental regimes, time-series of flows in the plankton compartments, as well as the microbial food web, will need to be assembled and analysed in more detail than it has been possible for the present contribution.

The productivity of the small pelagics, as well as the natural mortality of all dominant fish stocks, was also similar between systems, and can thus be regarded global properties. This should not be regarded as a pure artifact of model construction, as the models were balanced prior to any comparisons.

It also emerged clearly that small pelagics increase with primary production regardless of system and regime. This does not appear, at first glance, to go along with the findings of Cury and Roy (1989) and Cury *et al.* (1995) that moderate conditions are most beneficial to successful recruitment, but it should be kept in mind that the present approach dealt only with trophic interactions, and not with the transport processes that determine the survival of eggs and larvae.

The fraction of primary production used to sustain the five most important fish groups in the ecosystems was also quite similar between the systems (with exception of the Namibian ecosystem during the 1970s) and may thus be regarded as a global property. Furthermore, our results suggest that flows from the primary producers' level required to sustain the dominant fish species (in terms of production) may be a regime-specific property, anchovy using the largest fraction in anchovy-dominated systems, but hake or horse-mackerel using the largest fraction in sardine-dominated systems.

Characteristic / Property	'Global'[a)]	'Local'[b)]
General system structure	Species composition Major flow patterns	System size
Productivity of major fish species	Natural mortality of all dominant fish stocks, total mortality of small pelagics	Fishing mortality
Species interactions	Favoring of small pelagics	Favoring of medium-sized fish; Inhibition of all major fish groups; Strongest predators of all major fish groups
Sustenance of the major fish groups Sustenance of the fishery	Total fraction of primary production required (in general)	Fraction of primary production required by the dominant species Fishing regime, primary production required to sustain the fishery
Relation between production and fishery	Total catch vs. trophic level of fishery Total catch vs. primary production	–
System transfer efficiency	Low mean efficiency of energy transfer up the food web	Efficiency on 'medium scale' (?)
Goal functions	Overall low maturity; similar information content of flows, low relative ascendency	–

[a)] Similar between systems through time, i.e., (i) regime-dependent, or (ii) independent of system and regime

[b)] More similar within systems through time (i.e., regime-independent), or system- and regime-specific

Table 6: Summary of global versus local properties of the four upwelling ecosystems analysed.

Most system-level properties of these ecosystems, such as their generally low transfer efficiency, were also of global nature. Further attributes are discussed in detail in Jarre-Teichmann and Christensen (in press), notably those pertaining to the theories of Odum (1969) and Ulanowicz (1986). The generally low maturity, and low relative ascendency of these systems are global properties as well, and corroborate the grouping of upwelling systems in Christensen's (1992) maturity ranking of aquatic ecosystems. It should further be pointed out that the total catch was correlated with the trophic level of the fishery, and also with the primary production of the systems.

The most obvious local properties of the systems were related to system size, as primary production, total system biomass, or total catches. Furthermore, the factors most strongly favoring the medium-sized fish were more similar within systems through time. The strongest predators of the five most important fish species were rather variable, but their inhibition appeared to be a system-specific property, independent of the prevailing regime. Lastly, all properties related to the fishery, as fishing mortality of the groups, or the primary production required to sustain the fishery, were highly variable, not only among systems, but also among different regimes.

There are a number of inconsistencies in the properties that we have categorized as 'global'. In terms of multispecies management models, care should be taken before these estimates are transferred from one system to another. Additionally, all aspects related to the fishing regime will need to be modelled specifically for the system and period in question.

The complexity and interaction of the various factors influencing fish populations in upwelling ecosystems have been highlighted earlier (Crawford, 1991), implying blurred borderlines that have also made it difficult for us to categorize a given aspect as global or local. Nevertheless, time series, long required for improved understanding of any kind of variability in upwelling systems (see, e.g., Bakun and Parrish, 1980; Pauly, 1987; Sharp, 1991) are becoming increasingly suited for ecosystem approaches such as the one presented here, and may justify optimism that they will subsequently allow for refined future assessment of climatic effects on these four eastern boundary currents.

REFERENCES CITED

Bakun A. 1990. Global climate change and the intensification of coastal ocean upwelling. *Science*, 247: 198-201.

Bakun A. 1993. The California Current, Benguela Current and southwestern Atlantic shelf ecosystems: a comparative approach to identifying factors regulating biomass yields. *In*: K. Sherman, L.M. Alexander and B. Gold (eds.). *Stress, mitigation and preservation of large marine ecosystems*. American Association for the Advancement of Science, Washington D.C., USA.

Bakun A. and R.H. Parrish. 1980. Environmental inputs to fishery population models for eastern boundary current regions. Report on the workshop on the effects of environmental variation on the survival of larval pelagic fishes, Lima, 20 April - 5 May 1980. Organized by FAO as a contribution to the IOC Programme of Ocean Sciences and Living Resources. UNESCO, Paris, *IOC Workshop Rep.*, 28: 67-104.

Bakun A., V. Christensen, C. Curtis, P. Cury, M.H. Durand, D. Husby, R. Mendelsson, J. Mendo, R. Parrish, D. Pauly and C. Roy. 1993. The Climate and Eastern Oceans Systems Project. ICLARM, Naga, 15(4): 26-30.

Beverton R.J.H and S.J. Holt. 1959. A review of the lifespans and mortality rates of fish in nature, and their relation to growth and other physiological characteristics. *In*: G.E.W. Wostenholmen and M. O'Connor (eds.). *The lifespan of animals*. Ciba Found. Colloq. Ageing. 5, Churchill, London: 142-180.

Christensen V. 1992. *Network analysis of trophic interactions in aquatic ecosystems*. PhD Thesis, Royal Danish School of Pharmacy, Copenhagen. 55 p + 13 Appendices.

Christensen V. and D. Pauly. 1992. *A guide to the ECOPATH II software system (Ver. 2.1)*. ICLARM Software 6, Manila, International Center for Living Aquatic Resources Management, 72 p.

Christensen V. and D. Pauly. 1993. Flow characteristics of aquatic ecosystems. *In*: V. Christensen and D. Pauly (eds.). *Trophic models of aquatic ecosystems*. ICLARM Conf. Proc., 26: 338-352.

Crawford R.J.M. 1991. Factors influencing population trends of some abundant vertebrates in sardine-rich coastal ecosystems. *S. Afr. J. mar. Sci.*, 10: 365-381.

Cury P. and C. Roy. 1989. Optimal environmental window and pelagic fish recruitment success in upwelling areas. *Can. J. Fish. Aquat. Sci.*, 46: 670-680.

Cury P., C. Roy, R. Mendelssohn, A. Bakun, D.M. Husby and R.H. Parrish, 1995. Moderate is better: exploring nonlinear climatic effect on Californian anchovy (*Engraulis mordax*). *In*: R.J. Beamish (ed.). Climate change and fish population. *Can.Spec. Publ. Fish. Aquat. Sci.*, 121: 417-424.

Cushing D.H. 1982. *Climate and fisheries*. Academic Press, London, 373 p.

Daan N. and M. Sissenwine (eds.). 1991. Multispecies models relevant to management of living resources. *ICES Mar. Sci. Symp.*, 193, 358 p.

FAO. 1990. *Yearbook of fishery statistics: catches and landings 70*, 647 p.

James A. 1988. Are clupeid microphagists herbivorous or omnivorous? A review of the diets of some commercially important clupeids. *S. Afr. J. Mar. Sci.*, 7: 161-177.

Jarre-Teichmann A. 1992. *Steady-state modelling of the Peruvian upwelling ecosystem*. Doctoral thesis, University of Bremen, F.R. Germany, 153 p.

Jarre-Teichmann A., D. Pauly and P. Muck. 1991. Two approaches for modelling fish stock interactions in the Peruvian upwelling ecosystem. *ICES Mar. Sci. Symp.*, 193: 171-184.

Jarre-Teichmann A. and V. Christensen. In press. Modelling trophic flows in large upwelling ecosystems: temporal and spatial comparisons. *ICLARM Studies and Reviews*, 24.

Korrubel J.L. 1992. An age-structured simulation model to investigate species replacement between pilchard and anchovy populations in the southern Benguela. *S. Afr. J. Mar. Sci.*, 12: 375-391.

LeClus F. 1991. Hydrographic features related to pilchard and anchovy spawning in the northern Benguela system, comparing three environmental regimes. *S. Afr. J. Mar. Sci.*, 10: 103-124.

Lindemann R. 1942. The tropho-dynamic aspect of ecology. *Ecology*, 23: 399-418.

Lluch-Belda D., R.J.M Craford, T. Kawasaki, A.D. MacCall, R.H. Parrish, R.A. Schwartzlose and P.E. Smith. 1989. World-wide fluctuations of sardine and anchovy stocks: the regime problem. *S. Afr. J. Mar. Sci.*, 8: 195-205.

Odum E.P. 1969. The strategy of ecosystem development. *Science*, 164: 262-270.

Odum E.P. 1971. *Fundamentals of ecology*. Saunders, Philadelphia, USA. 574 p.

Parrish R.H., A. Bakun, D.M. Husby and C.S. Nelson. 1983. Comparative climatology of selected environmental processes in relation to eastern boundary current pelagic fish reproduction. *In*: G.D. Sharp and J. Csirke (eds.). Proceedings of the Expert Consultation to Examine Changes in Abundance and Species Composition of Neritic Fish Resources, San José, Costa Rica, 18-29 April 1983. *FAO Fish. Rep.*, 291 (3): 731-777.

Pauly D. 1980. On the interrelationships between natural mortality, growth parameters, and mean environmental temperature in 175 fish stocks. *J. Cons.*, Cons. int. Explor. Mer, 39(2): 175-192.

Pauly D. 1987. Managing the Peruvian upwelling ecosystem: a synthesis. *In*: D. Pauly and I. Tsukayama (eds.). The Peruvian anchoveta and its upwelling ecosystem: three decades of change. *ICLARM Studies and Reviews*, 15: 325-342.

Pauly D. and V. Christensen. 1995. Primary production required to sustain global fisheries. *Nature*, 374: 255-257.

Polovina J.J. 1984. Model of a coral reef ecosystem. I. The ECOPATH model and its application to French Frigate Shoals. *Coral Reefs*, 3: 1-11.

Polovina J.J. 1985. An approach to estimating an ecosystem box model. *Fish. Bull.*, U.S., 83(3): 457-460.

Polovina J.J. and M.D. Ow. 1983. *ECOPATH: A user's manual and program listings*. Nat. Mar. Fish. Serv., NOAA, Honolulu, Admin. Rep., H83-26, 46 p.

Shannon L.V., R.J.M. Crawford, G.B. Bundrit and L.G. Underhill. 1988. Responses of fish populations in the Benguela system to environmental change. J. Cons., *J. Cons. int. Explor. Mer*, 45(1): 5-12.

Sharp G. 1991. Climate and fisheries: cause and effect. *In*: T. Kawasaki, S. Tanaka, Y. Toba and A. Taniguchi (eds.). *Long-term variability of pelagic fish populations and their environment*. Pergamon Press, Oxford, UK. 239-258.

Siegenthaler U. and L. Sarmiento. 1993. Atmospheric carbon dioxide and the ocean. *Nature*, 365: 119-125.

Silvert W. and R.J.M. Crawford. 1988. The periodic replacement of one fish stock by another. *In*: T. Wyatt and M.G. Larraneta (eds.). *Long-term changes in marine fish populations*. Proceedings of a symposium held in Vigo, November 1986: 161-180.

Steele J.H. and E.W. Henderson. 1984. Modeling long-term fluctuations in fish stocks. *Science*, 224: 985-987.

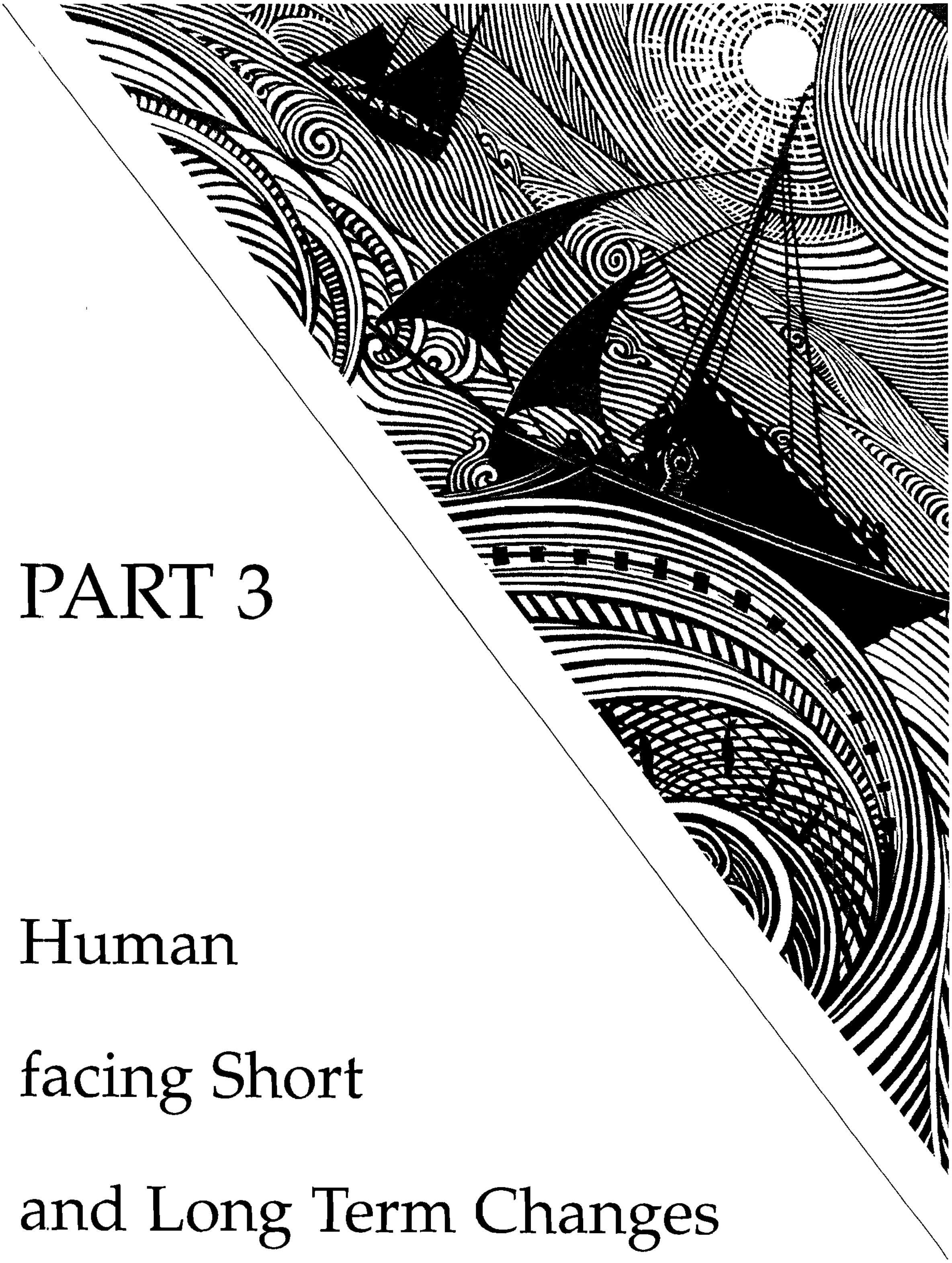
Ulanowicz R.E. 1986. *Growth and development: ecosystems phenomenology*. Springer, New York. 203 p.

Ulanowicz R.E. 1995. Ecosystem trophic foundations: Lindeman exonerata. *In*: B.C. Patten and S.E. Jørgensen (eds.) *Complex ecology*: The Part-Whole Relation in Ecosystems. Prentice Hall, Eaglewood Cliffs, New Jersey, USA.

Ulanowicz R.E. and C.J. Puccia. 1990. Mixed trophic impacts in ecosystems. *Coenoses*, 5(1): 7-16.

Ware D.M. 1992. Production characteristics of upwelling systems and the trophodynamic role of hake. *S. Afr. J. mar. Sci.*, 12: 501-513.

Walsh J.J. 1989. How much shelf production reaches the deep sea? *In*: W.H. Berger, V.S. Smetacek and G. Wefer (eds.). *Productivity of the ocean: present and past*. Dahlem Workshop Reports, Life Sciences Research Report. John Wiley & Sons, Chichester, UK. 44: 175-191.



PART 3

Human
facing Short
and Long Term Changes

Comparative Study of the Dynamics of Small-Scale Marine Fisheries in Senegal and Ghana

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ABSTRACT

The small-scale fisheries in Senegal and Ghana are described and compared. The structure of the canoe fleets, the trends in landing and the composition of catches are analyzed. Located in upwelling areas of the eastern Atlantic, these tropical multispecies fisheries are influenced by a strong environmental signal. Variability and instability of marine resources raise the problem of interactions among the different dynamics of the environment, of fish stocks and of fishing communities. The changes observed during a decade are interpreted from the perspective of the dynamics of the exploitation. Local and global changes were assessed in terms of fishing tactics and strategies that facilitate description of the adaptability of small-scale fishers to the variability of their environment.

RÉSUMÉ

Les pêcheries artisanales du Sénégal et du Ghana sont décrites et comparées. La structure des flottilles, les tendances des débarquements et la composition spécifique des captures sont analysées. Situées dans les zones d'upwelling d'Atlantique est, ces pêcheries tropicales multispécifiques, multiengins sont influencées par une forte composante environnementale. La variabilité et l'instabilité des ressources marines soulèvent le problème de l'interaction entre les dynamiques de l'environnement, des ressources renouvelables et des sociétés de pêcheurs. Les changements observés sur une décade sont interprétés sous l'angle de la dynamique du système d'exploitation. Les changements locaux et globaux sont abordés en termes de tactique et de stratégie de pêche qui permettent de décrire l'adaptabilité et la flexibilité des pêcheurs artisans aux fluctuations de leur environnement.

INTRODUCTION

This paper presents a comparative study of the small-scale fisheries of Senegal and Ghana, from the point of view of the dynamics of exploitation. With respect to fisheries, Senegal and Ghana have at least two things in common: a coastal upwelling system and an important small-scale fishery. The small-scale fisheries of Senegal and Ghana are the largest in West Africa and are among the most important economic activities in these countries. In terms of landings, these small-scale fisheries are the most important in the West African region (Everett and Sheves, 1991) and contribute over 70% of the total catch of fish in each of the two countries. The per-capita consumption of seafood per year is similar in the two countries, being about 25 kg per year (Horemans, 1993). The small-scale fisheries of Senegal and Ghana bear a number of other resemblance, notably in the way they changed over the years.

The main objective of this study is to establish a synoptic description of the fisheries with regard to the structure of their fleet and catch compositions. The evolution of the two fisheries in the last decade is compared, to analyze the responses to changes in their environment and to distinguish global and local changes.

Data on marine small-scale fisheries have been collected through sampling for over twenty years in Senegal and Ghana. The statistics used in this study were obtained from catch assessment surveys and canoe censuses that have been undertaken simultaneously since the beginning of 1980s. The statistics were gathered and preprocessed by the Research & Utilization Branch of the Fisheries Department (FRUB) at Tema in Ghana, and by the Centre de Recherches Océanographiques de Dakar-Thiaroye (CRODT) in Senegal.

1. CHARACTERISTICS OF SMALL-SCALE FISHERIES IN SENEGAL AND GHANA

Situated respectively in the northern and central part of the eastern central Atlantic, Senegal and Ghana are two West African countries separated by thousands of kilometers (Fig. 1); yet they have similar important small-scale fisheries. These fisheries have a long history and have undergone great changes during the last thirty years, especially the introduction of outboard motors and the development of the purse seine nets (Koranteng, 1992; Kébé, 1995).

Many types of fishing gears are used by small scale fishers. In both countries, small-scale gears are classified into five groups: purse nets, drifting gill nets, set nets, hooks-and-lines and beach seines. The group named 'others' includes diverse gears, such as traps or jigs for cuttlefish in Senegal, or no gear (with canoes used only for trans-shipment of catches).

Fig. 1: Location of Senegal and Ghana in Africa.

Table 1 gives the percentage of canoes in each type of fishing gear as enumerated in the most recent census in each country. The following features may be noticed:

i.) a large proportion of nets for small pelagic fishes in Ghana;
ii.) a large proportion of canoes with line gear in Senegal;
iii.) an almost equal proportion of canoes with set nets in Ghana and Senegal;
iv.) a much smaller proportion of canoes with drifting gill net and beach seines in Senegal compared to Ghana.

In Ghana, the common fishing craft is a dugout canoe carved out of a single trunk of wood. These canoes are symmetrical in shape, double-ended and range in sizes between 3 and 18 m long and 0.5 to 1.8 m wide. About 49% of the over 8 600 Ghanaian canoes are motorized, using outboard engines of between 25 and 40 hp (Koranteng *et al.*, 1993). The level of motorization depends on the size of the canoe and on the gear operated. For example the canoes operating purse nets are usually large and almost all of them are motorized. The engine is put on the side (normally on the right), at the rear of the canoe.

Senegalese canoes are almost completely planked except for the area close to the 'keel' which is carved out of a small log. The evolution of the canoe was dictated by geographic constraints, especially by the presence of a strong surf along the northern coast (Chauveau, 1984). The outboard engine is mounted at the rear or at the stern of the canoe through an incision made to the hull. About 90% of the 5 600 canoes used for marine fishing in Senegal are motorized (Kébé, 1995; Samba, 1995). The canoes operating pursing gears and long-range line with insulated ice boxes have outboard engines from 25 to 40 hp; canoes with line, set net or beach seine generally use outboard motors of 8 up to 15 hp (Ferraris, 1993).

In Senegal, the total number of canoes recorded for each gear is usually larger than the total number of operational canoes. This is because one fishing unit may have several gears and undertake different fishing activities depending upon the target

Feature	Ghana	Senegal
Length of the coastline	550 km	700 km
Number of fishing villages (N)	189 including 306 landing beaches	155 including 96 villages with marine canoes
Number of fishers	96,400	≈ 35,000
Number of marine canoes ($Q = \Sigma q_i$, i=1 to N)	8,688	5,661 (north of Sine Saloum in warm season)
Index of canoes distribution Shannon index $(- \Sigma ((q_i/Q) \log_2(q_i/Q))/\log_2 N$	0.902 (1989)	0.802 (maximum value in warm season 1988)
Gears (as % of canoes)		
Purse Seine (PS)	39.8	8.6
Drift Gill Net (DGN)	2.9	0.1
Set Net (SN)	29.7	25.9
Hand-Line (LN)	11.9	59.5
Beach Seine (BS)	8.9	1.3
Miscellaneous (DIV)	6.7	10.0
Catches ($t.10^3$)		
Pelagic	261	271
Demersal	46	46

Table 1: Main characteristics of the small-scale fishery sectors in Ghana and Senegal (1992).

species. This phenomenon of rapid gear switching is one characteristic of small-scale fisheries. In Ghana, only the main gear is taken into account during the census, but several cases of gear switching between set net and line or between the small-pelagic nets ('ali', 'poli' and 'watsa' nets) have been observed (Koranteng, 1990). Many fishing units may also have a set net. The joint utilization of different gears during the same fishing trip is best observed in the strategy of Senegalese fishers.

Migration is an important characteristic feature of small-scale fisheries in West Africa. According to Chauveau (1990), migration of fishers from the Gold Coast (now Ghana), for example, had been recorded by the beginning of the 20th century. Today, Ghanaian fishers may be found in many countries in West and central Africa, especially in Togo, Benin, Cameroon, Côte-d'Ivoire and Guinea. Senegal is also a net 'exporter' of migrant fishers (Diaw, 1991). Senegalese fishers may be found in Mauritania, Guinea, the Gambia, Guinea-Bissau and in other countries in West and central Africa. Distribution, abundance and movement of fish and fish schools are some of the factors that induce migration of fishers. Others are social and economic factors (Odotei, 1991; Haakonsen and Diaw, 1991; Koranteng *et al.*, 1993).

These migrations have, in part, contributed to the diffusion of small-scale fishing technology, skill and expertise. For example, it appears that the storage of fish in insulated, removable fish-holds on canoes was spread in the region by migrant fishers. Ghanaian fishers may have learnt this technique from their Senegalese counterparts in conjunction with long-range and long-duration line fishing. Another example of technology transfer through migration of fishers is the 'chorkor' smoking oven, which originated from a fishing village in Ghana but is now known throughout the West African region (Odotei, 1991; Koranteng, 1995). The major technical innovations have an impact on the relations between producers and tradesmen and consequently on the small-scale fisheries development (Lawson and Kwei, 1974).

Movement of fishers with their canoes also has serious effect on the assessment of the quantity of fish caught by the small-scale fishing fleets (Koranteng, 1992). In Ghana, small-scale fishers land their catches at a certain spot at the end of a daily trip, then return home with empty canoes. Assessment of catches is made by sampling and such an act introduces sampling and coverage errors in the estimations. Therefore, it is important to classify fishing villages between landing and refuge sites and to know and understand the temporal migratory flows between regions. As migration is influenced by variation of fish availability, considering a stable fleet during a long time might underestimate total catches because the migrant canoes are then associated with less productive regions and the most productive regions with an underestimated fleet (Ferraris, 1994).

The oceanographic regime of the Ghanaian and Senegalese coastal waters is characterized by seasonal upwellings. In Ghana, a major upwelling occurs for approximately three months each year, beginning late June or early July and ending in late September or early October, and a minor upwelling occurs three weeks either in January or February (Mensah and Koranteng, 1988). The Senegalese coast is under the influence of the trade winds which create local upwelling conditions and give rise to two main seasons: a cold season from December to May and a warm season from July to October (Roy, 1992). During the upwelling season, biological activity is high and most fishes, both demersal and pelagic, spawn and migrate. Stock availability and catchability are thus variable in the course of the year. These events result in variability in landings.

2. FLEET STRUCTURE AND DYNAMICS

The number of canoes at each landing area or village is obtained from the census of canoes which are conducted once in 2-4 years in Ghana and twice a year in Senegal. The census, also referred as 'frame surveys', form the basis of catch assessment surveys involving the small-scale fishing crafts.

The structure of the Ghanaian fleet (Fig. 2) shows marked differences in gear composition on regional basis. This is due to differences in specialization of the different ethnic groups. There are four regions for small-scale marine fisheries in Ghana (Volta, Greater Accra, Central, and Western; Fig. 4) and each region presents the characteristic gears of the dominant ethnic groups (Ewe, Ga, Fanti). The occurrence of a particular type of gear in a particular location is determined by the target species (Bennaseck, 1986). The same phenomenon is observed in the Senegalese small-scale fishery, pursued by three principal ethnic communities with long fishing tradition. These are the Wolof, Lebou, and Sérère-Nyominka, originating from Saint-Louis (Fleuve), Cap-Vert or Thies-Sud region and the Sine-Saloum Islands respectively (Fig. 5).

The frame surveys undertaken in Ghana show a relative stability in the structure of each region's canoe fleet (Fig. 2). For the country as a whole, the number of canoes increased by 25% between 1981 and 1992. The number of canoes dropped significantly in 1981, due to migration of fishers to neighbouring countries, possibly as a result of unfavorable economic conditions in Ghana at the time (Odoi-Akersie, 1982). Since 1986, the number of canoes operating drift gill nets has generally decreased. This decline has been attributed to the excessive and rising cost of operating this gear (Koranteng *et al.*, 1993). Another possible reason is that with the gradual depletion of the 'wawa' tree from which the dug-out canoes are produced, worn out large canoes are not being fully replaced (Wayo Seini, 1995). On the other hand, set net canoes have increased in number by about 50%. It is possible that the canoes used for techniques showing a decline may now be used for set net fishing.

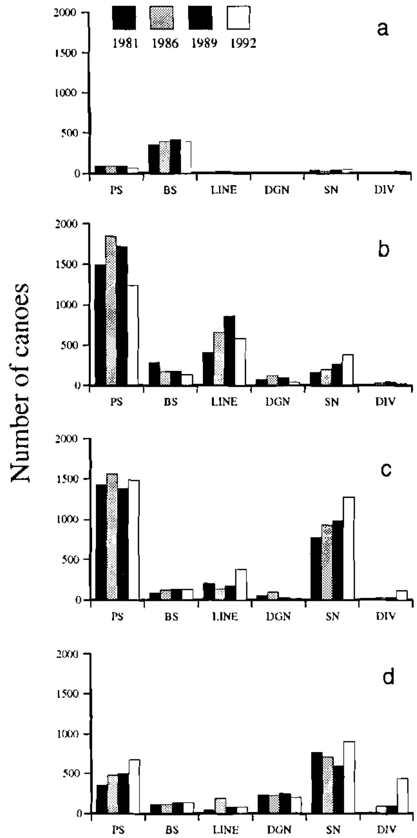


Fig. 2: Structure of the small scale fleet in Ghana: number of canoes by gear and by region from 1981 to 1992 (PS: Purse Seine, BS: Beach Seine, LINE: Hand Line, DGN: Drift Gill Net, SN: Set Net, DIV: Miscellaneous).
a) Volta; b) Greater Accra; c) Central; d) Western.

In Senegal (Fig. 3), there was an increase of 40% in the total number of canoes from 1982 to 1992. The increase was particularly important between 1989 and 1992 with the return of migrant fishers as a result of political conflict between Senegal and neighbouring Mauritania. The increase in line fishing in Senegal is due to the development of the activity of large canoes equipped with insulated ice boxes. Fishing is done far away from home bases. The increase of these canoes may be the sign that fishers prospect for new fishing places. There is the same phenomenon in Ghana, where 157 canoes with insulated removable fish-holds were counted during the frame survey in 1992 (Koranteng *et al.*, 1993).

The fleet structure established through the frame surveys exhibits seasonal variation. For example, in Ghana, the number of canoes with net for catching small pelagic species and located at specific landing beaches, reflects the seasonal pattern of the upwelling (Fig. 6a). This temporal variability in canoe numbers is well marked in the regions on the western part of Ghana where the sardinella season usually starts from (Ferraris and Koranteng, 1995). Fishers from other parts of the country migrate to the west at the onset of the sardinella season. The large fluctuations that occur annually correspond to migration of canoes within and between regions. This movement used to be very important during the major upwelling period (July-September) but in the last decade migration during the minor upwelling season (January-February) has also been remarkable. This could be linked to the increasing importance of the minor upwelling and the resulting increase in the production of sardinellas in the western Gulf of Guinea (Pezennec, 1995).

Fig. 3: Structure of the small scale fleet in Senegal: number of canoes by gear and by region from 1982 to 1992 - in warm season (PS: Purse Seine, BS: Beach Seine, LINE: Hand Line, DGN: Drift Gill Net, SN: Set Net, DIV: Miscellaneous.
a) Fleuve; b) Thies Nord; c) Cap Vert; d) Thies Sud.

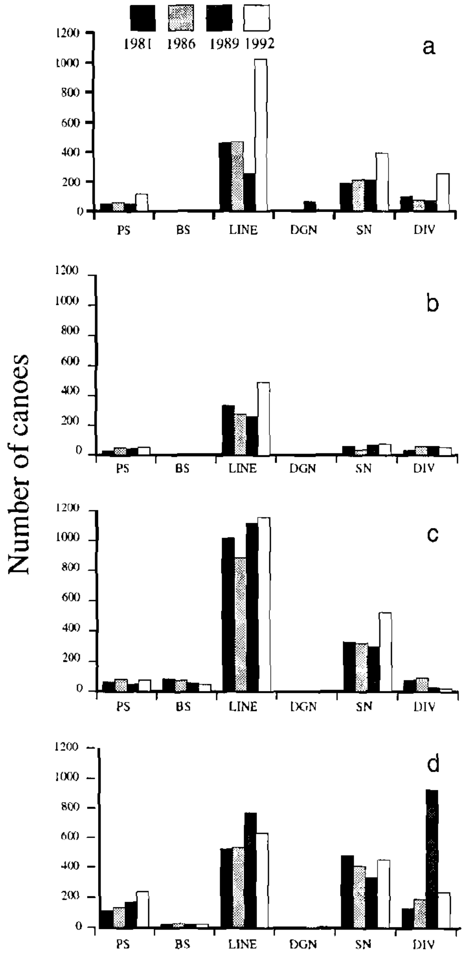
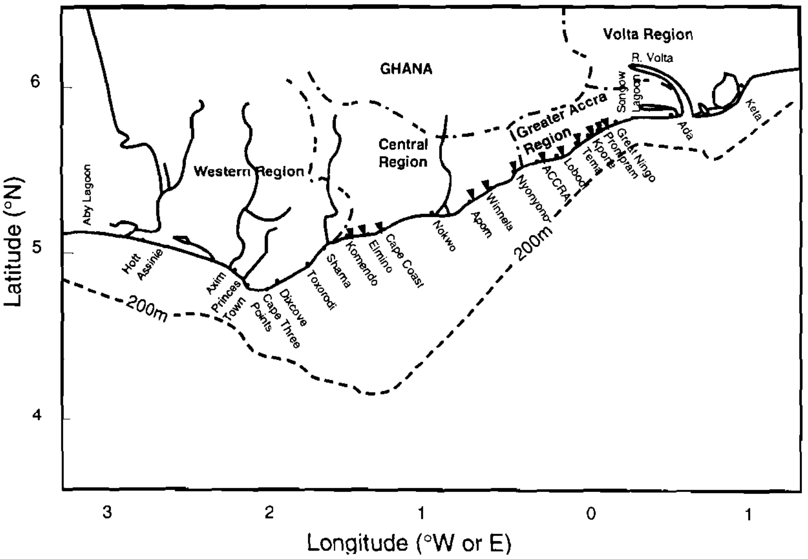


Fig. 4: Map of the Ghanaian coast, showing the four coastal regions considered here.



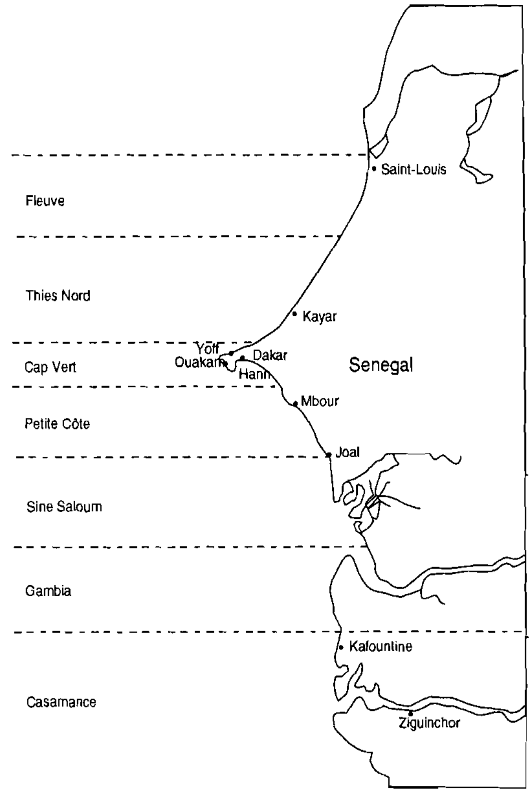


Fig. 5: Map of the Senegalese coastline showing the coastal regions considered here.

The same phenomenon of seasonal variation in the fleet is observable in Senegal (Fig. 6b). Here the profile of number of canoes in the Thies Nord region is complementary to that of the Fleuve region: during each upwelling season, some fishers migrate from the Fleuve region to the Thies Nord region and they return home after the upwelling period. This is related to seasonal migration of Saharian fish species such as grouper (*Epinephelus aeneus*), which migrate south and are then distributed all along the Senegalese shelf until the cold upwelled waters are replaced by warm tropical waters (Cury and Roy, 1988). Since 1991, a movement of fishers from the Thies Sud region to the Fleuve region is noticeable. These fishers, who have been in Senegal since the warm season 1989 (after the conflict with Mauritania), went back to Saint-Louis because of the reopening of the border, and also because of good fishing conditions in the north of Senegal during that time.

With a smaller coastline Ghana has two times the number of fishing villages as in Senegal and a larger number of fishers and canoes (Table 1). The distribution of canoes along the coast was measured by the Shannon index which depends on the relative number of canoes per landing beach (Table 1). This index is usually used in ecology to measure the diversity of species (Pielou, 1975). In this case, it was calculated during the period of low migration. The index was found to be higher in Ghana than in Senegal indicating that canoes are distributed more evenly along the Ghanaian coast than along the Senegalese coast. In Senegal, the canoes are concentrated in about ten main landing centers which are close to consumption centers with road infrastructure. As the distribution of canoes varies between the seasons, the index is low during the cold season when the fishers are concentrated in a few strategic centers. For example, in Kayar located in the Thies Nord region of Senegal, the number of canoes is two times as high during the upwelling period than during the warm season. In Ghana, large fluctuations of canoe numbers are observed at important centers like Elmina (Central

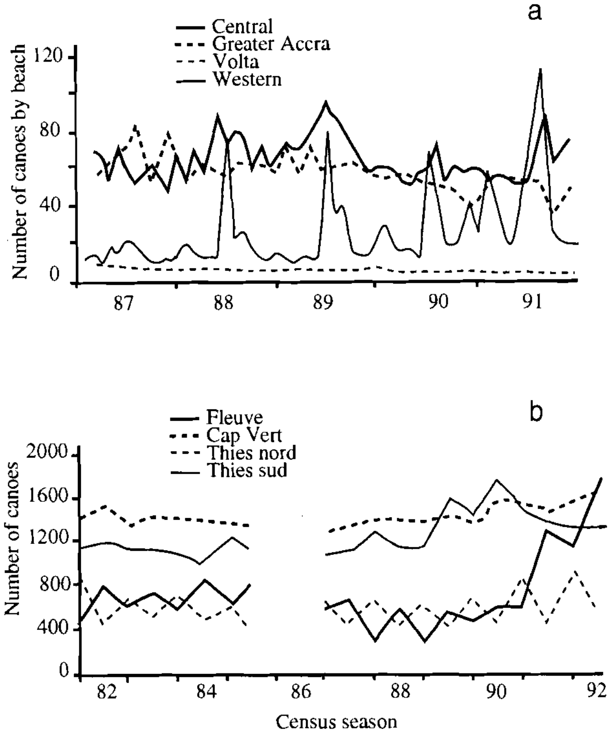


Fig. 6: Seasonal variation in the structure of the artisanal fleet by region in Ghana and Senegal.
a) Average number of canoes using pursing nets in Ghana;
b Total number of operational canoes in Senegal.

Region) and Sekondi (Western Region). Large canoe populations at these centers correspond to the sardinella season when many canoes migrate towards centers that are close to the bulk of the migrating fish and where they are likely to find market and better price for their catch (Ferraris and Koranteng, 1995).

In the last decade or so, the small-scale fisheries of the two countries have also undergone changes in nature as well as in the population of fishing craft. After the decline of the sardinella fishery in Ghana in the early 1970s, a classical case of technological innovation took place: the purse seine-type 'poli' net was developed from the 'watsa' ring net to catch anchovies (Koranteng, 1992). Today, poli net is the major fishing gear used in the sardinella fishery in Ghana. Long-range line fishing has also increased considerably. Some large-sized canoes that were used for purse seining may have been converted into long-range line canoes. These canoes carry ice and stay at sea for about three days (Koranteng, 1990). Set net fishers have also adopted the habit of attaching hooks on lines to the leadline of their nets (Koranteng, 1995).

In Senegal, the number of gears in all categories but 'line' and 'diverse' decreased between 1985 and 1989, due to a transfer of fishing effort to the exploitation of cephalopods as the biomass of octopus increased (Samba, 1995). New fishing methods for cuttlefish, traps and jigs were introduced in Senegal from Japan in 1975. With the increase of octopus stock size, the fishers adapted cuttlefish jigging for this species.

These changes reflect the nature of small-scale fisheries, in which there is the propensity for innovation by the fishers themselves, in response to changing circumstances.

3. TOTAL LANDINGS AND COMPOSITION OF CATCHES

Figure 7 shows the trend of fish landings by small-scale fishers in Senegal and Ghana from 1981 and 1992. The catch of small-scale fishers are composed mainly of pelagic fish species, although some demersal species are also caught. For example in 1992, pelagic species accounted for over 85 percent of the landing in each country (over 260 000 t). About 46 000 t of demersal fishes were landed by the small-scale fishers in each of the two countries in the same year (Table 1).

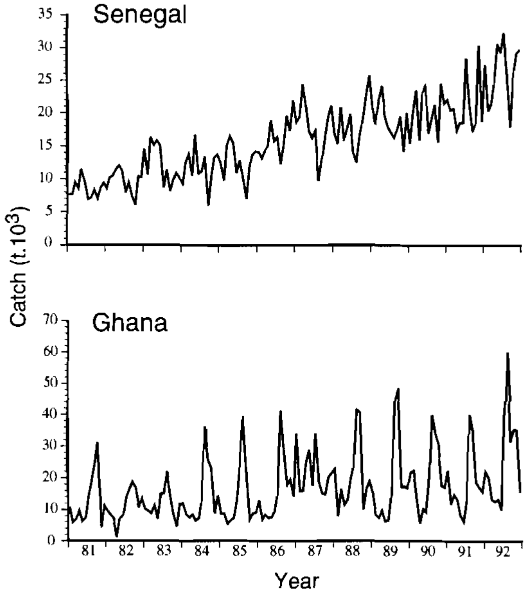


Fig. 7: Total catches of the small-scale fisheries in Senegal and Ghana from 1981 to 1992.

The changes in the composition of catches may be analyzed to detect changes in target species (Fig. 8, 9). In Ghana, the catches of pelagics are dominated by Engraulidae and Clupeidae (Fig. 8). The quantity of sardinellas and anchovies, therefore, greatly influence the percentage composition of the year's landings (Fig. 10a). *Sardinella aurita* is more abundant than *Sardinella maderensis*. Other important pelagic groups in the Ghanaian small-scale fishery are the Scombridae, Carangidae and Istiophoridae.

The pelagic catches in Senegal are dominated by Clupeidae (Fig. 8). The increase in landings since 1985 is due to *Sardinella aurita* (Fig. 11). At the beginning of the decade, catches of purse seine nets were relatively more diversified but less important than presently. Quite noticeable are the catches of bluefish (*Pomatomus saltator*) by purse seine and line gears, a species which disappeared after 1983. Samba and Laloë (1991) found a relation between bluefish catches, upwelling intensity and sea surface temperatures, supporting the idea that the upwelling is a favourable factor determining the migration pattern of migrant Saharian species in Senegal.

In the demersal sector, two families dominate the landings in Ghana (Fig. 9), the Pomadasyidae and the Sparidae. From 1973, the triggerfish (*Balistes capriscus*) became important in the landings of trawlers in Ghana (Mensah and Koranteng,

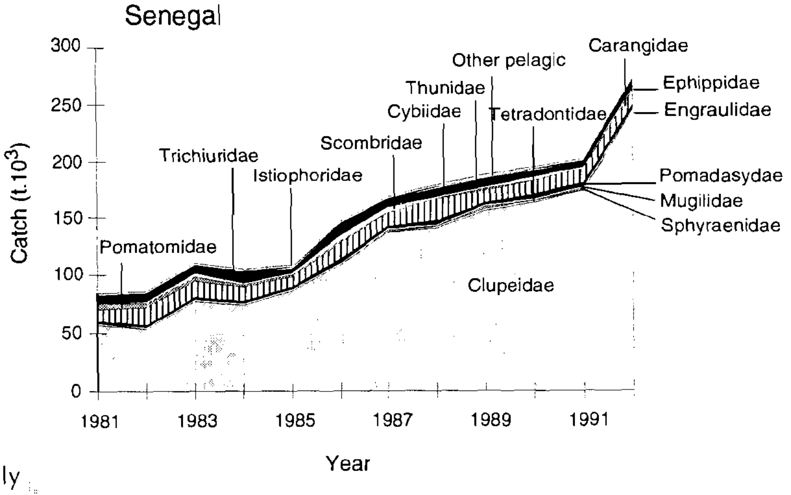
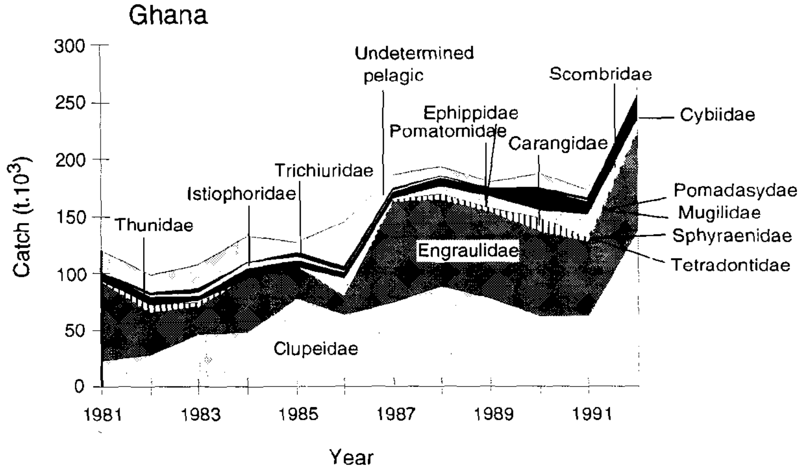
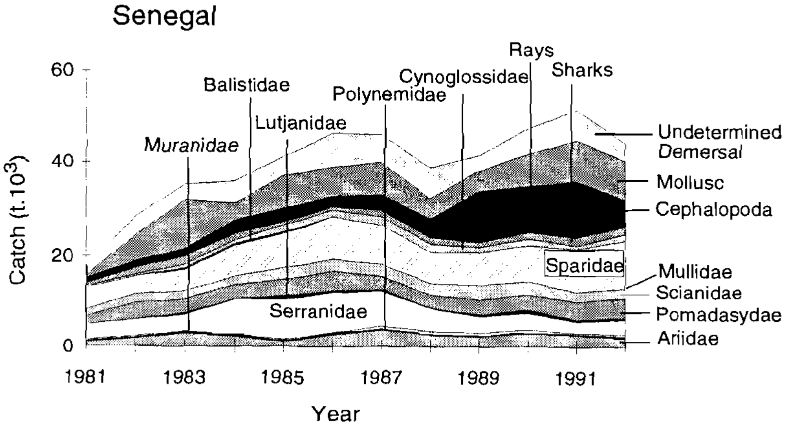


Fig. 8: Pelagic catches, by family and country from 1981 to 1992.



1988). However, the proliferation of triggerfish in the Gulf of Guinea did not show up early in the landings of small-scale fishers. Later increases of triggerfish in the landings of the canoes followed an increase in demand of the fish as a result of improvement in its utilization. The increase of triggerfish in the landings of small-scale fishers resulted essentially from trade between small-scale and industrial fishers on the high seas, with the former buying the catch from the latter. Triggerfish resources in the whole of the Gulf of Guinea have declined hence the reduction in landings of the species by the Ghanaian small-scale fleet since 1988 (Fig. 9). The increase in the landings unidentified demersal species by canoes in Ghana is also noticeable since 1987 (Fig. 9, 10). *Brachydeuterus auritus* (Pomadasyidae) and *Pagellus bellottii* (Sparidae) dominate demersal fish landings by small-scale crafts.

In the last decade, the demersal catches of Senegalese small-scale fishers were dominated by Serranidae, Sparidae and molluscs (Fig. 9). The increase in octopus catches since 1989 reflects the interest of fishers for a new target species



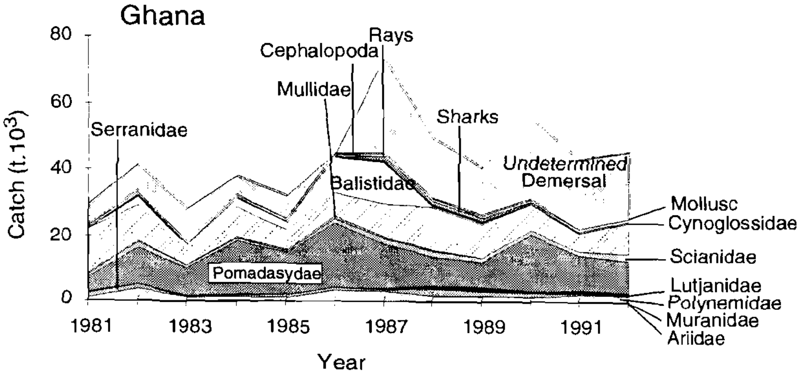
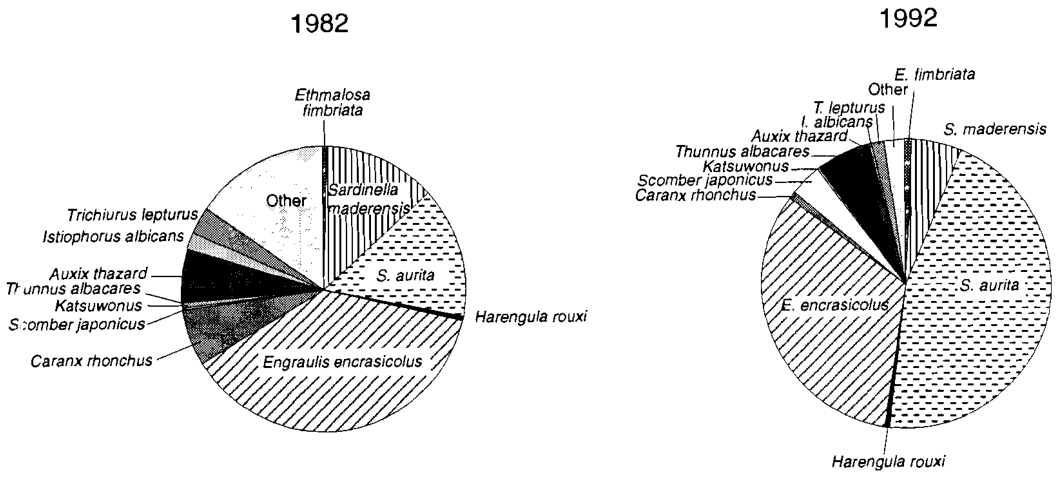


Fig. 9: Demersal catches, by family and country from 1981 to 1992

resulting from the increase in biomass of this species since 1986 (Caverivière, 1995a) and from the development of a market for octopus. There was a simultaneous decrease in the landings of groupers (Serranidae). At the end of the decade, catches of Sparidae (mainly of the genus *Pagellus* and *Sparus*) have increased with expansion of the export market and improvement in the organization of trading (Kébé, 1995). The increase in the landings of rays was a result of the introduction of long line fishing with multiple hooks and the development of the export of processed small-scale catches (Samba, 1995). The changes in catch composition of the line fishery shows a decrease in pelagic species following the disappearance of bluefish (Fig. 11).

There has never been a lucrative market for triggerfish in Senegal and the landings by the small-scale fleet were not important even though this species was abundant in the south of Senegal at the beginning of the 1980s (Caverivière, 1995b), then in the north. However, a trade between small-scale and industrial fishers at sea, similar to what has been observed in Ghana for the triggerfish also occurs in Senegal for cephalopods.

(a) PELAGIC SPECIES



(b) DEMERSAL SPECIES

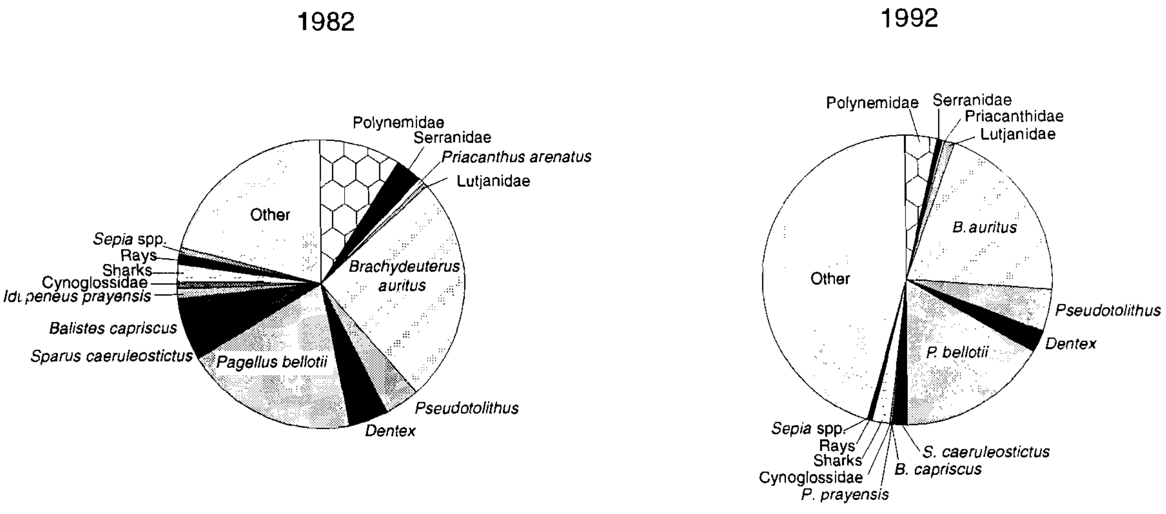
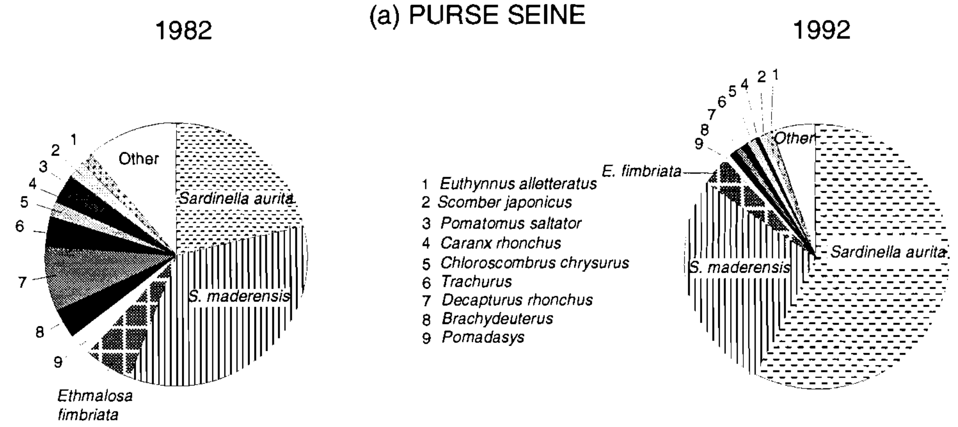
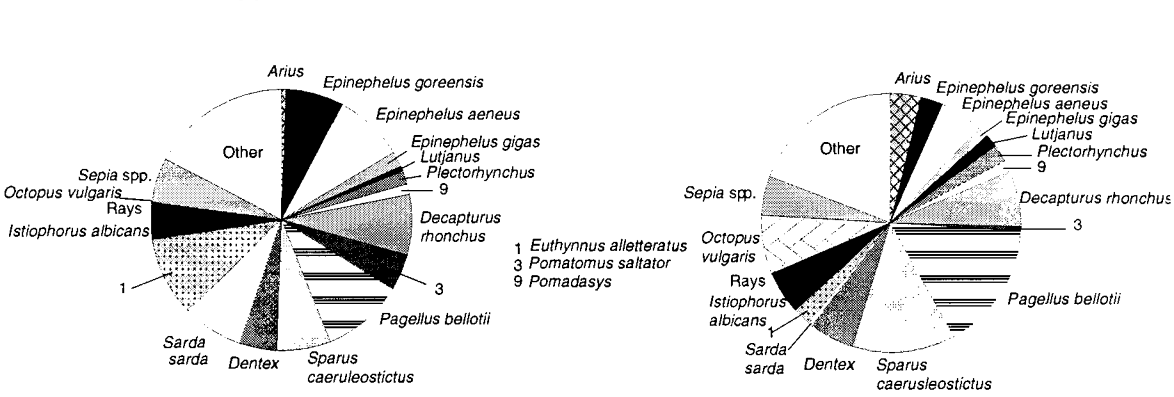


Fig. 10: Changes of species diversity of artisanal fish landings of Ghana, 1981and 1992; a: Pelagics; b: Demersals.

(a) PURSE SEINE



(b) LINE



(c) SET NET

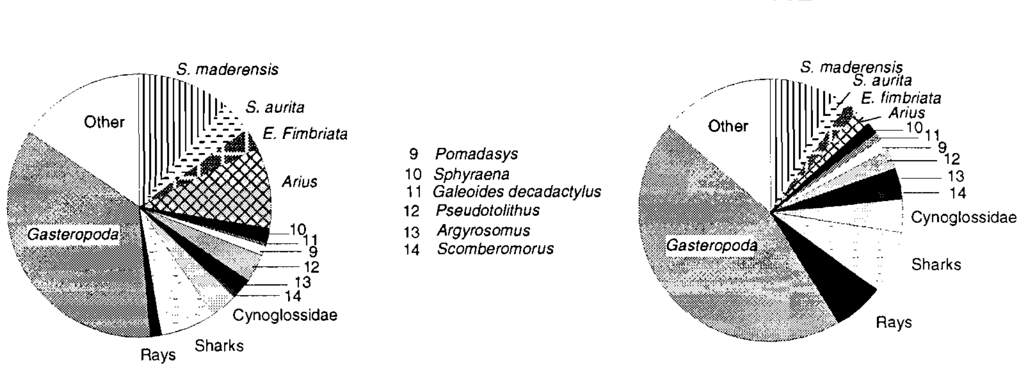


Fig. 11: Changes of species diversity, by gear, of artisanal fish landings of Senegal, 1981 and 1992; a: Purse seines; b: lines; c: set nets.

The species composition in the landings of set net and line fishing in Senegal (Fig. 11) shows a great diversity that reflects differences in target species which depend on the following factors:

i.) kind of set net (for soles, gastropods, sharks or rays, surface or bottom setting);

ii.) fishing season (line fishers target *Istiophorus* in the warm season and *Epinephelus* in the cold or upwelling season);

iii.) fishing practices in accordance with ecological characteristics, fishing villages, ethnic groups, etc. (e.g., in Kayar, Wolof fishers prefer to catch species such as *Pomatomus* or *Pagellus* with line and sole with set net whereas Lebou fishers prefer *Epinephelus aeneus* and do not use fixed gear such as set net).

4. DISCUSSION

The study of changes in the small-scale fisheries in Ghana and Senegal shows in both cases an expanding sector. The two upwelling systems in Senegal and Ghana induce similar characteristics in the small-scale fisheries; particularly a dominant fishery for small pelagic fish species. However, there are differences in species diversity. Environmental variability, a consequence of the upwelling fluctuations, results in uncertainty and instability in marine resources and raises the problem of interactions between the dynamics of the environment, fish stocks and fisher communities (Cury and Roy, 1991).

In the face of variability, small-scale tropical fisheries are characterized by their dynamics and adaptability. Small-scale fishing units have flexibility and ability to switch between various target species in response to trends in relative abundance of fish and to changes in market preference or technical innovation. The situation where a wide range of target species is exploited by boats, shifting seasonally or from one trip to another, is often described as the likely ultimate stage of development of industrial multispecies fisheries. Paradoxically, small-scale fisheries fall into this category (Gulland and Garcia, 1984).

Studies of long-term fishery development often show a 'fishing-up' sequence with an expansion of the fishery as fishers become more mobile and shift their effort to other species in response to a decline in landings of preferred species (Deimling and Liss, 1994). The fact that fishers in Senegal and Ghana developed canoes with insulated ice-boxes to exploit remote fishing grounds or adapted to joint utilization of fishing gears is, perhaps, a sign of the 'fishing-up' sequence in response to yields decrease. But migration and the use of a multiple fishing gears are two intrinsic characteristics of tropical multispecies small-scale fisheries. These characteristics, given alternatives, give them flexibility and provide stability.

There are similarities in nature, extent and evolution of the small-scale fisheries in Senegal and Ghana. In the comparative study of the evolution of these two fisheries over a decade, three principal factors were identified as common responses to changes in the environment. These are:

i.) Migrations: motivated by various causes (socio-economic or biological); they are either short- or long-term, between countries in the sub-region, or between regions within one country;

ii.) Technological mutations: introduction of new technology, innovation, knowledge transfer;

iii.) Switching and joint utilization of fishing gears.

For Senegalese fishers, Laloë and Samba (1990) identified two types of reactions: the strategic (migration and technological choice) and tactical (switching of effort depending on resource availability or market opportunities). The dynamics of exploitation is thus approached in terms of strategy and tactics. A model was developed to describe the dynamics of the small-scale fisheries in Senegal on the basis of a stock production model adapted for the multispecies and multigear fisheries (Laloë and Samba, 1991). In this model, the terms 'tactics' and 'strategy' are used to describe the decision making process of fishers in response to accessibility of resource, biomass changes, variations in market and/or socio-economic factors. A second model is being developed to simulate decision-making in the Senegalese small-scale fishery on the basis of an expert system and object-oriented formalism, where the whole fishery is viewed from a systemic point of view (Le Fur, this vol.).

The development of the fishery must be studied in a natural-cultural context where each fishery system is composed of interacting factors of physico-chemical, biological and cultural nature (Deimling and Liss, 1994). Catch is reflective of natural factors which create varying levels of abundance of species, and reflective also of cultural factors such as fishing technology, fisheries economics and market preferences. Catch is thus a product of the entire natural-cultural system.

From the point of view of fishing operation, catch is the result of the choice of one gear, one fishing place and one target species. The choice of these three factors may be presented as a tactical decision that needs to be taken by the fisher before or during a fishing trip. Ferraris (1995) defines 'tactics' as a combination of fishing grounds, target species and gears. One can study changes of fishery dynamics in the short term. 'Strategy' is defined as a set of tactics. This concept integrates fishing activity in a given period of time and allows the study of fishing dynamics on a longer term. Local and global changes, from a temporal point of view, may then be interpreted in terms of tactics and strategy. Tactics permit the analysis of the dynamics on the basis of daily fishing activity; a change in tactics is interpreted as a response to some local change in the fishers' environment. Strategy permits the analysis of the dynamics of a fishery on a seasonal or annual basis. A change in strategy reflects changes in global fishing conditions and it impacts on available tactics. However, a local change, for example the introduction of new tactics, may have an impact at the global level.

The responses to biological, ecological or socio-economic changes observed in the Senegalese and Ghanaian fisheries may also be described on a spatial scale. Local changes have reference to spatial peculiarities due to the natural-cultural system and the history of each fishery. Global changes, on the other hand, generated similar changes observed in the two countries. The local dimension refers to the specific tactics and strategies of each fishery, while global dimension led to common responses. Despite observed differences in the small-scale fisheries in the two countries, the changes observed on a decadal basis underline some generic fishing behaviors. These global changes may be due to similar changes in the natural system (e.g., increase in *Sardinella aurita* abundance, proliferation of triggerfish, development of cephalopods, etc.) or in the human system (e.g., the opening of export market and increasing domestic demand related to human demographic growth).

CONCLUSION

The study of the small-scale fisheries in Ghana and Senegal, through the structure and evolution of fleets and catches, underlines the importance of a good understanding of the dynamics of exploitation. The fishers' ability to adjust their activities and to react to perturbations in their environment confer on multispecies and multigear small-scale fisheries great flexibility and stability. The opportunistic behavior of the fishers may give some signals about the condition of the system and the wealth of the resource. Therefore, from a fisheries management point of view, it is important to better understand the reaction of fisher facing changes (Hilborn and Walters, 1992).

Comparative studies of the dynamics of the small-scale fisheries in Senegal and Ghana underlines three important factors in the fishing decision-making: fishing location, fishing gear and target species. The dynamics of the fisheries may be studied by these three factors, expressed in terms of tactics and strategy. Changes in species composition of catches and volume of landings were observed. However, changes in fishing strategy and in landings may be confused with 'real' changes in species composition or abundance. Similar migratory behaviors by fisher, resort to the use of a multiplicity of gears and technological mutation were identified. Thus we found, the specificity and common characteristics of the two fisheries facilitated the study of the dynamics of exploitation in the context of local and global changes.

REFERENCES CITED

Bernaseck G.M. 1986. Profile of the marine resources of Ghana. *CECAF/TECH, 86/71*, 105 p.

Caverivière A. 1995a. Le poulpe (*Octopus vulgaris*) au Sénégal: une nouvelle ressource. *In*: *Evaluation des ressources exploitables pour la pêche artisanale sénégalaise.* Coll. et Séminaires, ORSTOM: 245-257.

Caverivière A. 1995b. Les fluctuations d'abondance du baliste (*Balistes carolinensis*). *In*: *Evaluation des ressources exploitables pour la pêche artisanale sénégalaise.* Coll. et Séminaires, ORSTOM: 257-264.

Chauveau J.-P. 1984. *La pêche piroguière au Sénégal. Les leçons de l'histoire.* Revue Mer, n° spécial, automne 1984, 19 p.

Chauveau J.-P. 1990. The historical geography of fisheries migrations in the CECAF region (end XIX century to 1980's). *In*: J. Haakonsen and M. Diaw (eds.). *Fishermen's migrations in west Africa*, IDAF/WP/36, IDAF Project (FAO), Cotonou, Benin: 12-35.

Cury P. and C. Roy. 1988. Migration saisonnière du thiof (*Epinephelus aeneus*) au Sénégal: influence des upwellings sénégalais et mauritanien. *Oceanologica Acta*, 11(1): 25-36.

Cury P. and C. Roy. 1992 (ed.). *Pêcheries ouest-africaines: variabilité, instabilité et changement.* ORSTOM, Paris, 525 p.

Deimling E. and W. Liss. 1994. Fishery development in the eastern North Pacific: a natural-cultural system perspective, 1888-1976. *Fish. Oceanogr.*, 3 (1): 60-77.

Diaw M. C. 1991. Migrant fishermen from Casamance and southern river areas. *In*: J.M. Haakonsen and M.C. Diaw (eds.). *Fishermen's migrations in west Africa.* IDAF/WP/36, IDAF Project (FAO), Cotonou, Benin: 77-93.

Everett G.V. and G.T. Sheves. 1991. *Recent trends in artisanal fisheries and report on alternatives to canoes.* IDAF/WP/40, IDAF Project (FAO), Cotonou, Bénin, 33 p.

Ferraris J. 1993. *La pêche artisanale au Sénégal: atlas de variabilité spatio-temporelle.* Doc. int. CRODT. 79 p.

Ferraris J. 1994. *A critical look at the survey system on artisanal fisheries in Ghana.* Document de travail, Grand Programme Sardinelle, ORSTOM/CROA/FRUB, 29 p.

Ferraris J. 1995. Démarche méthodologique pour l'analyse des comportements tactiques et stratégiques des pêcheurs artisans sénégalais. *In*: F. Laloë, H. Rey and J.L. Durand (eds.). *Questions sur la dynamique de l'exploitation halieutique.* Colloques et Séminaires, ORSTOM: 263-293.

Ferraris J. and K. A. Koranteng. 1995. Statistical analysis of canoe fishery data in Ghana with particular reference to sardinellas. *In*: F.X. Bard and K. Koranteng (eds.). *Dynamics and uses of sardinella resources from upwelling off Ghana and Côte-d'Ivoire.* Colloques et Séminaires, ORSTOM: 205-22.

Gulland J.A. and S. Garcia. 1984. Observed patterns in multispecies fisheries. *In*: R.M. May (ed.). *Exploitation of marine communities.* Dahlem Konferenzen 1984. Berlin, Heidelberg, New York, Tokyo, Springer-Verlag: 155-190.

Haakonsen J.M. and M.C. Diaw. 1991. *Fishermen's migrations in west Africa*. IDAF/WP/36, IDAF Project (FAO), Cotonou, Benin. 307 p.

Horemans B. 1993. *La situation de la pêche artisanale en Afrique de l'ouest en 1992*. Cotonou, DIPA/WP/47, 36 p.

Hilborn R. et C.J. Walters. 1992. *Quantitative fisheries stock assessment. Choice, dynamics and uncertainty*. Chapman and Hall, N.Y., Lond., 570p.

Kébé M. 1995. Principales mutations de la pêche artisanale maritime sénégalaise. *In*: *Evaluation des ressources exploitables pour la pêche artisanale sénégalaise*. Colloques et Séminaires, ORSTOM: 43-58.

Koranteng K.A. 1990. *Ghana canoe frame survey, 1989*. Inf. Rep., Fish. Res. & Util. Branch, Tema, Ghana, 25, 57p.

Koranteng K. A. 1992. *The marine artisanal fishery in Ghana, recent developments and implications for resource evaluation*. Paper presented at the World Fisheries Congress, Athens, Greece, May 3-8, 1992.

Koranteng K. A. 1995. *Marine artisanal fisheries in Ghana and Senegal - similarities and differences*. Paper presented at the Workshop on 'Evaluation des ressources exploitables pour la pêche artisanale sénégalaise'. CRODT, 8-13 February 1993.

Koranteng K. A., O.O. Nmashie and A. N. A. Baddoo. 1993. *Ghana canoe frame survey, 1992*. Inf. Rep. Fish. Res. & Util. Branch, Tema, Ghana, 28, 48 p.

Laloë F. and A. Samba. 1990. *La pêche artisanale au Sénégal: ressources et stratégies de pêche*. ORSTOM, Etudes et Thèses, 393 p.

Laloë F. and A. Samba. 1991. A simulation model of artisanal fisheries of Senegal. *ICES Mar. Sci. Symp.*, 193: 281-286.

Lawson R.M.and E.A. Kwei. 1974. African entrepreneur ship and economic growth: a case study of the fishing industry of Ghana. Ghana Universities Press, Accra, 262 p.

Mensah M. A. and K. A. Koranteng. 1988. *A review of the oceanography and fisheries resources in the coastal waters of Ghana*. Mar. Res. Rep. Fish. Res. & Util. Branch, Tema, Ghana, 8, 35 p.

Odoi-Akersie W. 1982. *Canoe frame survey Ghana - October 1981*. Inf. Rep. Fisheries Dept, Accra.

Odotei I. 1991. Migrations of fante fishermen. *In*: J.M. Haakonsen and M.C. Diaw (eds.). *Fishermen's migrations in west Africa*. IDAF/WP/36, IDAF Project (FAO), Cotonou, Bénin: 168-179.

Pezennec O. 1995. Ecological importance of the Ivorian and Ghanaian minor upwelling season. *In*: F.X. Bard and K. Koranteng (eds.). *Dynamics and uses of sardinella resources from upwelling off Ghana and Côte-d'Ivoire*. Colloques et Séminaires. ORSTOM. 324-345.

Pielou E.C. 1975. *Ecological diversity*. Wiley, New York. 165 p.

Roy C. 1992. *Réponses des stocks de poissons pélagiques à la dynamique des upwellings en Afrique de l'ouest: analyse et modélisation*. Etudes et Thèses, ORSTOM, 146 p.

Samba A. 1995. Présentation sommaire des différentes pêcheries artisanales. *In*: *Evaluation des ressources exploitables pour la pêche artisanale sénégalaise*. CRODT, 8-13 February 1993. Colloques et Séminaires, ORSTOM: 1-9.

Samba A. and F. Laloë. 1991. Upwelling sénégalo-mauritanien et pêche au tassergal (*Pomatomus saltator*) sur la côte nord du Sénégal. *In*: *Pêcheries ouest-africaines: variabilité, instabilité et changement*. ORSTOM, Paris: 307-310.

Wayo Seini A. 1995. Economics of marine canoe fisheries in Ghana. *In*: F.X. Bard and K. Koranteng (eds.). *Dynamics and uses of sardinella resources from upwelling off Ghana and Côte-d'Ivoire*. Colloques et Séminaires. ORSTOM: 426-436.

Fishmeal Price Behaviour: Global Dynamics and Short-Term Changes

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ABSTRACT

About 80% of the world's pelagic fish resources are processed into fishmeal. The price of fishmeal is set on the world market and imposed to local producers. The high variability of fishmeal prices on the world market is not wholly connected with the fluctuations of aggregate supply and demand; interdependencies with other markets and speculative activities determine a large amount of this variability. This study considers the relationship between the fishmeal and soyabean meal markets. The hypothesis tested here concerns the existence of a long-term relationship directing the behaviour of the prices of these two commodities. Tests for cointegration are performed, and an equilibrium relationship is estimated. The results show that soyabean meal market induces short-term fluctuations into the fishmeal market because of speculative effects, while fishmeal price changes influence soyabean meal prices through a modification of the demand for soyabean meal.

RÉSUMÉ

Près de 80 % des espèces pélagiques capturées dans le monde sont transformées en farine de poisson. Le prix de la farine de poisson fixé sur le marché mondial s'impose à tous les producteurs quelles que soient les conditions locales de la pêcherie. Ce prix présente une forte variabilité qui n'est pas toujours en rapport avec l'évolution de l'offre et de la demande mondiale; les interactions avec d'autres marchés et les activités spéculatives déterminent en grande partie les variations de prix. Des tests de cointégration et l'estimation d'un modèle à correction d'erreur montrent l'existence d'une relation à long terme entre le marché de la farine de poisson et le marché du tourteau de soja qui dirige en partie l'évolution des prix sur ces deux marchés. C'est par un effet spéculatif que le marché du tourteau de soja induit des fluctuations à court terme du prix de la farine de poisson. L'évolution du prix de la farine de poisson provoque des modifications de demande sur le marché du tourteau de soja et entraîne des changements de prix.

INTRODUCTION

Fishmeal is usually prepared from pelagic species (anchovy, sardine, jack mackerel or capelin), the most important fish resource available, but also the most unstable: sudden pelagic stock 'outbursts' or, on the contrary, sharp resource declines are frequent. Above and beyond the amount of study that goes into the reasons behind them, such variations in the availability of fish do have an impact on the overall market.

While the available data are not very precise, it can be estimated that the pelagic catches used worldwide by the reduction industry represent roughly one third of world marine catches (i.e., about 30.10^6 t out of the $90\text{-}95.10^6$ t), and about 80% of world pelagic catches. Thus, fishmeal production is the main outlet of pelagic fisheries. World fishmeal production totals about $6.5.10^6$ t, more than half of which (around $3.5.10^6$ t) moves into international trade channels. About 90% of this international trade originates from five countries (Peru, Chile, Denmark, Iceland and Norway). The main areas of consumption are Europe (a traditional market centered mainly on Germany, a leading importer), East and Southest East Asia (China, now the biggest importer, Taiwan, Japan and, more recently, Indonesia, the Philippines and Thailand), and North America (essentially the United States, although Mexico has recently developed a broader demand base). These regional destinations represent roughly 35, 40 and 20%, respectively of total exports.

Fishmeal is a commodity whose sole end-market is the feed industry, itself located upstream from the animal and meat production sectors. Beyond the protective measures implemented in various regions as part of agricultural policy agricultural markets are all very competitive and under great pressure as far as pricing is concerned. The fishmeal market is a supply-limited market, and, due to the rapid development of aquaculture, an increasing demand helps to maintain a high price level. However, as for major commodities traded in an increasingly globalized and competitive world, the world fishmeal price shows a high variability. Apart from demand and supply factors, interdependence with other commodities and financial markets determine the evolution of prices. Local producers, facing instability in the input, are price-takers for their output.

It is common knowledge that prices of commodities such as raw materials and agricultural products follow similar patterns (Deaton and Laroque, 1992). Such similarities in the behaviour of commodity prices can often be explained by the broader underlying macroeconomic factors affecting all prices in general, e.g., world inflation, interest rates or evolving demand and industrial production (Pindyck and Rotemberg, 1990). Some commodities' prices, however, can be seen to be more closely interrelated and their common trends do show additional links. Certain factors more specific to these commodity markets — e.g., substitution possibilities, complementarity, or orientation towards a same demand — have to be taken into account when explaining their co-movements (Lord, 1991). It is generally admitted, for example, that substitutability among several commodities has the effect of decreasing prices.

The evidence of a link between the fishmeal and soyabean meal markets is well known, particularly to the animal feed mill operators and traders. However, this is only an empirical observation and, although generally postulated, it has never been tested as a formal hypothesis. The purpose of this study is to verify whether there really is a specific relationship between the prices of the fishmeal and soyabean meal markets. We test the existence of and quantify the common long-term trend to which both prices may be related; also we investigate the causality links explaining the behaviour of prices. Interpretations are offered of the long-run equilibrium between prices, as well as price-forming mechanisms on the two markets.

In the first section, we shall briefly describe the markets' specificities and the nature of the data we used. The second and third sections describe the model and discuss the results obtained before moving on interpretations.

1. THE WORLD FISHMEAL AND SOYABEAN MEAL MARKETS, SIMILARITIES AND DIFFERENCES

World fishmeal production is highly dependent upon the quantities of fish caught, which in turn depend on a variety of largely uncontrollable biological and environmental factors (see contributions in this volume). The close relationship between pelagic catches and fishmeal production (tied in with the fact that the raw materials cannot be stocked for long) brings about considerable variability in fishmeal supplies. This generates a degree of market uncertainty rather unusual in commodity trading environments. The market might be regulated through fishmeal stock management on the part of the producers. In past years, however, these stocks have only represented an average of around three months' worth of production, which is rather low compared with other commodities.

Unlike other commodity markets (e.g., soyabean) the world fishmeal market is not organized into any cash or futures markets. The London Commodity Exchange attempted a futures contract for fishmeal some decades ago, but the initiative was short-lived. So the fishmeal market is consequently not as 'transparent' as other major protein markets. Transactions usually remain private, not regularly publicized. Sales contracts are settled on a bilateral basis directly between fish-processing factories and a handful of traders (around thirty) working on behalf of livestock feed companies. There is one source of information available, though. Over the years, the Reuter agency has been establishing a price quotation reporting system on the Hamburg market (the world's biggest CIF — Cost, Insurance and Freight — market); this has progressively become a market reference and the only widely and regularly publicized quotation. This is the one we have selected for our work.

Traditionally, the soyabean crop is above all devoted to oil production, although, in the crushing process, meal (i.e., the protein-rich extract) constitutes approximately 80% of the raw oilseed. Soyabean meal is, thus, a by-product of the soyabean oil industry. As a matter of fact, this is also true of most other major oilseed meals marketed worldwide, e.g., cotton, rape, sunflower, etc. Consequently, the amounts of soyabean meal supplied are largely dictated by the market demand for oil, which is in fact the fundamental source of the crush margin, i.e., the oilseed crushers' profits.

Soyabean meal is used as a source of protein by the animal feed industry, either for direct use at farm level, or blended in with mixed feeds produced by the feed mills. Soyabean meal protein levels generally reach around 44% to 48% of the total dry matter as compared to 65% to 70% in the case of fishmeal (the richest source of protein available for feeding animals). Although our work has been concerned with its role as a protein supply, soyabean meal is also used to some extent by the European feed industry as a source of energy, bringing it into competition with grain, coleseed meal, sunflower meal and corn-gluten-feed. Hence, soyabean meal prices are also linked with grain prices, which are known to be largely influenced by the subsidy or protection policies implemented by the main purchasing and producing entities, Europe and the USA (Tavéra and Dronne, 1991).

Fishmeal and soyabean meal show some similar characteristics, yet also differ in a number of ways.

Similarities include:

- A very high proportion of both commodities' production output is traded internationally. World soyabean meal production totals about 75.10^6 t, 35% of which circulates on the international market. Although this proportion is relatively lower than for fishmeal (50%), this international trade/production ratio still remains high with regard to the agricultural commodities sector. These products are consequently both very sensitive to worldwide changes in the balance of supply and demand, which has a huge impact on price levels.
- The same end-users; both commodities are competing directly with each other as sources of protein for animals (essentially poultry, pigs and aquaculture).

Differences include:

- The nature of the raw product. Soyabean is a cultivated seed harvested once a year (although the wide planting range allows two major crops per year, one in the Northern Hemisphere in September/October; one in the Southern Hemisphere in March/April). For any given year, total soyabean supply is well identified and estimated as early as harvest time and can therefore affect the markets or even be anticipated by the operators, in spite of the fact that crushing may take place at a later stage.
- Fishing remains a highly uncertain activity. Although fish stock assessments are made, these estimates do not influence the markets until the fish have been caught. However, as soon as the fish is landed, the equivalent fishmeal production becomes a market factor, because processing is done within a few hours of the catch, in order to establish a high product quality.
- The more predictable soyabean production is valuated differently on three separate well-organized and informed markets. Soyabean prices are determined worldwide on the basis of supply and demand. There are futures markets for soyabeans, soya oil and soyabean meal which are active on the Chicago Board of Trade.
- As far as fishmeal is concerned, the final product is the same without there having been any distinction whatsoever between either the species processed or the fishing zones where they are caught. However, levels of profitability can differ greatly according to species and fishing zones. What's more, it is sold on a unique and 'confidential' market that makes little information available to the public.

The competitiveness at the end-user level is the interesting point for understanding the long-term price relationship between these two commodities.

2. A COINTEGRATION APPROACH

Economic time series are generally non-stationary. It has been shown that most of them have unit root and that they are integrated of order one. Sometimes, it happens that a linear combination of integrated series gives a stationary series. In such cases, the series are said to be cointegrated (Engle and Granger, 1987; Durand and Mendelssohn, this vol.). This property is confirmed when two non-stationary series have a common trend. Such a stationary link between two non-stationary series underscores the fact that they never drift apart in the long run. If the series diverge in the short-run, then there is a mechanism to bring the two variables back towards their 'equilibrium relationship'.

If the prices of fishmeal and soyabean meal are both integrated and cointegrated, we will be led to conclude that there is a mechanism linking them in the long-term. We may then measure their structural interdependency. It should be pointed out that non-cointegration does not mean that the markets are independent. It still remains possible to find some causal links and to show that a price variation in one of the two markets can affect the other.

If the prices are integrated yet non-cointegrated, the repercussions of any market event or shock affecting its price at any given moment will persist in the future. Such processes are known as 'long-run memory processes'. A crash in fishmeal prices could be attributed to an occasional event, such as an 'El Niño' event, which brings about a sharp decline in the amount of fish caught. Or, soyabean meal prices may tumble as a result of a bad soyabean harvest in the USA or Brazil. On both markets, one-off incidents like these will have a lasting effect. Prices can be subjected to a succession of such shocks with effects that are either positive or negative. Thus, although these effects may be lasting, this does not mean that prices are sent onto an irreversible upward or downward trajectory. The sum total of these effects will result in erratic patterns of behaviour in the price level. This is what is meant by the term 'random walk'.

Cointegration, if there is any, means something else: i.e., that there is a long-term equilibrium relationship between prices which is a causal factor in price variations on at least one of the two markets, independently of other market conditions. Cointegration also implies that the two prices cannot drift too far apart for very long. Should a shock cause these prices to drift apart, a correction mechanism will bring them back into their long-term relationship, and the random walk behaviour will be reduced or disappear.

The fact that cointegration exists means that there is also a relationship of causality as defined by Granger. Granger-causality can arise for two reasons: one 'real' and the other 'speculative' (Campbell and Shiller, 1988). 'X causes Y' is commonly understood to mean that any change in X will produce a change in Y. According to the other interpretation of Granger-causality, X could cause Y if X is an anticipation or forecast of Y. In this latter case, even if we have a causality going from X towards Y, a change in the past behaviour of Y is what determines a current change in its anticipation X.

With regard to the fishmeal and soyabean meal markets, causality can be interpreted in either of these two ways without the other being ruled false.

One 'real' reason why fishmeal prices can 'cause' soyabean meal prices (and vice versa) is the products' substitutability. Both have the same end-users. Feed mill operators trying to minimize their production costs, will buy greater or lesser quantities of fishmeal or soyabean meal for use in feed rations, according to their price ratio. Thus, their long-term equilibrium relationship can be interpreted in terms of a balanced price ratio acceptable to feed millers. Any deviation from the balanced price ratio will lead to changes in purchasing behaviour. These changes in demand can in turn cause changes in price.

The fishmeal market is a 'confidential' one where little information is made public. What's more, the medium or short-term evolution of supply is not easy to anticipate. The soyabean meal market, on the other hand, is well-organized and provides such a wealth of public information as to facilitate price forecasts. Campbell and Shiller (1988) have shown how cointegration can occur between the prices of any two markets when "agents have more information about the variable they are trying to forecast than is contained in the history of that variable alone". In this case, one variable reflects the agents' rational expectation of the future of the other. Agents on the fishmeal market are known to keep a close watch on the fishmeal/soyabean meal price ratio. The key value of this ratio is fixed at 2. Any movements away from this value are taken to indicate forthcoming changes in the price of fishmeal and give rise to buying or selling. This is a 'speculative' interpretation of Granger-causality.

Being aware that when two variables are cointegrated, their cointegrating relationship is unique, we set out to check the validity of the market agents' empirical model which sets the equilibrium price ratio at 2.

3. TESTING FOR MARKET COINTEGRATION

3.1. Data used

Soyabean meal and fishmeal price series covering a period of about 13 years were set up. In order to be consistent, both series were established on the basis of CIF quotations. For fishmeal prices, we used the monthly average CIF prices quoted in Hamburg, in US dollars. For soyabean meal prices, we used the monthly average CIF prices quoted in Rotterdam until 1989 (when data ceased to be available), and then those quoted in Hamburg from 1990 on. So the results of this study are chiefly representative of the European market, the world's largest importer of fishmeal up until the beginning of the 1990s. In 1990, Europe accounted for 48% of the world fishmeal imports; this fell to a 1993 level of 37% as demand rose in Asia, due to the region's economic growth and more particularly, its development of aquaculture. Europe's share of world soyabean meal imports over the period 1987-1991 stood close to 50%. Our data sample covers January 1977 to June 1993 (Fig. 1).

3.2. Unit root tests

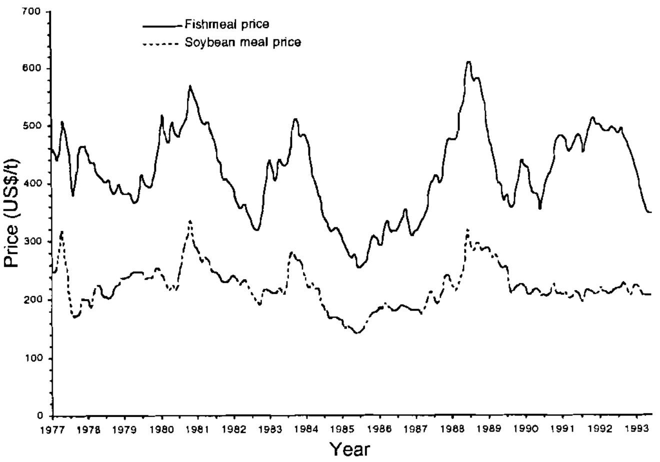
Several unit root tests have been developed from the first papers of Fuller (1976) and Dickey and Fuller (1981). They are based on the regression :

$$\Delta y_t = \varphi y_{t-1} + e_t \qquad \text{where } \Delta y_t = y_t - y_{t-1} \text{ and } e_t \text{ is white noise Nid } (0,\sigma^2)$$

We test the null hypothesis $H_0 : \varphi=0$ which implies that Y_t is a random walk, against the alternative hypothesis H_a: $\varphi<0$ which implies that y_t is stationary. Under the H_0 hypothesis, we are within a non-stationary framework and the ordinary least square estimator of φ does not follow the usual probability distribution. Fuller (1976) and Dickey and Fuller (1981) have tabulated the critical values of the test-statistics for various different versions of this regression.

When performing unit root tests, one must have a prior understanding of the data-generating process, especially of the autoregressive order, so as to correct any possible autocorrelation. The autocorrelation and partial autocorrelation

Fig. 1: Fishmeal and soyabean meal prices ($/t) January 1977 - June 1993.



functions of both fishmeal and soyabean prices indicate that they behave in the manner of an AR(2). This is confirmed by carrying out Akaike and Schwartz tests which indicate that these two level series are AR(2) and that the first differences are AR(1). The Augmented Dickey-Fuller (ADF) and Phillips-Perron (Z_t) tests have been designed to account for the series' autoregressive structure.

In order to test for a unit root leaving open the possibility of there being a deterministic trend, we used the following sequential procedure. We firstly regress thus:

$$\Delta y_t = \alpha + \beta t + \varphi y_{t-1} + \sum_{j=1}^{p} a_j \Delta y_{t-j} + \varepsilon_t \qquad \text{(ADF test - Model 1)}$$

With an ADF test, an autoregressive term is added to the regression model; p is the order of autoregressivity. For the two series p is equal to 1.

Otherwise:

$$\Delta y_t = \alpha + \beta t + \varphi y_{t-1} + u_t \qquad (Z_t \text{ test - Model 1})$$

With a Phillips-Perron (Z_t) test, the u_t term, no longer restricted to being white noise, and is an autocorrelated process. It is generally set up of order 4.

We test the null hypothesis, H_0 : $\varphi=0$, against the alternative hypothesis, H_a: $\varphi < 0$. If H_0 is rejected, we conclude that y_t is I(0). If H_0 is not rejected, we test to see if the trend coefficient is significant. If the deterministic trend is significant, it will 'dominate' the stochastic trend and the usual laws can be applied. In such case, the critical values of the gaussian distribution N(0,1) are used to test H_0. If β is not significant when H_0 is true, we run a new regression without trend (Model 2) to retest H_0 once again using the Dickey-Fuller (DF) critical values.

Note that if the Δy_t series has a deterministic trend in t, then the y_t series will have a quadratic deterministic trend.

$$\Delta y_t = \alpha + \varphi y_{t-1} + \sum_{j=1}^{p} a_j \Delta y_{t-j} + \varepsilon_t \qquad \text{(ADF test - Model 2)}$$

or else:

$$\Delta y_t = \alpha + \varphi y_{t-1} + u_t \qquad (Z_t \text{ test - Model 2})$$

If H_0 is rejected, we conclude that y_t is I(0). If H_0 is not rejected, then we test to see if the drift α is significant. If it is, we conclude that y_t has a linear deterministic trend. In this case, the deterministic trend will dominate the stochastic trend, α has a gaussian distribution and H_0 is therefore tested with this probability distribution. If α is not significant when H_0 is not rejected, then we run a regression without intercept (Model 3):

$$\Delta y_t = \varphi y_{t-1} + \sum_{j=1}^{p} a_j \Delta y_{t-j} + \varepsilon_t \qquad \text{(Model 3)}$$

We again test H_0 with the appropriate DF critical values. If the null hypothesis is rejected, then y_t is definitely I(0). If it is not rejected, this implies that y_t is integrated to an order of at least 1. Since we are unable to reach a conclusion with regard to higher orders of integration, we have to rerun the same test procedure with, for example, regressions for I(2):

$$\Delta^2 y_t = \varphi y_{t-1} + e_t$$

The results of the unit root tests for fishmeal and soyabean meal prices are summarized in Table 1. As the I(2) hypothesis was always rejected for both series, the results of these tests are not reported.

	Model 1		Model 2		Model 3
Soya	ADF	Z_t	ADF	Z_t	ADF
	t_φ =-3.58	t_φ =-3.10	t_φ =-3.56	t_φ =-3.07	t_φ=-0.69
	t_α = 3.38	t_α = 3.49	—	—	—
	t_β =-0.48	—	—	—	—
Fishmeal	ADF	Z_t	ADF	Z_t	ADF
	t_φ =-2.75	t_φ =-2.44	t_φ =-2.76	t_φ =-2.44	t_φ =-0.70
	t_α = 2.60	—	t_α = 2.68	—	—
	t_β =-0.03	—	—	—	—

Table 1: ADF and Z_t unit root tests.

The "t" statistics are of a "student ratio" type.

Critical value at (1%, 5%, 10%) for a sample of 250 observations:

t_φ : (-3.99,-3.43,-3.13)　t_φ : (-3.46,-2.88,-2.57)　t_φ : (-2.58,-1.95,-1.62)
t_α : (3.74, 3.09, 2.73)　t_α : (3.19, 2.53, 2.16)
t_β : (3.49, 2.79, 2.38).

For the fishmeal price series, Model 1 allows us to accept the unit root hypothesis with coefficients α and β being null. So we must therefore refer to Model 2, where the unit root hypothesis is accepted every time. Here, however, we can consider, with a 5% risk margin, that this series also has a drift. So this price series is integrated of order 1 and behaves in the manner of a random walk with possible drift.

As far as soyabean meal prices are concerned, the conclusions are less obvious. In Model 1, the unit root hypothesis is rejected with the Dickey-Fuller test and accepted with the Phillips-Perron test. In Model 2 (β not being significant), the unit root hypothesis is rejected with the Dickey-Fuller test, and accepted with the Phillips-Perron test (with only 1% risk). With the Dickey-Fuller test, results are very sensitive to the number of lags added to the regression. It is therefore generally preferable to use the Phillips-Perron test.

Although the power of these two tests when applied outside of their standard hypotheses, i.e., (ε_t Nid($0,\sigma^2$)), is still the subject of much discussion, it has been shown that residual heteroscedasticity leads to a far too frequent rejection of unit root hypothesis H_0 and, that the critical values should be readjusted (Kim and Schmidt, 1993). We should mention that some heteroscedasticity is present in the soyabean meal price series and in the residuals of its regression. Beck (1993) has shown that heteroscedasticity in commodity prices is attributable to speculative storage behaviour. Although the results of these tests are not very convincing, we nonetheless accept the unit root hypothesis for the soyabean meal series. The ambiguity of these results stem from the feeble 'size' of the random walk with regard to soyabean meal prices (Cochrane, 1988) and, that the deterministic trend is not very significant either. These tests are known, in certain cases, not to be very good at discriminating between Trend-Stationary and Difference-Stationary series. With these ADF and Z_t tests, the null H_0 hypothesis always stands as a pure random walk.

We shall therefore consider the fishmeal and soyabean meal price series as being I(1), with drift in the latter and the possibility of drift in the former.

3.3. COINTEGRATION TESTS

Having found from the previous results that these price series are I(1), we have to test for cointegration. Three cointegrating regressions can be performed:

$$SJ_t = \alpha + \beta t + \delta FP_t + z_t \qquad \text{(demeaned - detrended);}$$

or

$$SJ_t = \alpha + \delta FP_t + z_t \qquad \text{(demeaned);}$$

or

$$SJ_t = \delta FP_t + z_t \qquad \text{(standard).}$$

SJ_t and FP_t stand for the soyabean meal price and fishmeal price respectively. If the error term z_t is I(0), then SJ_t and FP_t will be 'cointegrated', with a cointegrating vector of $(1\ -\delta)'$.

As before, the cointegration tests are based on unit root tests, but this time, these tests are performed on the z_t residuals' series. The two price series are cointegrated if the null hypothesis H_0 is rejected, i.e. if z_t. is stationary. They are not cointegrated if H_0 cannot be rejected i.e. if z_t is non-stationary. The unit root tests are performed on the following regression :

$$\Delta \hat{z}_t = \varphi \hat{z}_{t-1} + \sum_{j=1}^{p} a_j \Delta \hat{z}_{t-j} + \varepsilon_t$$

As we are performing the tests on an estimated series (the residuals), the critical values for the tests are not the same. They have been tabulated by Phillips and Ouliaris (1990).

The usual properties of the OLS estimators cease to be valid here, because the explanatory variables are non-stationary. However, these coefficients will be 'super-convergent', because they converge towards the theoretical value of the regression parameters twice as fast as usual.

Theoretically speaking, normalization on either SJ_t or FP_t will give the same results. However, we have performed the two following regressions :

$$SJ_t = \alpha_1 + \delta_1 FP_t + z_{1t}$$

$$FP_t = \alpha_2 + \delta_2 SJ_t + z_{2t}$$

In some cases, z_{1t} can be considered as stationary yet z_{2t} cannot. This occurs when the R^2 is not close enough to 1. Both tests must then be performed on z_{1t} and z_{2t}. Table 2 gives the cointegration test results.

Demeaned - detrended : critical values at 1%, 5%, 10%: (-4.36, -3.80, -3.51)				
$SJ_t = 84.62 - 0.12t + 0.35FP_t + z_{1t}$	$R^2=0.58$	DW=0.28	p=1	$t\varphi=-4.50$
$FP_t = 38.46 + 0.22t + 1.61SJ_t + z_{2t}$	$R^2=0.58$	DW=0.21	p=2	$t\varphi=-3.30$
Demeaned : critical values at 1%, 5%, 10%: (-3.96, -3.36, -3.06)				
$SJ_t = 74.13 + 0.35FP_t + z_{1t}$	$R^2=0.55$	DW=0.26	p=1	$t\varphi=-4.34$
$FP_t = 72.70 + 1.56SJt + z_{2t}$	$R^2=0.55$	DW=0.19	p=2	$t\varphi=-3.26$
Standard : critical values at 1%, 5%, 10%: (-3.38, -2.76, -2.45)				
$SJ_t = 0.52FP_t + z_{1t}$	$R^2=0.41$	DW=0.23	p=1	$t\varphi=-3.95$
$FP_t = 1.88SJ_t + z_{2t}$	$R^2=0.53$	DW=0.22	p=1	$t\varphi=-3.92$

Table 2: Cointegrating regression and ADF tests for cointegration.

The Durbin-Watson and R^2 statistics are sometimes used in order to test for cointegration, but this procedure has been much criticized and has to be interpreted with care (Perron and Campbell, 1992). The DW and R^2 statistics cannot be interpreted here to the usual ends.

Going on the demeaned-detrended regression, the hypothesis of stationarity will be accepted for the z_{1t} residuals, but rejected for the z_{2t} series. Going on the demeaned regression, we end up with the same results. As mentioned earlier on, these tests can produce different results according to the normalization vector chosen (SJ_t or FP_t). They are particularly sensitive to the presence of deterministic trends in the explanatory variables of the cointegrating regression. These results tend to confirm that drift only occurs in the soyabean meal price series, thus making SJ_t the most appropriate vector to choose for normalization.

So we therefore accept the hypothesis of cointegration and conclude that there is a specific relationship between these two prices: a specific value of the FP_t/SJ_t price ratio drives the behaviour of prices on these markets. The cointegrating vector is estimated as (1 -0.35)', which puts the price ratio for the period studied at $SJ_t/FP_t = 0.35$ (or $FP_t/SJ_t = 2.85$), once the gradual downward trend of soyabean meal prices has been taken into account.

We were also interested to know if the price ratio, FP/SJ=2 (a key value for the agents on the fishmeal market) can be considered as a stationary process. If so, we would be able to say that the agents on the market are right to keep such a close watch on this particular ratio value. So we therefore carried out another set of unit root tests on the calculated series $u_t = FP_t - 2SJ_t$. Since this series is calculated rather than estimated, the appropriate critical values were supplied by the Dickey-Fuller tables.

The u_t series is AR(1) and the ADF and Phillips-Perron statistics are equal to -3.78 and -4.03 respectively. As we can reject the unit root hypothesis, u_t is stationary. We can therefore consider the cointegrating vector to be (1 -2)' for normalization on the fishmeal price or, equally, (1 -0.5)' for normalization on the soyabean meal price. The standard regression for cointegration tests confirms this fact and gives us a cointegrating vector of (1 -0.52)'.

Theoretically speaking, there can only exist one cointegrating vector for two integrated I(1) series. The fact is that both (1 -0.35)' and (1 -0.5)' have been found to be acceptable as cointegrating vectors. This may appear contradictory, but it reflects the difficulty in dealing with deterministic trends, a problem which remains open to question both with regard to unit root and cointegration tests, and estimating cointegration models. Our interest in performing standard regression, was confined to the fact that it allowed us to confront the validity of the agent's empirical model. From the statistical point of view, the standard test regression was not suitable, because it leaves drift in the z_t series and cointegration tests are not established in such a case. That is why it is often necessary to demean or detrend the test regression. The cointegrating vector which has to be considered is then (1 -0.35)'.

3.4. Error correction representation

If two series are I(1) and cointegrated, and they both have a deterministic trend, then there is a linear combination of them which is stationary and which will remove both their deterministic and stochastic trends. In such cases, we are talking about "deterministic cointegration". So the model representing the short-run adjustments for AR(1) cointegrated series, is the standard cointegration model:

$$\begin{pmatrix} \Delta SJ_t \\ \Delta FP_t \end{pmatrix} = -\begin{pmatrix} \gamma_1 \\ \gamma_2 \end{pmatrix} (1-a) \begin{pmatrix} SJ_{t-1} \\ FP_{t-1} \end{pmatrix} + \begin{pmatrix} \Gamma_{11} \Gamma_{12} \\ \Gamma_{21} \Gamma_{22} \end{pmatrix} \begin{pmatrix} \Delta SJ_{t-1} \\ \Delta FP_{t-1} \end{pmatrix} + \begin{pmatrix} u_{1t} \\ u_{2t} \end{pmatrix}$$

If two series are I(1) and cointegrated but only one of them has a deterministic trend, then this deterministic trend cannot be removed by the cointegrating vector. In such cases, we are talking about "stochastic cointegration". The cointegration model should therefore account for this deterministic trend and is written thus:

$$\begin{pmatrix} \Delta SJ_t \\ \Delta FP_t \end{pmatrix} = \begin{pmatrix} \mu_1 \\ \mu_2 \end{pmatrix} - \begin{pmatrix} \gamma_1 \\ \gamma_2 \end{pmatrix} (1-a) \begin{pmatrix} SJ_{t-1} - \delta(t-1) \\ FP_{t-1} \end{pmatrix} + \begin{pmatrix} \Gamma_{11} \Gamma_{12} \\ \Gamma_{21} \Gamma_{22} \end{pmatrix} \begin{pmatrix} \Delta SJ_{t-1} \\ \Delta FP_{t-1} \end{pmatrix} + \begin{pmatrix} u_{1t} \\ u_{2t} \end{pmatrix}$$

The value of the coefficient δ does not reflect the influence of the deterministic trend because a part of it is caught in the intercept μ_i.

These cointegration models stem from the time series analysis field developed by Box and Jenkins. In the field of economics, at the end of the 1970s, Davidson, Hendry, Sbra and Yeo began developing a new econometric approach aimed at testing the equilibrium relationships generally postulated by economic theory. The idea was to model the behaviour of economic variables as a dynamic process of adjustment towards a equilibrium relationship. This approach is known as the Error Correction Model (ECM). In 1987, Engle and Granger pointed out the equivalence between the ECM and cointegration models. The difference between these two approaches lies in the fact that with the ECM, the equilibrium relationship is known, postulated by economic theory and static, whereas with the cointegration model, the equilibrium relationship remains to be estimated.

If we assume that $FP_t / SJ_t = 2$ is a fixed price ratio, to which fishmeal and soyabean meal prices will adjust, we can thus estimate an ECM which, in our case, will take the form of one of the following two equations:

either:

$$\Delta FP_t = \beta_0 + \beta_1 \Delta FP_{t-1} - \beta_2 (SJ_{t-1} - 0.5 FP_{t-1}) + \beta_3 \Delta SJ_t + \beta_4 \Delta SJ_{t-1} + \varepsilon_t$$

or:

$$\Delta SJ_t = \beta_0 + \beta_1 \Delta SJ_{t-1} - \beta_2 (SJ_{t-1} - 0.5 FP_{t-1}) + \beta_3 \Delta FP_t + \beta_4 \Delta FP_{t-1} + \varepsilon_t$$

Although in principle only one of the three models (deterministic, stochastic, ECM) would be the right one to select, we estimated all three to compare their results. The deterministic and stochastic cointegration models were compared because the unit root test results were ambiguous as to whether there was a deterministic trend or not in the fishmeal price series. We estimated the ECM in order to represent the market agents' empirical model. The first two models were estimated by NLS, and the ECM by OLS.

The results of the stochastic cointegration model show the coefficient of the deterministic trend of soyabean meal to be non-significant, while the intercept is significant (cf. Table 3). The soyabean meal price series really does have a significant mean trend: a downward trend over the period studied. Although weak, it had to be introduced, and the stochastic cointegration model is the one that best represents the data process and must hence be selected.

$$\Delta SJ_t = 16.67 - 0.18\,((SJ_{t-1} + 0.11(t-1)) - 0.34\,FP_{t-1}) + 0.39\,\Delta SJ_t - 0.12\,\Delta FP_{t-1} + u_{1t} \qquad R^2=0.16 \qquad DW=1.99$$

(6.11) (0.04) (0.08) (0.06) (0.08) (0.05)

$$\Delta FP_t = 4.52 - 0.05\,((SJ_{t-1} + 0.11(t-1)) - 0.34\,FP_{t-1}) + 0.58\,\Delta SJ_{t-1} + 0.18\,\Delta FP_{t-1} + u_{2t} \qquad R^2=0.24 \qquad DW=1.95$$

(5.59) (0.06) (0.08) (0.06) (0.11) (0.07)

Variance/covariance residuals matrix:

	u_{1t}	u_{1t}
u_{1t}	154.17	
u_{2t}	95.55	317.45

Table 3: Stochastic cointegration model.

It is interesting to note that while errors around the long-term relationship have a significant influence on soyabean meal prices, this is not so in the case of fishmeal. Soyabean meal prices determine a current fishmeal price change solely through its price variations in the previous period. Fishmeal prices meanwhile determine changes in soyabean meal prices through both short and long-term effects.

The results of the deterministic cointegration model confirm the statistical validity of the fishmeal market agents' empirical model, since the estimated FP_t/SJ_t price ratio is close to 2 — here, with a cointegrating vector of (1 -0.52)' we have an 'equilibrium ratio' $FP_t/SJ_t=1.92$ — (cf. Table 4). In the light of our previous findings, the fishmeal market agents have been found to make the sole mistake of neglecting the long-run downward trend of soyabean meal prices. As before, the errors around the equilibrium relationship will only have an impact on the short-term variations in soyabean meal prices, and none on short-term fishmeal price changes.

$$\Delta SJ_t=-0.111\,(SJ_{t-1} - 0.525\,FP_{t-1}) + 0.356\,\Delta SJ_{t-1} - 0.122\,\Delta FP_{t-1} + u_{1t} \qquad R^2=0.12 \qquad DW=1.96$$

(0.03) (0.01) (0.08) (0.05)

$$\Delta FP_t = 0.038\,(SJ_{t-1} - 0.525\,FP_{t-1}) + 0.534\,\Delta SJ_{t-1} + 0.204\,\Delta FP_{t-1} + u_{2t} \qquad R^2=0.24 \qquad DW=1.94$$

(0.05) (0.01) (0.11) (0.07)

Variance/covariance residuals matrix:

	u_{1t}	u_{2t}
u_{1t}	162.13	
u_{2t}	103.29	317.89

Table 4: Deterministic cointegration model.

With the Davidson-Hendry ECM, the fixed price ratio has a positive influence on the changes in soyabean meal prices and, for the first time, on fishmeal price changes too. This model is not useful for 'revealing' that these two markets are interlinked in a price relationship because it postulates the fact from the outset. It indicates what might be the impact of an $FP_t/SJ_t = 2$ price ratio arbitrarily fixed at 2 on the evolution of prices. Fishmeal market agents consider this seldom observed value of the price ratio to be an important signal. The ECM shows us what the consequences of the agents' empirical model might be if they (the agents) are right, and if there really is a mechanism making this price ratio a price-determining factor. The results of this model (Table 5) show that when the price ratio is less than 2, i.e. when the agents think that fishmeal prices are undervalued in relation to soyabean meal prices — i.e. that $(SJ_t - 0.5\,FP_t)$ is positive —, this brings about a rise in the prices of fishmeal and a fall in those of soyabean meal. If the $FP_t/SJ_t = 2$ price ratio acts as a signal for anticipating future price changes, then any modification in this ratio will spark off a spate of buying or selling which, in turn, modifies the prices.

$$\Delta SJ_t = 1.51 - 0.132\,(SJ_{t-1} - 0.5\,FP_{t-1}) + 0.188\,\Delta SJ_{t-1} + 0.323\,\Delta FP_t - 0.188\,\Delta FP_{t-1} + u_{1t} \qquad R^2=0.30 \qquad DW=1.98$$

(0.90) (0.03) (0.07) (0.04) (0.05)

$$\Delta FP_t = -1.50 + 0.108\,(SJ_{t-1} - 0.5\,FP_{t-1}) + 0.279\,\Delta FP_{t-1} + 0.637\,\Delta SJ_t + 0.307\,\Delta SJ_{t-1} + u_{2t} \qquad R^2=0.39 \qquad DW=1.95$$

(1.28) (0.05) (0.06) (0.09) (0.10)

Table 5 : Davidson and Hendry type Error Correction Model.

The market agents are right to keep a close watch on the price ratio. It really does to some extent dictate short-term variations in price. They are only mistaken with regard to its value because they do not account for the long-term downward trend in soyabean meal prices. This trend does not affect the prices of fishmeal whose mean remains stable. The 'true' long-term equilibrium price ratio, which can include the substitution mechanism between the two commodities, is far higher as it is close to 3 (the cointegrating vector (1 -0.34)' in the stochastic cointegration model we selected gives the equilibrium price ratio $FP_t/SJ_t = 2.94$). Agents tend to neglect long-run tendencies in their efforts to anticipate short-run price movements. The 'apparent' price ratio, as given by the deterministic cointegration model and which does not take the decline in soyabean meal prices into account, remains close to 2. Thus, in appearance, the agents are not entirely in the wrong.

3.5. Granger causality links

It is known that between any two cointegrated series there is at least one causality relationship: "(...) the stationary linear combination of levels must Granger-cause the change in at least one of the cointegrated variables" (Campbell and Shiller, 1988). From the cointegration model, we conclude that the equilibrium errors have a recall effect on soyabean meal prices but none on those of fishmeal. On the other hand, short-run variations in either price will influence the other. Cointegration models, however, are not suitable for conducting valid Granger-causality tests.

The correct way of testing for Granger-causality is to use a stationary VAR model, i.e. taking first difference series when they are I(1). When the variables are cointegrated, however, a VAR model built with first difference series will be misspecified due to a loss of part of the information. So it is therefore preferable to use the level data to test the causality. Certain authors, such as Lütkepohl, have shown that the definition of Granger-causality established within a stationary framework is also valid within a non-stationary framework, i.e. VAR systems using levels of I(1) variables. The problem of using non-stationary VAR models is that the Wald statistics normally used to test for linear restrictions no longer follow the usual asymptotic χ^2 distribution. According to Lütkepohl and Reimers (1992), however, Wald statistics only continue to have a χ^2 distribution in bivariate VAR processes alone.

$$\begin{array}{llllll} SJ_t = & 17.20 & + 1.21\, SJ_{t-1} & - 0.38\, SJ_{t-2} & - 0.07\, FP_{t-1} & + 0.11\, FP_{t-2} + u_{1t} \\ & (5.90) & (0.07) & (0.07) & (0.05) & (0.05) \end{array} \qquad R^2=0.88 \qquad DW=1.98$$

$$\begin{array}{llllll} FP_t = & -22.70 & + 0.53\, SJ_{t-1} & - 0.56\, SJ_{t-2} & + 1.18\, FP_{t-1} & - 0.21\, FP_{t-2} + u_{2t} \\ & (8.27) & (0.10) & (0.10) & (0.07) & (0.07) \end{array} \qquad R^2=0.94 \qquad DW=1.98$$

Wald tests (likelihood ratio):

$\lambda = 9.83$ SJ causes FP

$\lambda = 26.94$ FP causes SJ

Table 6: Var(2) representation and Granger-causality tests.

Granger-causality cannot be rejected in both directions (i.e., SJ causing FP and FP causing SJ). These results thus lead us to conclude that fishmeal price partly determines soyabean meal price, even if the fishmeal market is smaller-sized and the international trade in soyabean meal is of a far smaller scale. Although these two commodities have always been known to be linked, the influence fishmeal prices exert on soyabean meal prices is quite a new finding.

We should point out that the sum of the SJ_t coefficients in the FP_t regression is non-significant, meaning that soyabean meal prices have no lasting effect on fishmeal prices. Soyabean meal prices mainly exert a short-run causality on fishmeal prices. The latter react very quickly to changes in the former; soyabean meal prices only have an impact on fishmeal prices through their period-to-period changes. However, the fishmeal market has a more lasting and thus less speculative influence on the soyabean meal market. This confirms the cointegration model findings.

A recall mechanism can come into being, either through the long-run effects of the cointegration relationship or, through the short-run effects of period-to-period changes which are either positive (ΔSJ_t on ΔFP_t) or negative (ΔFP_t on ΔSJ_t). These cross-effects will restrict any strong price variations on either market.

CONCLUSION

This study has shown that fishmeal and soyabean meal prices behave in the manner of a random walk, meaning that the best price forecast that can be made is given by the current value. These prices are non-stationary processes, characterized by their great variability. This is frequently the case with commodity prices that quickly react to shocks in supply and demand. It has also been shown that despite their non-stationarity making forecasting difficult, these two prices are linked by a stationary relationship, and that they can never drift apart for very long.

In 1991 and 1992, fishmeal production collapsed partly because of the El Niño phenomenon along the Pacific coast, but also due to a collapse in Japanese pelagic catches and the dismantling of the former Soviet-Union's fishing fleet. Fishmeal prices consequently rocketed during this period. Since 1993, there has been a sharp decline in fishmeal prices. This is partly due to an increase in Peruvian production, but worldwide demand that year reached an all-time high and physical stocks of fishmeal fell to their lowest ever level. That high level of demand must have prevented the fall in prices. This confirms the effect of the link we have found between the fishmeal and the soyabean meal markets. In 1991-1992, rising fishmeal prices drifted too far apart from soyabean meal prices, for too long. The recall effect between these two prices is also the reason behind a fall in fishmeal prices.

An equilibrium price ratio between these two commodities exists because they both respond to the same demand (feed mill companies) and substitute for each other. The evolution in prices is driven by a demand which is basically for proteins. The protein contents of these two products is not of the same quality. Some amino-acids which are essential growth factors for animals are only provided by fishmeal, making it a necessary component in feed rations. However, the ingredients of the feed ration may change; there are no set rules to determine the proportions of vegetal and animal proteins. Feed mixes are prepared according to an optimization process whose aim is to reduce production costs and maximize benefits. Quantities used of these two components are readjusted in tune to how their prices are evolving. Otherwise production costs would be very unstable. Any evolution in the price ratio brings about changes in the relative demand for these two products and, hence, changes in their prices.

In this context, it is important to note that soyabean meal prices alone will be affected by any deviation from the equilibrium price ratio, the ensuing effects of which will be negative. This means that if fishmeal becomes too expensive in relation to soyabean meal, there will be a rise in demand for soyabean meal and its price will rise accordingly. Conversely, if fishmeal becomes cheaper in its relation to soyabean meal more fishmeal will be incorporated in feed mixes, there will be a fall in the relative demand for soyabean meal and its price will fall. Fishmeal prices are not affected by these kinds of changes in purchasing behaviour. The fishmeal market is supply-limited, and demand adjustments are made on the soyabean meal market, which, on the contrary, is an excess-of-supply market.

Short-run effects stem more from anticipation phenomena. Fishmeal prices exert a long-run causality on soyabean meal prices, whereas soyabean meal prices only exert a short-run causality on fishmeal prices. So it is through anticipatory mechanisms that soyabean meal prices influence fishmeal prices, and through demand phenomena that fishmeal prices influence soyabean meal prices. Further investigations into how speculative effects occur and drive the prices on the fishmeal market will inevitably have to account for the storage management.

REFERENCES CITED

Beck S.E. 1993. A rational expectation model of time varying risk premia in commodities futures markets: theory and evidence, *Int. Econ. Rev.*, 34: 149-167.

Campbell J.Y. and R.J. Shiller. 1988. Interpreting cointegrated models. *J. Econ. Dyn. Contr.*, 12: 505-522.

Cochrane J.H., 1988. How big is the random walk in GNP? *J. Polit. Econ.*, 95 (5): 893-920.

Deaton A. and G. Laroque. 1992. On the behaviour of commodity prices. *Rev. Econ. Stud.*, 59: 1-23.

Dickey D.A. and W.A. Fuller. 1981. Likelihood ratio statistics for autoregressive time series with a unit root. *Econometrica*, 49: 1057-1072.

Engle R.F. and C.W.J. Granger. 1987. Cointegration and error correction representation, estimation and testing. *Econometrica*, 55 (2): 251-276.

Fuller W.A. 1976. *Introduction to statistical time series.* Wiley, New-York.

Lord M.J. 1991. Price formation in commodity markets. *J. Appl. Econom.*, 6: 239-254.

Lütkepohl H. 1991. *Introduction to multiple time series analysis.* Springer-Verlag, 545p.

Lütkepohl H. and H.E. Reimers. 1992. Granger-causality in cointegrated VAR processes, the case of the term structure. *Econ. Lett.*, 40: 263-268.

Kim K. and P. Schmidt. 1993. Unit root tests with conditional heteroscedasticity. J. *Econometrics*, 59: 287-300.

Perron P. and J.Y. Campbell. 1992. Racines unitaires en macroéconomie: le cas multidimensionnel. *Ann. Econ. Stat.*, 27: 1-50.

Phillips P.C.B. and S. Ouliaris. 1990. Asymptotic properties of residual based tests for cointegration. *Econometrica*, 58 (1): 165-193.

Pindyck R.S. and J.J. Rotemberg. 1990. The excess co-movement of commodity prices. *Econ. J.*, 100: 1173-1189.

Tavéra C. and Y. Dronne. 1991. Interactions des prix mondiaux des produits de l'alimentation animale sur le marché de Rotterdam. *Ann. Econ. Stat.*, 23: 115-135.

Modeling Fishery Activity Facing Change: Application to the Senegalese Artisanal Exploitation System

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ABSTRACT

A computer model is presented which formalizes the responses of the Senegalese artisanal fishery to changes in its environment. The problem of a fishery's response to change is first considered at a global system level. There, adaptive processes are defined as the major determinant of the fishery's response to change. The system's structure and function are then formalized at the most local possible level (that of communities) and related, through successive embedded schemes, to the global level. An artificial intelligence formalism is used to generate this progression. In a third part, some simulation results of the fishery model response to change are discussed in support of the adequacy of this approach.

RÉSUMÉ

Un modèle informatique est décrit qui représente les réactions d'une exploitation halieutique artisanale à des changements de son environnement. Le problème du changement est appréhendé à un niveau global où les processus adaptatifs sont considérés comme les principaux déterminants de la réponse de l'exploitation. La structure et le fonctionnement de l'exploitation sont d'abord formalisés au niveau le plus local (communautés). Un formalisme multi-agent issu de l'intelligence artificielle est utilisé pour la modélisation. Par emboîtements successifs, ce cadre élémentaire est relié au niveau global initial où l'exploitation et sa réponse au changement peuvent être étudiés. Dans une troisième partie, quelques résultats de simulation sont présentés comme support à une discussion sur la validité de l'approche.

INTRODUCTION

Ferraris *et al.* (this vol.) and other authors have discussed the responses of fishing exploitation systems to changes in their environment. Knowledge of these different networks and interactions leads to various questions about human activities facing long or short term changes. For instance, for a monitoring purpose, it may be useful to formalize how changes can affect these complex systems, identify likely responses, or help determine through which means this evolution may be steered. On a modeling point of view, it is also interesting to provide new tools for these difficult problems.

This work proposes a modeling scheme which answers some of these questions. The results presented here are based on a modeling experiment pertaining to the Senegalese artisanal fisheries. The issues and hypotheses are first presented and the system is defined. In a second part the model is described. The third part presents and discusses simulation results.

1. THE PROBLEM OF CHANGE (WORKING HYPOTHESES)

1.1. The fishery exploitation as a global adaptive system

To provide a working framework, the generic problem of fisheries' response to change is first considered at a global system's level (as in Quensière, 1993). At this scale, change can be considered to have four possible effects on the exploitation (Fig. 1):

The first response type (Fig. 1a) occurs when the exploitation system takes advantage of the change and reaches a new,

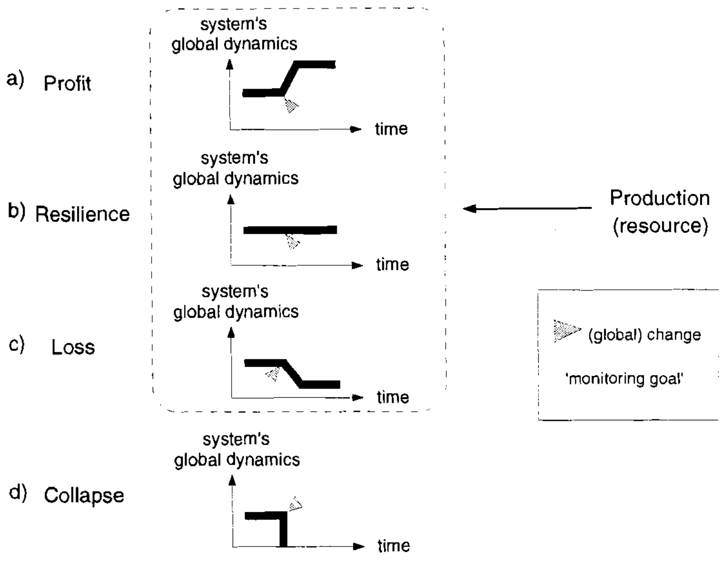

Fig. 1: Schematic representation of four possible responses of a system confronted to change.

different, stationary state. For example, at the beginning of the 1950s, outboard engines suddenly became available to artisanal fishers ('technological change'). This drastically changed fishing practices, and impacted on fish landing, both in terms of quality and of quantity. The Government took interest in the artisanal fisheries, roads were built, and marketing activities evolved towards this promising sector (Chauveau, 1988).

In the second case (Fig. 1b), the fishery exploitation system resists the change, and goes on with the same structures and functions, the same level of activity or the same outputs. For instance, in the 1970s, the artisanal fishery of the north coast of Senegal was greatly dependent on bluefish (*Pomatomus saltator*). Scientific appraisals concluded that if the bluefish species resource happened to disappear, this would have 'disastrous consequences' for the artisanal fishery (Champagnat *et al.*, 1983). This resource has nowadays almost completely disappeared from the artisanal catches. The fishers responded to this perturbation by quickly switching to other species and no major change, only weak fluctuations were observed to occur at the level of the exploitation system (Laloë and Samba, 1990).

In Fig. 1c, the fishery system is negatively affected by the change. It remains active but loses some functionality or output. A Senegalese example can be provided here: in June of 1985, an important resource of sole became suddenly available in the surrounding of Kayar, one of the main landing site of the country. This induced a migration flow of gill-net fishers towards this fishing area and landing site. The resulting competition between sedentary and nomadic fishers led to violent conflicts between the two communities, which have persisted to date (pers. obs., September 1993).

Fig. 1d depicts a 'non-adaptive» system: such system does not occur in Senegal, but has been described elsewhere, e.g., for upwelling-dependent fisheries (Glantz and Thompson, 1954; Chaboud, 1992). In this case, the fishery system cannot adapt to global change and collapses.

In any of these four cases, the evolution process can be related to the adaptability of the system. Thus we have here a tool to understand, and to formalize, the ways a given fishery system responds to change.

1.2. Local constraints to representation

1.2.1- Human activity

If the fishery exploitation system as a whole can present adaptive characteristics, it is mainly due to the human actors within this system. Indeed, through the past half century, most of the major changes observed in the Senegalese system have been 'processed' by human communities (see the examples above). It therefore appears necessary to take into account the various modalities of actions and reactions of the actors. This however, is best done at the local level.

1.2.2- Monitoring

In the case of resource exploitation, after a change whatever becomes of a fishery exploitation, its basic functionality remains such as providing seafood, a positive currency balance, employment, etc. (Fonteneau and Champagnat, 1977; Chauveau, 1984; Chaboud and Kébé, 1989). The means society at large has to impact the system dynamics may belong to the macro scale (e.g., the recent currency devaluation in Senegal; Kébé and Dème, 1994). These means are often local such as fishing quotas, defining fishing zones, etc.

To take these local aspects into account, the adaptive properties of an exploitation system must be understood as a result of the interactions of lower-level elements of this system. This 'neo-systemic' approach of dynamics is presently developed in several different fields such as physiology (Bagley and Farmer, 1991), ethology (Drogoul and Ferber, 1993), sociology (Nowak and Latané, 1992), or fisheries sciences (Bousquet *et al.*, 1992).

1.3. Choosing a 'granularity'

Several levels can be selected for describing a system's behavior, ranging from the global, systemic view to the most local mechanisms (i.e., individual behavior). It thus appears necessary to select the level or 'granularity' that is best adapted to the objectives at hand.

The individual level appears computationally difficult, since it implies too many little-known processes to consider. On the other hand, if a more global level is chosen (e.g., trading, fishing, consuming), important lower-scale mechanisms will be missed. Moreover, it will prevent the study of the means that can be used to bear on global dynamics.

The granularity retained here is the community level, which is intermediate between the two above extremes. A community is here defined as a set of human actors whose individual behavior can be considered equivalent. For example, every trader in a given landing site can be assumed to sell fishes at the same market places, while fishers owning the same type of gear will be considered to display the same behavior when faced to a change in their environment. In this sense, they belong to the same community.

2. THE COMPUTER MODEL

The growing power of computer simulations leads to increasing investigations of complex systems in the modeling field. It now appears that most of the major concepts to be manipulated in this field (e.g., interaction, diversity, organization, memory, evolution, catastrophe, emergence) can be depicted fairly well. Scientists working on artificial intelligence have provided new, powerful formalisms to represent these concepts. From this new panel of techniques, distributed artificial intelligence (DAI) and multi-agents' formalism are being used more and more for complex systems and artificial life modeling and simulation. This technique is based on communication between objects and their environment (Ferber, 1994; Erceau, 1994). It has also been here retained for it allows the fine granularity that suits our purpose.

Using DAI, a model was structured through different embedded levels. This chapter describes the different levels modeled, from the most local (components) to the most global (exploitation system). Here, the first steps of the modeling effort is to represent how the different components of the fishery system are organized and how they get information from their environment.

2.1. Structure representation

Structurally, the fishery exploitation system is formalized as a few set of meaningful components (i.e., communities, stocks, markets, fishing zones, etc.). In the model these components are translated in a class hierarchy. For the Senegalese exploitation system, the model class hierarchy is presented in Figure 2, which identifies the limits within which the investigated system is defined.

A given class is defined by a set of fields and may contain several different objects or agents. For example, the agent described in Figure 3 belongs to the 'fisher-active-community' class. It is defined by several fields whose value characterize it. These fields are for example its size (number of fishers belonging to this community), the equipment it owns (fishing gears, canoe), the species it can harvest, the sites where it can go (landing sites, fishing zones), or the fishing tactics[1] it may use. The set of fields is given by the class, the field proper values define each particular instance (e.g., particular fishing community). The field values can change depending on context.

Other type of agents are related to this community agent. The Kayarland current site for instance refers to another agent belonging to the 'landing site' class. It is characterized by the different communities that are currently acting in it, the species that are exchanged or eaten in this site, and the last price at which these species have been sold (to the customers) or bought (by the fish traders).

By defining several agents in each of the various classes, one may obtain a global representation of the exploitation system thus modeled.

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[1] *A tactic corresponds to the practice of a given fishing gear in a given fishing zone, used for targeting given fish species. This notion has been extended and also corresponds to a particular landing site.*

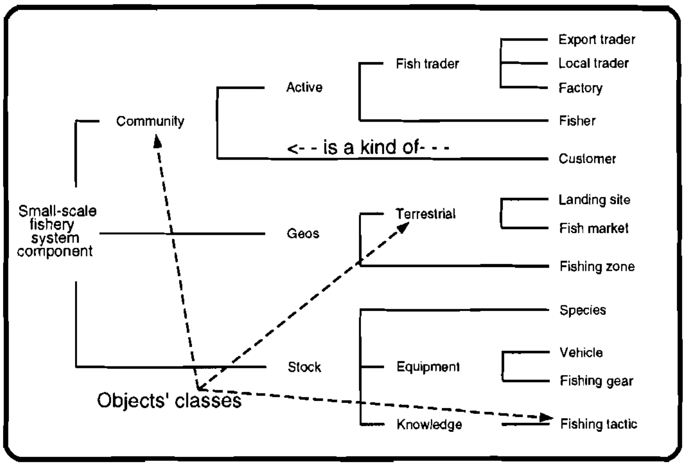

Fig. 2: Structural limits defined for the Senegalese artisanal fishery exploitation system (multi-agent class hierarchy).

2.2. The communication step

The only actions a computer agent can perform are sending messages to other agents, receiving messages from other agents and providing 'back-answers' by means of new messages[2]. The arrows on Figure 3 present an example of the relations constructed is this fashion. In this example, the *st-ky-2* fishing community needs to know the traders' demand for its species of jacks (Carangidae) in its current landing site. *st-ky-2* sends to the landing site Kayarland the message: "what is the trader's demand for jacks?" (messages 2+2'). The 'landing sites' specific behavior to this message is to send itself a message to know which traders are currently acting in it (*3,4*). The 'site' agent then sends the same message to all of these known fish trading communities (*5,5',5''*). Each trading community receiving this message is then able to answer it after an internal evaluation (step 6 stands for another combination of messages taking into account information about vehicles' maximum capacity, room available in vehicles, the market as demand for fish, the species preferred, the money available). The landing site then processes all the traders' answers and returns the answer back to the fishing community (*7,8,9*).

This process can be perceived as communication between agents (e.g., community *st-ky-2*) and their environment (e.g., landing site, known traders)[3]. In the sense of the model presented here, this corresponds to communities gathering information from their environment.

Almost all the functional representations of the fishery exploitation system are governed by this message-sending formalism: by successive nesting, sets of messages such as those just described can be gathered for more global tasks (e.g., 'knowing the traders' demand') which can in turn become part of an upper-level behavior (e.g., 'comparing different traders' demand at different, known landing sites'). Thus, sophisticated tasks and global behaviors can be represented.

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[2] *The messages are small computer routines;*

[3] *The filtering protocol enables the representation of uncomplete information. For example, in this case community C is not allowed to know about traders which are not at their usual landing place.*

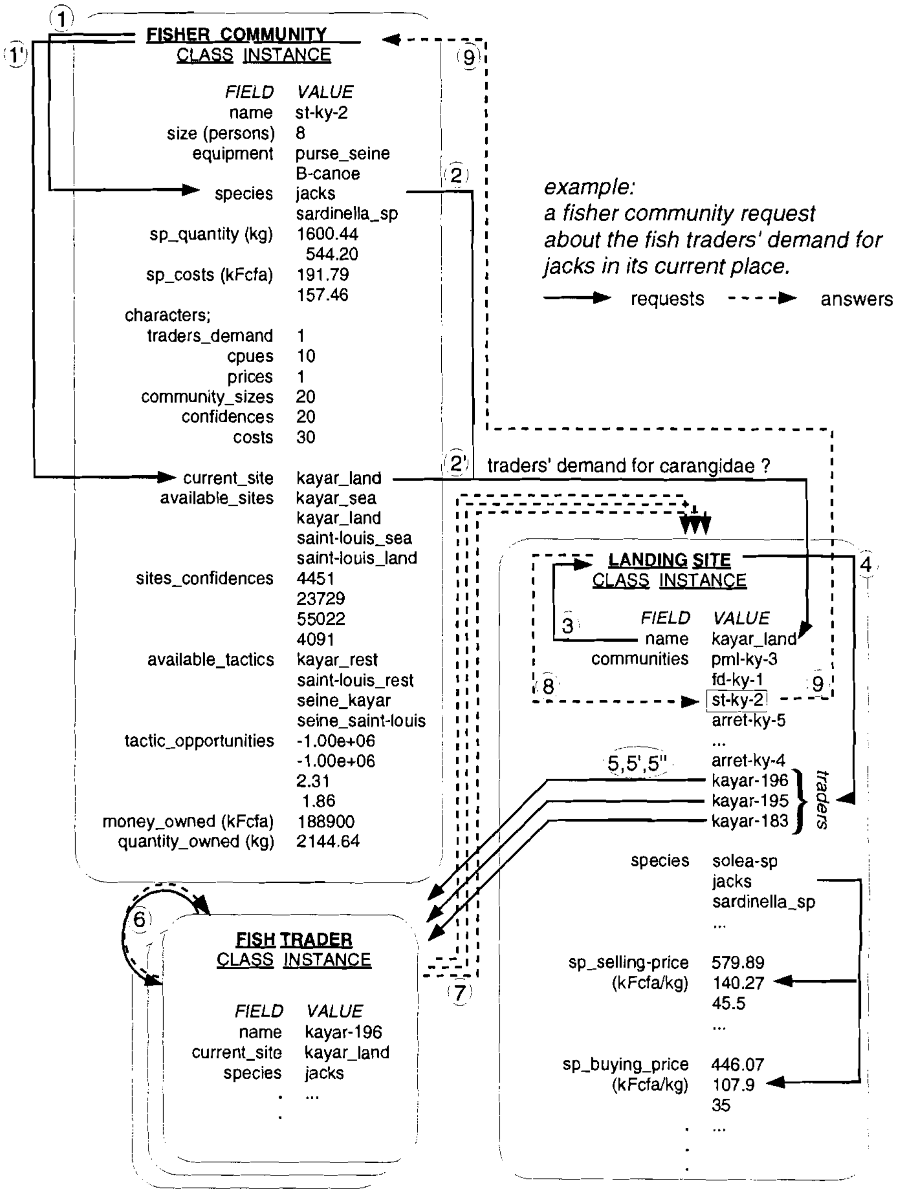

Fig. 3: Structure and communication between (computer) agents in the Senegalese artisanal exploitation system.

2.3. The decision step

When communities gather information of different kinds about their environment, they must decide what to do with this information (this need for choice is probably more acute when change occurs in the communities' environment). Under this hypothesis, decision processes must be paid particular attention.

Using previous works on communities' behaviors, common sense rules and *in situ* interviews, several criteria have been selected that may be involved in the communities decision processes. The conceptual scheme retained and represented undertakes three classes of criteria: the objectives to reach (e.g., fishing, earning money) at the time of the decision process, the information gathered from the environment, and the communities' character and habits.

Using the representation described in the communication step, local tasks can be represented. The example in Figure 4 represents the decision process of a fishing community agent. In this example, the community already sold its fish, needs to go back to fishing (objective) and must decide which kind of fishing tactic it will use (from the different behaviors it can exhibit).

The process follows the circular path. The community objective is assumed to be already defined (here: 'going fishing') and not represented here. The process begins with an 'information step' divided in three main parts: the community first considers what equipment it owns related to its objective, in this case, a canoe, gillnets and lines (a,b). The community can then obtain information from the corresponding fishing tactics (here, gillnet fishing tactic or line fishing tactic 's agents). Thus, it gets connected to a new information flux constructed by the particular tactics[4]. In this case the community may know about the species potentially targeted , their fishing yields, their prices at the different landing sites (c,d,e). Also, these communities are related to other contexts such as fish traders' demand for the species they can target or the moves needed to practice a given tactic. Each time they practice the tactic, the fishing communities' own confidence for this tactic will change: when, at preceding time steps, fishers 'succeed' or 'fail' in practicing a given tactic, they gain or lose confidence in their action. This implementation, partly based on confidence theory (Le Cardinal and Guyonnet, 1994), provides an evaluation criterion for the corresponding decision processes: the communities become experienced and take into account this experience during the decision processes.

Each of the evaluation criterion can be given a priority depending on the 'social characters' of the community. For example, depending on the fishery investigated, a community can be more influenced by the cost implied by its choice than by the benefit it can gain from it. In this example, the 'moving costs' choice criterion will be given more weight than the selling price of species or fishing yields. The character field described in Figure 3 accounts for this balance between each evaluation criterion. The weight given to each criterion (e.g., *confidence* 0.20) will lead each community to different choices when faced to a given situation. By combining these weights, it is possible to represent different types of communities (e.g., communities of young men preferring yields and prices or of old men to whom confidence or community size may be more important). This quantitative transcription can be used to input qualitative or fuzzy knowledge about the system's actors. An example is provided for the community size's criterion in the simulation results (first simulation, t_{26}).

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[4] *In the computer model, fishing tactic are agents in the strictly same way the communities are. They are able to send and receive message depending on the value of their differents defining fields. They can therefore communicate with other types of agents.*

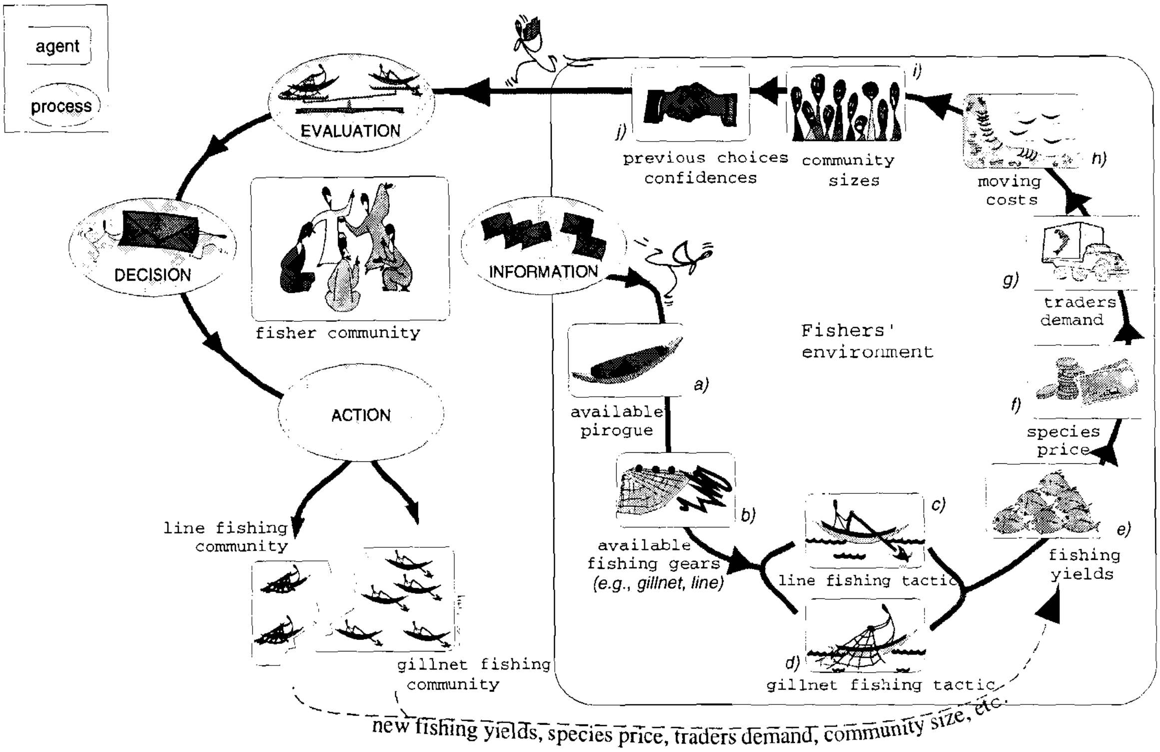

Fig. 4: Schematic representation of a community agent decision process.

In the following step (*evaluation*), the communities weigh each of these information, depending on their experience and character and produce a decision. This decision leads one part of the fisher community to choose line fishing and the other one gillnet fishing (given *VL* the expected value of line fishing and *VG* the expected value of gillnet fishing, the community percentage choosing gillnet will be *VG/VL+VG*). The resulting action leads to dividing the community agent into two community agents, one practicing gillnet fishing, the other one going on with line fishing. This partition induces changes in the fishery system. For instance, the distribution of fishing effort will be different from before; it will lead to new fishing yields, new species prices, new traders demand, new community sizes, different confidences for each of the new communities and, therefore, changes in all further evaluations and decisions (i.e., the next simulation's time step).

Since 'good' or 'bad' choices may govern adaptation to change, this decision-process level constitutes an important step to represent whole system's dynamics. Observed dynamics of Senegalese artisanal fisheries were thus simulated using a simplified version of this model (Le Fur, 1995). Good agreement was obtained between *in situ* observations and model simulation. It was concluded that this decision process model would be reliable in simple cases.

2.4. The activity step

Apart from choosing, fishers also move, practice fishing, sell or give their catches. Through change, performance and results of these activities can also determine communities' dynamics. A decision process sub-model was completed to account for these processes. These tasks have been implemented and organized through an 'activity cycle' in which the decision process model is included.

The resulting activity cycle of this third modeling step is presented on Fig. 5 for the case of the fisher communities. The whole cycle accounts for one time step. It arbitrarily begins when the fishers at a landing site decide what would be the best fishing behavior. The decision process first occurs (the DP symbol locates the decision process model that was previously described). Once the fishers have chosen what fishing tactic they want to practice, they split into two communities and with one sailing towards the selected fishing site. This task performs the removing unsold fishes, spending money for the journey depending on the available equipment, informing related agents concerned by this move (e.g., traders at the landing site left, arrival in the fishing zone). When fishers arrive at a fishing zone, they actually fish[5] and, depending on their success, change their confidence for the particular fishing zone and tactic choice selected. The

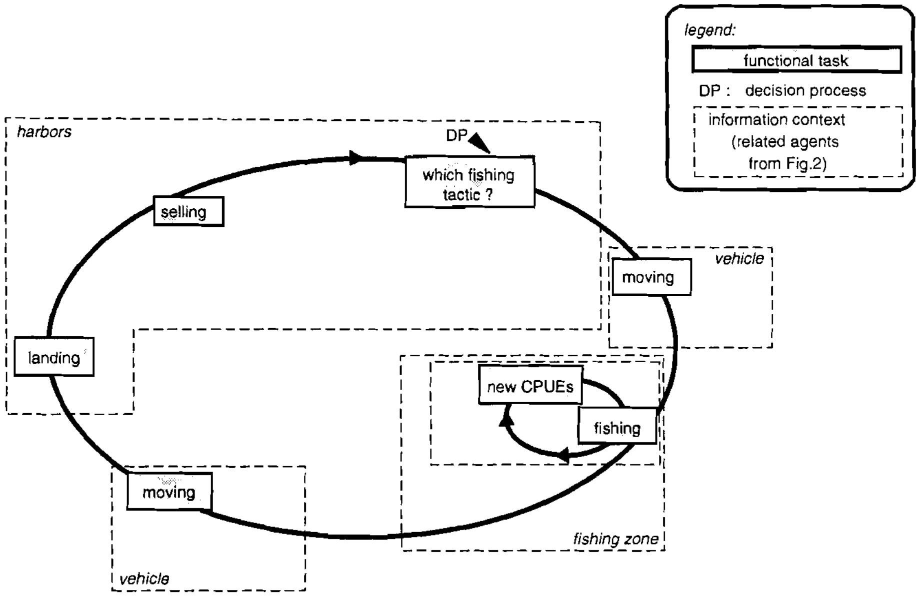

Fig. 5: Fishermen communities' activity cycle.

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[5] *In this step, fishing yields can be generated through various means such as observed data files or multispecies and multi-gears production model (Laloë and Samba, 1991). Response curves can also be introduced to simulate any event affecting fish stocks (e.g., stationery yields, catastrophe-like decrease/increase, sudden appearance of new species, etc.). The DAI formalism can be also used to make this task dependent on the gear the fishers own and choose, the species availability in this fishing zone and the number of fishers from other communities currently acting in this fishing zone.*

next task makes them go back to the landing site (given by the chosen tactic, see decision process step). Selling occurs, money and fishes are exchanged, new confidences and new information are gained. The results of this activity will lead to new choices in the next time step.

In Senegal, fish-traders play as an important role as fishermen in the artisanal exploitation system's dynamic (Chaboud and Kébé, 1989). A second cycle accounts for fish-traders' choices and activity. It has been formalized in the same way as the fishers' (Fig. 6). The traders' cycle starts when the fish traders have sold their fishes in a given market place. They then have to choose a harbor where they will supply for new fishes. Another task makes them move towards a given landing place. There, money and fishes are being exchanged.

To account globally of the exploitation system's dynamics, these two cycles have been connected and organized in an upper level 'interaction step'.

2.5. The interaction step

Exchanges of fish and money are the main links between traders and fishers, and thus, transactions play an important role in the dynamics of the system. In Senegal fish prices may change fourfold during the same day (Chaboud and Kébé, 1989). Moreover in Senegal, bargaining is an important social phenomenon; almost a social duty. Price setting was formalized to account for this through a 'bargaining' sub-model which represents selling as private contracts between different communities. At the beginning of the 'transaction task' (Fig. 6), each selling community gets information from its surroundings (i.e., send messages). It evaluates the cost caused by the previous activity (moving, fishing) and proposes its price. The buyer (fish trader, customer) considers its previous costs or needs and put forth its own proposition.

In particular game theory applications (i.e., in cases where information is incomplete), the Bayes equilibrium states that, in an auction, the best choice for an actor is to propose a third of its maximum price (Guerrien, 1993). As bargaining may appear functionally close to auctions, we adapted this hypothesis for the selling transaction: sellers propose three times their lowest price, buyers propose a third of their maximum buying price. The final price of the transactions will be values between the sellers' lowest price and the buyers' highest price. In decision theory, given A a set of acts, E the possible states of an environment, the possible consequences (C) can be described through a probability distribution. A rule of thumb (Charreton and Bourdaire, 1985) establishes the possible mean of this distribution (i.e., final price) as:

$$\frac{\begin{array}{c}\text{maximum of the distribution } (\textit{i.e., fishers' price proposal}) \\ + \text{ minimum of the distribution } (\textit{i.e., traders' price proposal}) \\ + \text{ mode } (\textit{i.e., final price in this port for the last transaction concerning this species})\end{array}}{3}$$

In a given time step, the evolution of the traders' arrival in the port and their successive transactions cause the harbor's fish prices to evolve. These fluctuations will again intervene in the agents' choices.

Once the fish traders have bought their fishes, they proceed to another decision process, choose a selling market place and move towards it. To obtain an equilibrated presentation of the interaction's cycle and a controlled input/output for the fish and money fluxes, two more simple cycles have been provided. The first accounts for the local consumers in the country — fish is the major source of protein in Senegal (Chaboud and Kébé, 1989). The other cycle accounts for the

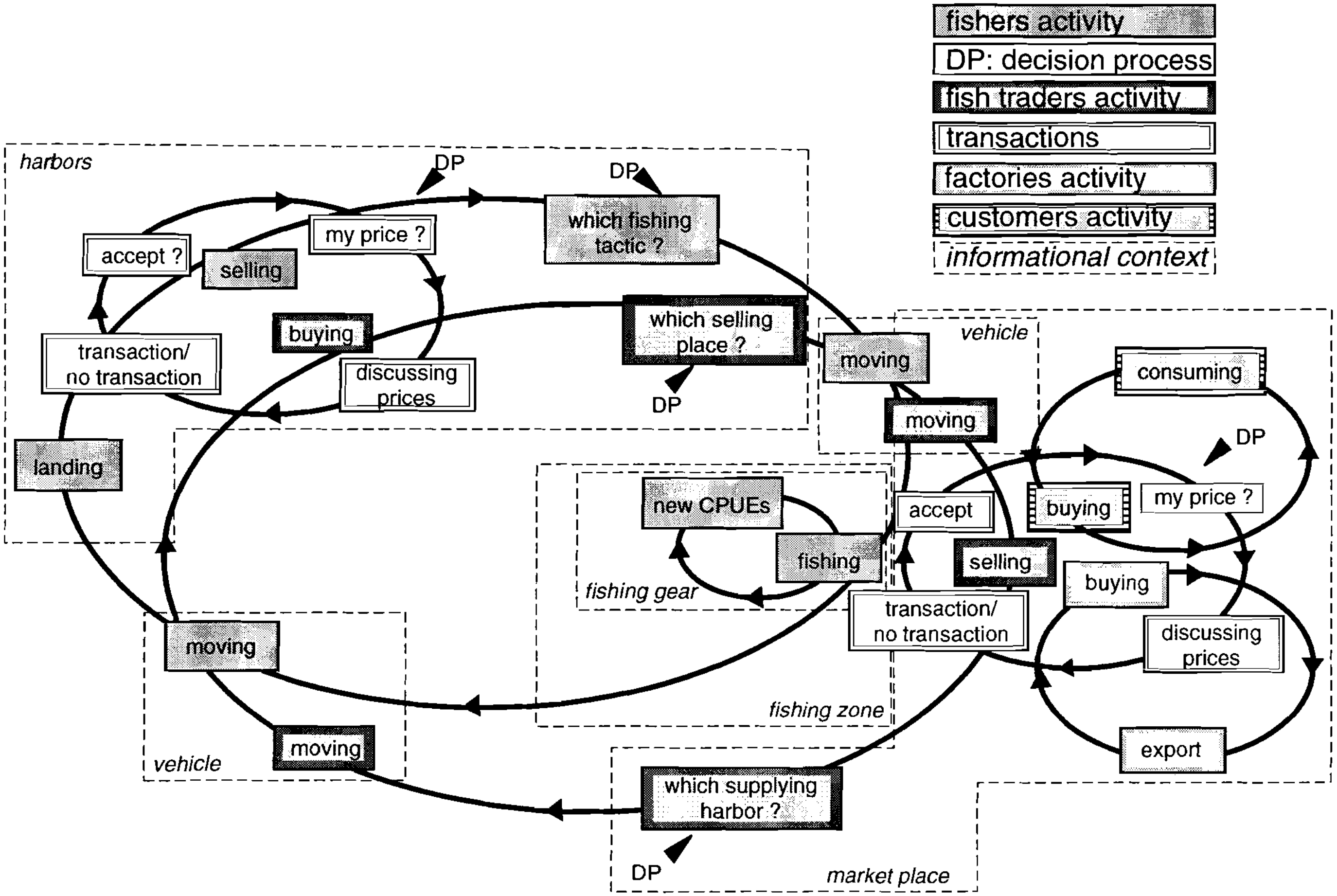

Fig. 6: Dynamics of the fishery system interaction model.

plants involved in fish exports — exports represent 40% of the Senegalese artisanal fishery production (Dème, 1988). Bargaining was duplicated to account for interactions between consumption requirements and supply fluctuations and was modeled as part of the fish traders' activity cycle. This bargaining generates the market prices. This also allows to take into account the fish market as another factor of change in the exploitation system.

At the end of this step, the exploitation model is a reliable functional system of interconnected levels. The external sources of fluctuations can be generated by the dynamics of the resource, by changes in national consumption, by international market prices, or by equipment and fuel costs. From the dynamics point of view, during a simulation, the communities' objectives will change depending on the phase where they stand in the activity cycle (fishing, selling, moving, buying, consuming). Then, from one objective to the other, from one type of community to another and from one environment to the other, the decision process will lead to different (adaptative?) choices. The resulting activities will modify the contexts through time and, by feed-back, influence the various evaluations processed by the human communities.

3. SIMULATION RESULTS

Using this model, we attempted to simulate the observed Senegalese fishery exploitation. For this purpose, available observed data were selected and formatted. Several quantitative data sets were used: artisanal fleet monitoring data, by fishing gears and fishing places (CRODT, 1990), fishery yields for several species and types of engine, monitored daily at the various landing sites in Senegal (Ferraris *et al.*, 1993; Laloë, 1992), species composition for each fishing tactic (Laloë and Samba, 1990; Ferraris and Samba, 1992; Périnel, 1992), markets and fish traders characteristics and distributions of traded species (Chaboud et Kébé, 1990), geographical information on the different sites, technical information such as vehicle costs, capacities and abilities (Chaboud, 1985), fish consumption rates in the different cities of Senegal (Chaboud and Kébé, 1990) etc. Most of the data selected for the simulations refer to 1986-1987, where the largest set of markets and consumption data was available. The communities simulated are distributed through the different fishing and trading communities, markets and harbor places, tactics and habits. In the initial conditions of the experiment (t_0), the whole system communities represent 3 193 fishing teams, 1 278 traders, 75 479 customers, 1 factory (standing for all exportation fluxes). 14 market places, 9 landing-sites, 13 fishing zones, 5 fishing gears and 6 vehicle types; 21 types of fish species and 43 fishing tactics are also described. Each community agent is given 200 000 FCFA/day (1 US $ ≅ 280 FCFA in 1986/87) for the first step of the simulation and allowed to act for several time steps. Fishing yields are tactic-specific and remain constant throughout the simulations.

Global activity indicator: The initial issue is defined as the fishery's response to change. For feed-back at this level, we developed an indicator of global system's response: in the multi-agent simulation model, each time a message is sent or received by an agent, information can be obtained from the computer (in one simulation time step, million messages are sent). Depending on the aspects of the system, that are studied (e.g., productivity, strategies, distributions), printed messages can be filtered to keep only the ones corresponding to the investigated fields (e.g., moving, selling, fishing, choosing, bargaining). Depending on the intensity of the activity, the amount of messages at a given time step will fluctuate. The procedure thus saves, at each time step, all printed messages onto the hard disk. Depending on communication intensity, these messages' files can contain from several hundreds to several hundreds of thousands lines. The evolution of the file sizes was traced from the beginning to the end of the simulations as an indicator of the 'system's activity' (when no messages are produced, that the system is 'inactive' or 'dead').

Some results obtained from these simulations are described below[6].

In the first simulation, only the fishers' activity cycle (Fig. 5) is considered. The total number of fishers in the system is kept constant throughout the simulation as are the selling prices at the different harbors. Moreover, fishers' communities are allowed to sell their entire catch every time they proceed to the selling task.

The curve on Figure 7 provides the evolution of the system's activity indicator for these simulation. System's activity quickly expands at the start of the experiment, producing diversity in the communities[7]. Activity then decreases through time. The system was allowed to run for 60 time steps (one step equals 15 days in this example). During the simulation, three kinds of change have been introduced; a 'biological' change at t_{11}, a 'behavioral change' at t_{16} and a 'technical change' at t_{45}. The resulting reactions of the system were studied.

A) For perturbation introduced at time t_{11}, the catches of sardinella species was lowered by a factor of 10 (from 300 kg per trip for a purse seine to 30 kg/trip). This resulted to no reaction of the whole system (Fig. 7, point A). In the simulated fishery, sardinella is mainly caught by purse seine; analysis of the simulation results (not shown) revealed that at that time, a purse seine tactic would have survived this change, by switching to jacks (carangidae) (in the model, purse seine fishing tactic allows fishers' communities to target both sardinella and jacks species; this type of behavior is observed in the artisanal Senegalese purse seine fisheries (CRODT, 1989)).

As the ports' prices were maintained constant throughout the simulation, the price of jack could have remained sufficiently high to maintain interest in seine fishing.

B) The second change consisted in giving more weight to the 'community-size' criterion. During the decision processes, this criterion provides a mean for fishers to take into account the size of the other communities as a confidence indicator for the practice of their tactic (see 'decision step', Fig. 4): the more people practice a given tactic, the safest it will be to choose it, and vice versa. Previous studies, for instance, in economics (Lesourne, 1990) and in fisheries (Allen and McGlade, 1986) have pointed out the role of risk-aversion in dynamics where both 'followers' and 'risk takers' coexist. The change introduced here consisted in accentuating this character, e.g., more old fishers in the fishery, or more uncertainty in the input dynamics.

When this change was introduced (t_{26}, point B), the systems' activity dropped, while the number of agents remained constant. The modeled system lost activity because of this change. Nevertheless, it did not collapse, but reached a new, and lower stationary state. After the period of change, the system remained at this low level, but with a slightly descending slope.

C) To investigate the absence of the systems' reaction to the change in sardinella purse seine fishing yields at t_{11}, a final perturbation was induced at t_{42}. This consisted of allowing purse seine fishers to practice line fishing (i.e., 'providing suitable canoes for practicing both types of fishing'). The effect of this change on the whole system results in an 'electric potential' type response (Figure 7, point C). The fishers activity suddenly dropped a new, higher level (it 'benefited' from the change). The system's activity thereafter went on with a slightly decreasing slope.

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[6] *At the time of this paper's writing, the results were work in progress: from the technical point of view the coherence of the system was entirely validated and some of the basic sub-tasks not represented in satisfactory fashion (e.g., the task for evaluating the costs involved by the community activities only takes moving costs into account).*

[7] *At the start of the experiment, some choices are forbidden until the community agents gather all available information. After the agents get more information, their range of choices enlarges. As these choices are considered, these very new possibilities create new communities, which increase the systems' activity.*

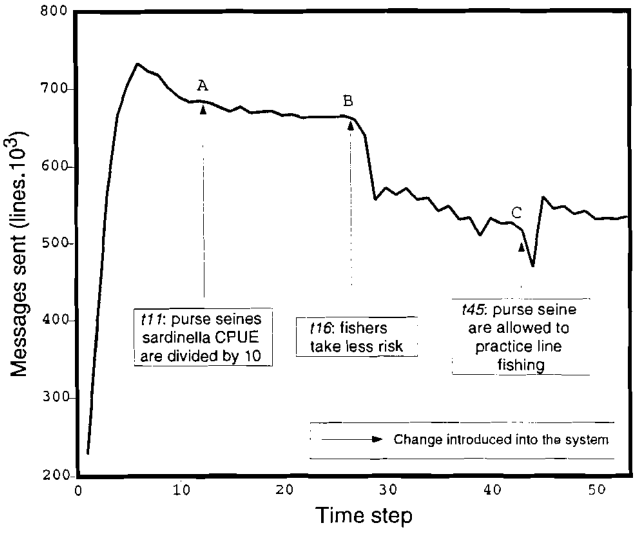

Fig. 7: Change of the 'system's activity' indicator during the first simulation (see text).

In a second simulation, the extended exploitation system described in Figure 6 was investigated in some details. The model was allowed to simulate traders' activity cycle, bargaining and transaction processes and the dynamics of other, related agents (markets, factories, customers, vehicles). This simulation was first run during 50 time steps, with the total number of individuals in the system kept constant. However, economically unadapted communities were rejected: when, through successive activity cycles, a given community comes to the point where it is in debt by more than 1500 kFcfa/person, it is ruled out of the system (the agent is removed). During the simulation, two changes were introduced in the system.

* at t_{11}, a sudden increase in the 'fish demand' was simulated. This was realized at the local level (communication step) by multiplying the size of each consuming community agent in the different market places by ten;

* at t17, the past experience of the fishery was removed (i.e., the confidence fields described in the communication step of all communities have been set to zero);

* Finally, a test simulation was run with the same initial conditions, but with no change introduced in the system.

The results, in Figure 8, present two evolutions of 'system's activity'. The first curve accounts for the simulation with changes introduced in the system and the other one without change (control). As in the first experiment, the system's activity first explodes when the fishery model becomes 'accustomed' to its new environment. The activity then starts to decrease.

Unexpectedly, the first perturbation at t_{11} has no effect on the system. Two selected generic variables were plotted on Figure 9: the total size of agents (whole community size) in each active type (fish-traders and fishers) and the amount of money earned by each agent from the start of the experiment (money/agent). It appears from the figure that multiplying fishing consumption (first change) provided more possibilities for traders to sell their fishes. This resulted in an increase of traders' incomes but no change on the fishers' earnings. Nevertheless, the systems' activity did not benefit from this change and went on decreasing (the reference curve on Figure 8 presents another possible scenario for the system's evolution).

The second perturbation, at t_{17}, relates to the loss of the experiences by the agents. System's activity drastically declines but the system does not collapse. The activity goes on in another slowly decreasing dynamics. The community size's slopes did not change nor did the money earnings.

The simulation was run, finally through 400 steps with no more change introduced. The results are presented on Figure 10. Some of the variables clearly fluctuate when others remain similar. Moreover, in several parts of the simulation, the monetary benefit of one of the two types of community (fishers, traders) occurs to the prejudice of the others (see arrows 'inverted evolution'). Finally, for the whole range of the simulation, activity constantly declines. However, the system does not collapse but becomes a very small, undiversified system (48 fishers only practicing in 3 harbors, 189 fish traders with small vehicles selling in 2 markets). At the same time, the agents' personal benefit increases. It can be here noticed that this configuration of a small fishery exploitation is similar to that described earlier by McGlade and Allen (1984).

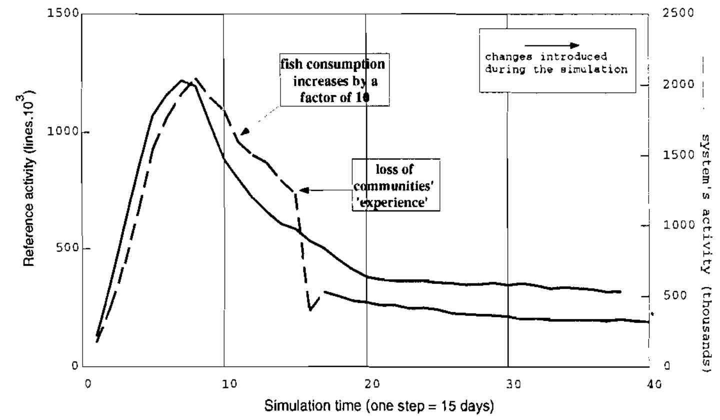

Fig. 8: Activity observed during extended system's simulation (with and without changes).

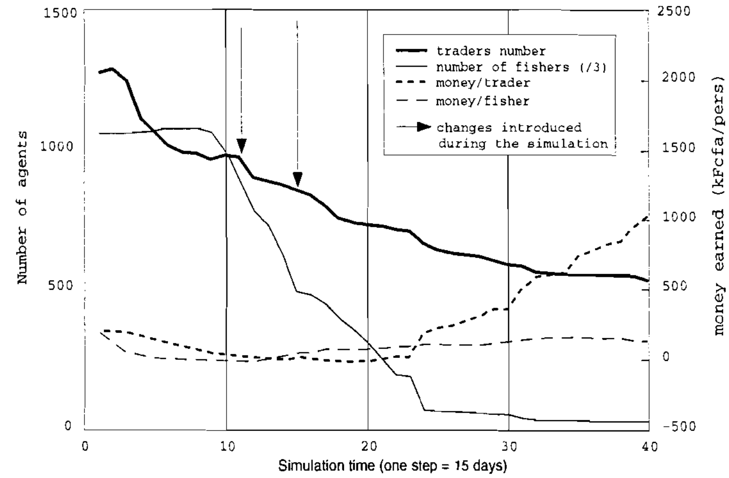

Fig. 9: Sizes and earnings of communities during the extended system's simulation.

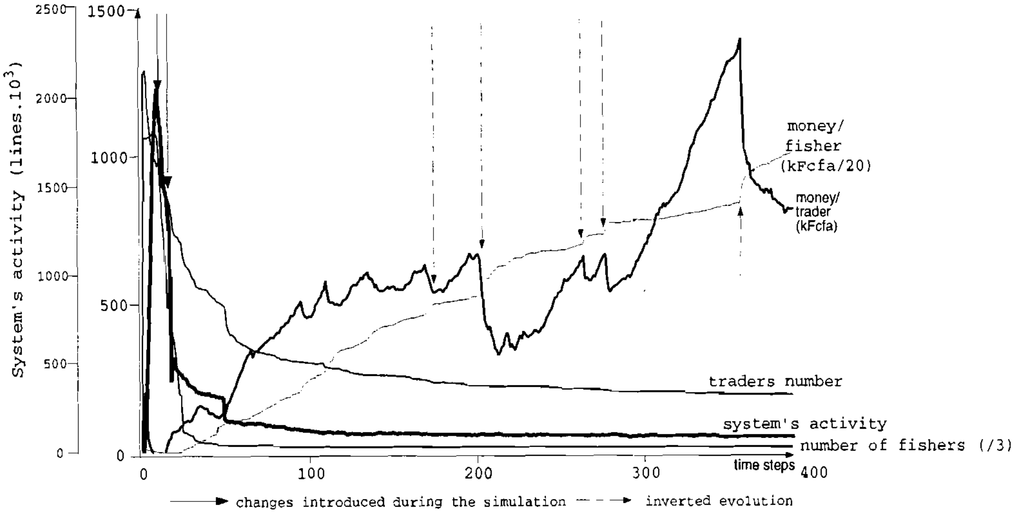

Fig. 10: Long term simulation of the extended system (extension of Figures 8 and 9).

4. DISCUSSION

Some parts of our modeling approach are discussed, notably: the modeling tools and limits of the hypotheses, the results of the simulations and the possible use of the approach.

4.1. Modeling tool and hypotheses limits

The choice of a thin 'granularity' implies that a large set of information must be introduced at the beginning of the simulations. The model structure then generates a huge amount of intermediate and final results, which makes such a system hard to validate.

The 'systems activity' indicator closely depends on the filter chosen for the messages. In this case, the indicator was mostly composed of choices, and bargaining messages (offer a price, refuse, etc.). It was therefore closely dependent on the number of communities (i.e., behavior diversity). More objective methods (e.g., statistics) should make this indicator more robust.

The communication step may not be viewed as occurring at the same conceptual level as the other steps of decision, action, interaction, etc. Indeed, message sending between agents are computer processes that intervene at each level or cycles where reality is simulated (Treuil, pers. comm.). Information therefore appears to create the ability of the exploitation system to adapt, but this may be a bias of the multi-agent formalism that was used.

4.2. Results

At a global level, a given change can produce unexpected effects as well as expected effects or no effect at all. In the first simulation example, the increase of communities' aversion to risk produced a large modification of the systems' dynamics, whereas a drastic lowering of sardinella fishing yields did not. Sensitivity analysis seems necessary, therefore, to better understand the results.

In the second simulation, an increase of fish consumption led to an increase of traders' earnings, but this monetary effect did not propagate all the way towards the fishers. A similar example was recently encountered in the Senegalese exploitation system: just after the currency devaluation at the beginning of 1994, artisanal fish exports increased. The fish traders interviewed in Kayar felt satisfied with the new situation whereas the fishers were negatively affected by the change. It appeared that the fishers went on selling their fishes at the same price, while fish traders were selling theirs at the new international price (without telling the fishers). The problem was finally partly solved by the fishers 'syndicate' which ruled on the prices (Le Fur, pers. obs.).

In each of the reported simulations the systems' activity slope is always descending. It therefore looks as if the system tends to collapse (other simulations not shown here confirm this result). From the processes represented in the model, it appeared that the agents' possibilities are too restricted to fully explore their environment. Indeed, if a fisher community can get information about two possible tactics, if a drastic change occurs in the environment that greatly affect both of the tactics, the community will not have the mean to adapt[8]. This case occurred for the purse seine in the first simulation: when the sardinella catches were lowered at t_{11}, no change occurred since the communities went on fishing for jacks. When these purse seine fishing communities were allowed to practice another fishing tactic (line fishing at t_{42}), most of them changed to the new tactic, as if they were unsatisfied with their current earnings (poor catches of sardinella). It will be noticed that this also resulted in a higher level of activity in the system (and thus, to better adaptation of the system).

4.3. Extension of the model

The communities fish, sell, move, they become experienced through several decision processes. Nevertheless, they still are only concerned with one activity objective. For example, the fisher communities can only decide which fishing

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[8] *At the computer level, this phenomenon seems to come from unexploited possibilities: since the agents' fields are defined at once, a fisher community with its usual species or a fish trader with its potential selling markets will be unable to change if their knowledge remains static. These field values define the information networks available to each agent. The problem there appears to give the ability for the agents to change their sources of information (see adaptation step, next paragraph).*

behavior to go on with. To better model change, it would be interesting to complete the adaptation scheme with new 'reality-like' choices such as 'am I satisfied with my current situation?', 'do I get the best context to work?', 'is it profitable to invest?' or 'am I happy to be a trader?'.

To represent these processes, the model could formalize a new adaptation step embedding the interaction step. This 'adaptation step' is tentatively described in Figure 11. The whole model described is here considered as one global task, part of an upper level system's cycle where a generic decision task concerns every agent. In the DAI formalism, the previous cycle is considered as a one unique task corresponding to producing (i.e., working). In the same way two other cycles (i.e., tasks) can be produced. In each of these new cycles, communities can decide not to produce, fish, sell, move, but also to adopt new fishing tactics (buying gillnet for example will acknowledge new available information on species, traders, etc.), to buy bigger vehicles or new fishing gears. In the computer model, this gives the possibility for the agents to obtain more information from other agents in the system. The community can even decide to change more drastically ('mutate' in Fig. 11). This last task can express, for instance, changing jobs (fishers becoming traders), leaving the fishery, becoming industrial workers, etc. At this upper level, communities can adapt through several goals and not only through their producing activity (they have more choices and possibilities to adapt). These three upper cycles are driven by another upper level cycle. In this 'adapt' cycle, the community agents evaluate their current state and, using the same decision process model, choose the best from the three activity cycles.

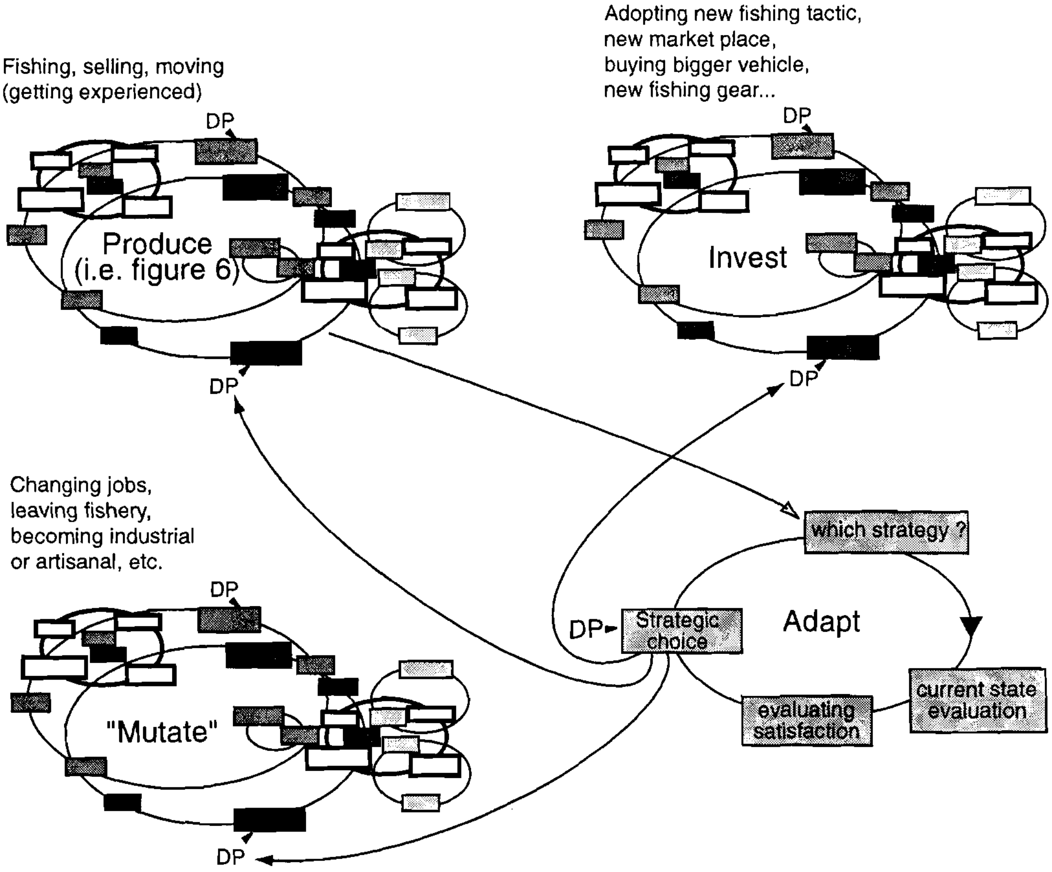

Fig. 11: Towards an adaptation step?

CONCLUSION

The initial issue was founded on a global perception within which the reactions of fisheries to change can be studied as a reduced set of global response curves. This approach is as a simple way to study and understand change and its possible effects on a complex fishery exploitation system.

The hypothesis of a global system, and multi-agent formalism makes it possible to represent a system's global behavior based on local mechanisms. Moreover, through successive modeling steps, we can successively deal with *communication*, *decision*, *activity* and *interaction* steps. We finally proposed a new *adaptation* step. This modeling scheme, 'from global to global through local processes', may be proposed as a generic mean to model and investigate the dynamics of exploitation systems in general.

Some of the simulation examples provided unexpected results and may require the current 'reality' transcription to be improved (this was discussed as a possible bias of the approach). Despite this, it proved possible to simulate different local changes in the same system, and to simultaneously analyze a global systems' behavior[9]. The fine 'granularity' selected for the model also made it possible to study a large array of local indicators (species fluctuations, community confidences, prices' evolution, distributions of tactics, etc.). Thus, if change occurs in real systems, it appears possible to better identify that part of the system from which good or bad consequences may be expected.

ACKNOWLEDGMENTS

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[9] *The simulations presented here are only concerned with static, punctual change. It would be interesting to study the effect of dynamical changes such as trends, inflations, continuous depletion, etc.*

REFERENCES CITED

Allen P.M. and J.M. McGlade. 1986. Dynamics of discovery and exploitation: the case of the Scotian Shelf groundfish fisheries. *Can. J. Fish. Aquat. Sci.*, 43(6):1187-1200.

Bagley R.J. and D.J. Farmer. 1991. Spontaneous emergence of a metabolism. *In*: C.G. Langton, C. Taylor, J.D. Farmer and M.S. Rasmussen-Addison-Weslay. *"Artificial life II", SFI Studies in the Science of Complexity*, 10: 93-140.

Bousquet F., C. Cambier, C. Mullon and J. Quensière. 1992. Simulating fishermen society. *In*: *Proceedings, simulating societies symposium*, University of Surrey, April 1992.

Chaboud C. 1985. Le mareyage au Sénégal. *Doc. Scient. Cent. Rech. Océanogr. Dakar-Thiaroye*, 87, 112p.

Chaboud C. 1992. Etude de cas : la pêcherie d'anchois du Pérou - la crise de 1972-73. *In*: Recherches interdisciplinaires et gestion des pêcheries. CIEO-890276, Halifax: 111-151.

Chaboud C. and M. Kébé. 1989. La distribution du poisson de mer au Sénégal: commerce traditionnel et interventions publiques. *Cah. Sci. Hum.*, 25(1-2): 125-143.

Chaboud C. and M. Kébé. 1990. *Commercialisation du poisson de mer dans les régions intérieures du Sénégal (données statistiques)*. CRODT-ISRA, contrat FAO 695 TCP/SEN/6653(t), septembre 1990, 300p.

Champagnat C., A. Caverivière, C. Conand, P. Cury, J.R. Durand, A. Fontana, A. Fonteneau, P. Fréon et A. Samba. 1983. *Pêche, biologie et dynamique du tassergal (Pomatomus saltator, L., 1766) sur les côtes sénégalo-mauritaniennes.* Trav. Doc. ORSTOM, Paris, 168, 279p.

Charreton R. and J.M. Bourdaire. 1985. *La décision économique*. Presses Universitaires de France., Coll. Que sais-je?, ISBN 2-13-039042-0, 125p.

Chauveau J.P. 1984. Histoire de la pêche maritime et politiques de développement de la pêche au Sénégal. *In*: *Colloque Littoral, Milieux et Sociétés, Boulogne/mer*, nov. 1984, 37p.

Chauveau J.P. 1988. *Note sur l'histoire de la motorisation des pirogues de pêche maritime artisanale au Sénégal: préconditions et rançon d'un succès précoce.* Séminaire d'Economie rurale CIRAD/MESRU - Economie de la mécanisation en région chaude, Montpellier, sept. 1988.

CRODT. 1989. Statistiques de la pêche artisanale maritime sénégalaise en 1987. *Arch. Cent. Rech. Océanogr. Dakar-Thiaroye*, 175, 85p.

CRODT. 1990. Recensements de la pêche artisanale maritime sénégalaise entre Djifère et Saint-Louis, mai et septembre 1987. *Arch. Cent. Rech. Océanogr. Dakar-Thiaroye*, 181, 49p.

Dème M. 1988. Les exportations de poissons de la pêche artisanale sénégalaise. *Doc. Scient. Cent. Rech. Océanogr. Dakar-Thiaroye*, 85: 1-27.

Drogoul A. and J. Ferber. 1993. *Multi-agent simulation as a tool for modeling societies: application to social differentiation in ant colonies. Decentralized AI, 3.* C. Castelfranchi and E. Wesner (eds.). North Holland Pub.

Erceau J. 1994. Complexité et simulation: les systèmes multi-agents. *In*: *44èmes rencontres du programme Modélisation de la Complexité: l'intelligence stratégique de la complexité, Aix-en-Provence, 9-10 juin 1994. Cahier des Contributions*, 11p.

Ferber J. 1994. La Kénétique: des systèmes multi-agents à une science de l'interaction. *Rev. Int. Systémique*, 8 (1): 13-28.

Ferraris J. et A. Samba. 1992. Variabilité de la pêche artisanale sénégalaise et statistique exploratoire. *In*: *Seminfor 5: Statistique impliquée*, F. Laloë (coordon.), ORSTOM, Paris, coll. Colloques et Séminaires: 169-190.

Ferraris J., V. Fonteneau et A. Sy Bo. 1993. Structuration de la base de données "Pêche Artisanale" et chaîne de traitement informatique. *Arch. Cent. Rech. Océanogr. Dakar-Thiaroye*, 192, 207p.

Fonteneau A. et C. Champagnat. 1977. Vers une politique de pêches: éléments pour un aménagement rationnel des ressources marines vivantes. *La Pêche Maritime*, Mars 1977: 3-7.

Glantz M.H. and Thompson. (eds.). 1954. *Resource management and environmental uncertainty: lessons from coastal upwelling fisheries*. John Wiley, New-York: 81-106.

Guerrien B. 1993. *La théorie des jeux*. Economica, Paris, 1993, Economie Poche, ISBN 2-7178-2470-7.

Kébé M. et M. Dème. 1994. *Impact de la dévaluation sur le système pêche artisanale maritime sénégalaise.* Cent. Rech. Océanogr. Dakar-Thiaroye. Bur. Anal. Macro-économiques Agricoles, mars 1994:1-9.

Laloë F. and A. Samba. 1990. *La pêche artisanale au Sénégal: ressource et stratégies de pêche*. ORSTOM, Paris, coll. Etudes et Thèses, 395p.

Laloë F. and A. Samba. 1991. A simulation model of artisanal fisheries of Senegal. ICES Marine Science Symposium, 193:281-286.

Laloë F. 1992. Collecte d'information sur la pêche artisanale au Sénégal. *In*: *Seminfor 5: Statistique impliquée*. F. Laloë (coordon.), ORSTOM, Paris, coll. Coll. et Séminaires: 37-45.

Le Cardinal G. and J.F. Guyonnet. 1994. Comparaison de trois approches stratégiques de la coopération. *Rev. Int. Systémique*, 8 (1): 105-122.

Le Fur J. 1995. Modeling adaptive fishery activities facing fluctuating environments: an artificial intelligence approach. *AI Applications in natural resources, agriculture, and environmental sciences*, 9(1): 85-97.

Lesourne J. 1990. *Economie de l'ordre et du désordre*. Economica, Paris, introduction:7-25.

McGlade J.M. and P.M. Allen. 1984. The fishing industry as a complex system. *In*: R. Mahon (ed.). Towards the inclusion of fishery interactions in management advice. *Can. Tech. Fish. Aquat. Sci.*, 1347: 209-216.

Nowak A. and B. Latané. 1992. Simulating the emergence of social order from individual behavior. *In*: N. Gilbert (ed.). *Simulating societies*. Symp. Univ. Surrey, Guilford, UK, 2-3 april, 1992, 13p.

Périnel E. 1992. *Analyse numérique/symbolique des tactiques de pêche artisanale au Sénégal*. DEA Univ. Paris Dauphine, 54p.

Quensière J. 1993. De la modélisation halieutique à la gestion systémique des pêches. *Natures, Sciences, Sociétés*, 1 (3): 211-220.

Dome or U-Shaped Physiological Responses of Populations, and Ecosystems

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There is nothing so difficult as to hypothesize plausible causal relations in biophysical systems as to be without understanding of, or concern for underlying principles.

ABSTRACT

Clearly human manipulation and exploitation have taken the projected tolls in aquatic ecosystems, and show little promise of relent. The contrast between the successes of the two contemporary approaches to better understanding aquatic systems ecology, one based on principles of empirical physiological ecology, and the other based on parameterized population dynamic responses, is invoked to explain the present impoverished status of marine fisheries management. Decades have passed with few or no good examples of how to secure either 'sustainable yield', or even how to define it in a rational context. Given the historical perspectives on global patterns of climate-driven resource variabilities, the basic 'stability' concept is certainly inappropriate as a prime objective. Basic tenets of economics and general ecological principles have also been ignored as one resource population after another has been 'defined', regulated, negotiated, and litigated, while being systematically decimated in the name of economic stability, and short-term profit taking. Within this same

period the numbers of environmental and resource scientists have multiplied, yet the results of their efforts have been devastation, not conservation. Peer-induced mediocracy through vetted agency fund chasing has replaced quest for applicable knowledge. In fact, we have come full circle, to the point where all the emergent observing technologies and information systems that were suggested to be enhanced during the late 1960s and 1970s for needed monitoring of resource habitats and ocean and atmosphere systems, so that ecological resource status could be understood, have been dismantled, their promoters retired or moved on, and replaced by a generation of inept resource modellers. Agency funds, once available for primary research, are increasingly squandered on bureaucratic councils, committees, and litigation. It is no wonder that we are having to start over again, to link knowledge that we have had, with system knowledge that we could not obtain, to manage resources that are already pressed beyond any reasonable limits, by social systems that are in perennial denial.

RÉSUMÉ

Les activités anthropiques ont fait beaucoup de dégâts dans les écosystèmes aquatiques et font preuve de peu de signes d'amélioration. Le contraste entre les deux approches contemporaines utilisées pour comprendre l'écologie des systèmes aquatiques, l'une fondée sur les principes empiriques de l'écologie et de la physiologie, l'autre fondée sur les modèles quantitatifs de la dynamique des populations, est évoqué pour expliquer les pauvres résultats de l'aménagement des pêcheries. Les décennies ont passé sans apporter aucun exemple permettant d'assurer un niveau soutenu des captures, ou proposant un contexte rationnel à l'aménagement. L'observation sur longue période montre que la variabilité des ressources est déterminée par des changements climatiques globaux et se donner la stabilité comme objectif premier est certainement inapproprié. Les principes de base en économie et en écologie ont été ignorés, les ressources ont été les unes après les autres « définies », administrées, objets de conflits et de négociations, alors qu'elles étaient systématiquement décimées au nom de la stabilité économique et du profit à court terme. Durant la même période, le nombre de scientifiques spécialisés dans l'environnement et les ressources s'est multiplié ; aujourd'hui, on constate que les résultats de leurs efforts ont été plus dévastateurs que conservateurs. La médiocrité auto-entretenue par les scientifiques à la chasse de fonds de recherche a remplacé la recherche d'un savoir applicable. Les techniques d'ob-

servation et les systèmes d'information mis au point à la fin des années 60 et des années 70 étaient nécessaires au suivi de l'habitat des ressources, des océans et des systèmes atmosphériques, de façon à comprendre le statut écologique des ressources. Ils ont été démantelés, leurs promoteurs sont partis et remplacés par une génération d'inaptes modélisateurs des ressources. Les agences, bailleurs de fonds jusqu'alors disponibles pour la recherche de base, ont alors commencé à gaspiller leur argent pour des conseils et autres comités bureaucratiques. Il n'y a pas de doute, il faut tout reprendre à la base, repenser le savoir que nous avons acquis, identifier dans la dynamique des systèmes les éléments que nous ne pourrons pas obtenir, pour aménager les ressources déjà exploitées au-delà des limites raisonnables.

INTRODUCTION

Fishery science is an applied science, fraught with conflicting perspectives, and short, fragmentary information sets. Fortunately, we have the legacies of von Bertalanffy, Fred Fry, and their myriad intellectual grandchildren to guide us in interpretations of physiological responses by fishes to physical environmental variables. Kinne (1970, 1971) provides a thorough summary of the variety of known responses. Nearly all of these responses, alone, or particularly when combined, form U- or domed relationships with fish distribution and behavior.

Otherwise, we have a morass of virtual populations, computer generated pseudo-biological 'virtual reality', generally with more basis in mathematical convenience than precise empirical observations. The problems facing groups such CEOS include the responsibilities of explaining the patterns of cause and effect that have been hypothesized, and described. This is not a new challenge, it is simply a professional responsibility.

The vast information base from which anyone has to draw experience and help support innovations includes a huge, aging literature based on decades of careful laboratory studies, and long-term comparative studies of the sort advocated in recent decades by A. Bakun, R. Parrish and their colleagues. This tactic has been long practiced within the Fred Fry school of physiological ecology, originally with a focus on the fishes of the Great Lakes.

It was recently brought to my attention that William Ricker, putative father of North American stock assessment, spent his early efforts at the University of Toronto studying the consequences of environmental variability on trout populations. The global marine resource management focus on Ricker's equilibrium-based stock assessment methods is thus another example of a good start gone awry. Historically, most innovations tend to fail, although at their inception they often appear to be appropriate within the local context of the problems being faced.

In fact, this is a good example for problems in resource conservation science. Although it might have appeared that equilibrium-based population concepts might be applicable within the human life-span, it is the minuscule nature of a single generation, whether of humans, fishes, or daisies, and the denial of the naturally induced population variabilities, and the importance of marginal subpopulations, that has cost the world so dearly within recent decades.

In support of the CEOS effort to identify the causal processes in coastal pelagic fish population variations, and eventual development of rigorous forecast models, I hope to reawaken the concepts of physiological ecology within the context of a not-always-random, even quasi-cyclic series of environmental changes. These are not new concepts. They just get denied.

Laboratory studies are the reproducible, critical information sets that provide 'corrective lenses' that can facilitate interpretations of what are now distinct, but poorly defined illusions of understanding. Neill *et al.* (1994), using of Fry's (1947) concepts of 'environmental factors and scope', provide a unique series of discussions and insights into ecophysiological responses of fishes.

Due to the poverty of physical context observations since the adoption of ritual stock assessment tools, systematic translations of carefully constructed fisheries data sets have yet to provide sufficient evidence of direct causality, or even of firm categories of measurable and traceable processes with direct, predictable results. This goal will be difficult to obtain, but worth the effort. Once achieved it will mark the maturation of fisheries research into a predictive, rather than hind-cast science. Unless the interpretive process is completed, the CEOS efforts might well be labeled as only another 'novel' methodology, with little or no genuine basis. Such are the problems of getting a new concept onto the table for more than discussion as another oddity.

1. ENVIRONMENTAL FORCING AND SOCIO-ECOLOGICAL CONSEQUENCES: WHAT'S NEW?

Sears and Mérriman (1980) provide historical insights into oceanographic observations and the birth of oceanography as a science. An important consequence of the age of exploration by sea, via the sequence of events arising from ancient Persian astrology, through western civilization's fixation on astrology, were the developments of navigational tools. The chronometer eventually provided sailors means for locating themselves on the high seas, providing the capability to chart paths to and from new found opportunities. The history of exploration of our planet is about integration of known but poorly understood processes, technologies, and occult phenomena.

Some few examples will suffice to initialize my concerns. In 1786 Deputy Postmaster General of the American Colonies, Ben Franklin published the now famous map of his Nantucket sea captain cousin, Timothy Folger, to help navigators avoid the time consuming countercurrent motion of the Gulf Stream for vessels headed from England to the Colonies. A century later, in 1878, the U.S. Coastal and Geodetic Survey was formed, to provide mariners with information about the U.S. coastal environment, and harbors.

Alexander Agassiz (1835-1910) inherited a naturalists eye for biological correlates in his long career as an ocean scientist. He became an icon for the 'Father of Oceanography', in its broadest sense. Realistically, the first ancient mariner that logged his observations, and shared them, holds rightful claim to that title. Another historically important scientist, among a cohort of 19th Century 'naturalists', was Charles Darwin. His notebooks while a naturalist observer aboard the H.M.S. Beagle gave birth to an array of oceanographic, geologic, and 'marine science' questions, many of which remain largely unanswered to this date. In fact, we have a long list of true scientific heroes that can share the responsibility for progress in oceanography and related resource sciences.

It is difficult to conceive of where we might be without the influence of Matthew Fontaine Maury. He was first to organize ocean and atmosphere observations, initially for use in constructing his Wind and Current Charts in the 1850s. These became the first quality controlled records comprising the recent Comprehensive Ocean and Atmosphere Data Set (COADS), which CEOS utilizes in its formulations (see Roy and Mendelssohn, this vol.). These various stages of organized observations comprise a legacy of millennia of mariner's notes and maps of hazards and places since the advent of sea trade (Sears and Merriman, 1980).

The legendary disagreements between Norwegian Johan Hjort and his countryman colleague O. Dannevig initiated research into early life histories of fish resources around the turn of the 20th century. Alfred C. Redfield and his North American contemporaries, Henry B. Bigelow, Gordon Riley and their cohort, initiated a formal organization of thought, study and interpretation of constantly varying primary production processes in the ocean domain. There were undoubtedly many more local contributors leading to the increasing numbers of ocean resource scientists. The Challenger Expedition and the discourse over 'calcareous ooze' set the stage for the future scientific approaches to measuring and documenting ocean features and processes.

Most of the principle forcing functions in the upper ocean are well described, most within the recent fifty years. They have been studied individually, as well as in combination, and reported throughout the rapidly growing physical oceanographic literature. Since the beginning of organized ocean science, more biology and ecological interactions have been documented. Responses of fisheries to environmental variability has been studied and documented for nearly as long, but both sciences have only recently been converging onto the common objective of explaining the role of physical forcing on ocean production (Hjort, 1914, 1926; Cushing, 1969; Southward, 1974a, 1974b; Fasham, 1983; Csirke and Sharp, 1983; Sharp and Csirke, 1983; Platt, 1981; Longhurst *et al.*, 1995).

The recent Intergovernmental Panel on Climate Change reports (IPPC, 1990) on the potential climate change scenarios accept the basic tenets of 'Green House' warming arguments. Even though the analogy is imperfect, at best, it serves as a simple, if inappropriate, coded statement of a 'dread factor' and may thus stimulate research funding.

The importance of long-term climate records, and careful integration of ecological responses is well recognized by geologists (Soutar and Isaacs, 1969, 1974; Soutar and Crill, 1977; Anderson, 1989; Baumgartner *et al.*, 1989) and many enlightened geophysicists. These long term data sets are keys to understanding climate change, and credible forecasting.

For example, Figure 1 provides proxy indications of decadal and longer scale production of two pelagic fish species within the Southern California Bight over the recent 2 000 years. Note particularly the long term decline in apparent fish production. This accompanies the long term decline in global temperatures since 9 000 years before present. Note also, the changes in apparent system production after about 1100 AD.

The Medieval Warming epoch (~850-1200 AD) and the Little Ice Age (~1450-1780 AD) provide examples of extremes in climate within the recent millennium. The fact that the Little Ice Age ended only about 1780 or so provides the backdrop for the warming trend over the recent two centuries. Note also in Figure 1, that there appears to be a correlation between the dates of the little Ice Age, and fish debris abundance in the Southern California Bight. The general cooling of the period was interrupted by warm periods, probably inducing changes in global thermal balances that induced changes in coastal winds, and short periods of localized production evidenced within the data set. Likewise, there were short periods in the preceding 'warm' period, during which cool epochs would have reversed these patterns, contributing to the lower production periods within that sequence.

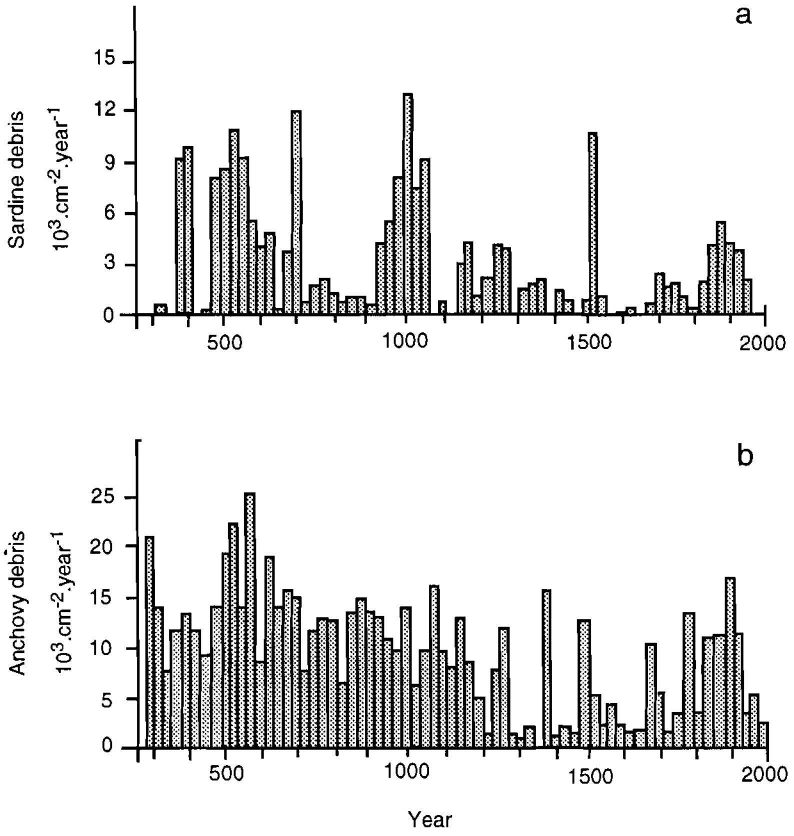

Fig. 1: The annual varve sediment records of the Santa Barbara Basin have been sorted and fish debris (e.g., scales, otoliths, hard parts) identified, and enumerated for contiguous segments for the recent two thousand year period (provided by Dr. Andrew Soutar. SIO, La Jolla, CA.). a) Pacific sardine ; b) Northern anchovy. These records have been the inspiration for much speculation about the periodic ebb and flow of pelagic species, and the climatic regimes that dominated each period. Similar records from dysaerobic sediments from Walvis Bay and from Peru record similar patterns of population responses to climate-driven ocean changes.

In fact, the greatest rate of warming during the recent two centuries occurred in the period from the 1920s through about 1940, accounting for 0.3°C of the 0.5°C temperature rise for the period around the globe. This is often touted as evidence for 'anthropogenic Global Warming'. If anything, the northern hemisphere temperature was in decline from about 1945 until about 1972, at which time many changes were experienced around the globe (Sharp, 1992). Figure 2 shows example historical ocean records from the COADS. There has been relatively little global climate variation during the recent fifty year period, particularly considering the concerns about increasing positive biases over the period as the anemometer has been phased into use.

Climate change is the most dependable paradigm that we have. The issue is in response to what, and on what time and space scales? My colleagues in the paleoclimate research fields have little doubt that normal, natural climate variations occur well within a few decades, and over major geographic regions. The major forcing appears to be exogenous, with frequent and obvious punctuations by volcanic events. The popular concerns about anthropogenic forcing causing 'Global Warming' may even be misplaced given that we are nine thousand years into the next Ice Age. Surveys of paleological, and anthropological evidence would suggest that the worst things that have happened to humanity occur during cool, dry periods, and within the few warm and wet decades following the termination of these cool periods. Human populations have been devastated by over-growths of pests in response to natural lower trophic level ecosystem blooms. This is a result of declines (natural or human-induced) of limiting predator species during lowered trophic flow-through periods. Considering the present distributions and abundances of humans, and of natural predators, perhaps it is time to rethink the issues. Fish and fisheries will respond to climate change, as always, but the more important issues are related to reduced biodiversity.

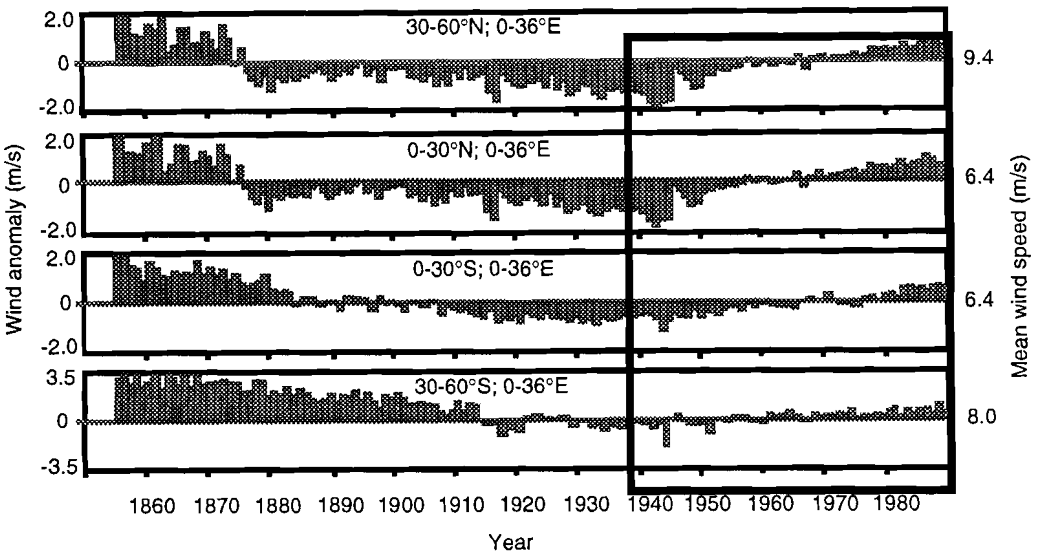

Fig. 2: The winter season scalar surface wind speed departures from the long term mean, from the COADS are portrayed for four 30 degree latitude swaths around the globe. The instrumental period is outlined by the box. The trends within the four examples are similar to the one that Bakun (1990) found in his upwelling index data, as expected. There are, however, some very notable patterns that this series of graphics show us. First is that the northern latitudes tend to lead the changes in the more southerly latitudes, which likely indicates the relative sea surface to land surface ratios. Second, the long term patterns of change are far more extreme than anything that has been observed during the recent five decades of the instrumental period.

2. PHYSIOLOGICAL RESPONSE PATTERNS AND NATURAL VARIATION OF CONTEXT

The following examples of known response patterns are presented only to rekindle the flame of several generations of careful experimentalists, so that CEOS might benefit from the insights of these, and thereby prove to be not only more credible, but more explicit about what causes the empirical relationships reported e.g. in this CEOS volume. These are principally behaviorally based, physiological and ecological responses, not mere mathematical 'truths'.

Ambient temperature is a primary variable in physiological ecology, particularly for poikilotherms. **Respiration rate**, as a measure of energy throughput, is the common currency of physiological studies. **Growth** is the record of success, and **reproduction** is the adult's reward for having at least survived the first course. The array of complexities and options that are exhibited by participants in this ecological game of life are myriad, yet there are generalities and principles by which the game is played. Most of these are simple confirmations of the well known Laws of Thermodynamics. Others include unique genetic adaptations for coping with local habitat variabilities. These local variations are the important variables, each of which has certain limitations, hence constraints of context within which individuals within species must operate, or die.

Although a great amount of attention is given to mortality in aquatic resources research, there are insufficient documented records of when, where, which, and how individuals die. What we have, instead, are most often limited life tables, in which frequency distributions of size classes from samples collected after a fish takes a hook or is caught by net, and are then sorted into presumed age bins that are the bases for Life Table-based interpretations. Edward Deevey (1947) provided remarkably clear insights into the requirements for interpreting Life Tables, as he defined and introduced them. The missing key for the Life Table approach is a fast, automated technology that can age, credibly, any fish that is sampled. A representative sampling scheme then needs to be devised for each category of fish, and applied. Too much of present aging technique is poorly validated, and fraught with errors.

Another common-problem-solution in historical stock size estimation procedures has been the application of 'constant' mortality parameter (M). Vetter (1988) examined consequences of fishery-related mortality estimation procedures, and refutes the common assumption of constant mortalities, no matter where or how applied. This is particularly problematic in early life history stages of aquatic species, as their daily progress through size classes within any trophic pyramid can vary remarkably, with the issue being a simple binary situation in which they are either encountered by a predator, and eaten, or not. Which predator is encountered may not be consequential. Moreover, in coastal upwelling environments, where a single species can be overwhelmingly dominant, cannibalism may turn out to be a significant density dependent action (MacCall, 1990).

Another significant issue in the predator-prey relationships is the ecological efficiency of each predator, and how the consumed prey's energy resources are eventually distributed within the trophic web. One obvious, but often ignored direct consequence of temperature structure, whether horizontal, vertical, or in time, is the overall decline in ecological efficiencies as temperature increases, hence the decrease in resulting standing biomass at each higher trophic step with temperatures rise. The general response of aquatic ecosystems to warming perturbations is to speed throughput of energy, the expenditure of larger portions of that throughput on respiration, rather than growth and reproduction. Cooling causes the converse response.

There are also major consequences regarding both egg production in quantity, and quality. This issue is complex because the actual onset of gonadal maturation involves the mobilization of lipid stores from the somatic tissues, and their redeposition in the ovaries. The subsequent dissipation of this energy at each spawning event is important, too. Seasonal changes in somatic fat content and reproductive cycles are therefore inversely related. While less energy is stored at higher temperatures, and adult sizes are smaller due to hormetic effects, there is also a diminution of the size and numbers of eggs, although since onset of reproduction occurs earlier, at smaller size, there are often many more eggs produced. These issues are rarely fully resolved in present day stock models. Delivery of even these lesser quality, yet more abundant eggs into a recently warmed (e.g., ENSO-event) recently productive environment (with fewer predators) would seem to be one short-term Darwinian Game Winner. This may be the least complex reason for some of the great abundance variations in upwelling environments.

I like to think of each fish as a two-system entity. The somatic fish, and the gonadal fish, each of which has its own imperatives. The prime imperative of the somatic fish is to grow, and deliver a well stocked gonad to a location where the gametes stand a high chance of encounter with an opposite sex gamete, and where the fertilized eggs have some probability of hatching out into an environment where appropriate larval food will be available. The means by which each gonad goes about arriving 'there', to reproduce, is the key to understanding both species diversity, ecosystems, and environmental dynamics.

The prime imperative of the gonadal fish is to deliver healthy gametes, well stocked to support early development in an uncertain, but often carefully selected environment. This can be anywhere within a fairly vast gradient system. Both the somatic fish and the gonadal 'symbiont' are preprogrammed to carry out their respective roles, but the gonadal imperative dominates the somatic needs after a developmental stage set by whole organism respiration processes (Pauly, 1984).

In many text books, it is presumed in the balance of energetic equations leading to energy for maturation of gonads that only energy in excess of a preprogrammed growth pattern is available. For fish, it is more realistic to describe the gonadal energetics as a complex forcing function that defines somatic growth potentials, where somatic growth is supported only up to some critical relative ratios of food intake, respiration rate, and a related apportionment between growth and somatic fat storage. Once a set of hierarchic physiological response criteria are met, and the soma begins to lose ground with respect to energy stores and respiratory demand, the gonadal imperative kicks in, and a series of hormonal signals are sent, mobilizing the somatic energy, and enhancing the gamete development and maturation system. That point in time is irreversible, and sets the parameters for remainder of the somatic fish growth. These are species specific, and plastic, as a function of individual experience. We call that plasticity adaptability, within the species' scope.

Life history strategies and somatic properties of individual species are harshly selected by their environment, in its broadest context. As long as the parent can sustain a positive energy balance that restores energy (primarily in the form of lipid), then a fish can spawn repeatedly, as per Hunter and Goldberg (1980). Sardines, anchovies and many scombrid fishes have been proven to spawn iteratively. Spawning potential is spread over a much larger area, and time, to enhance the likelihoods of survival of a next generation of gonads. Individuals can start the cycle at any time during the year. This also suggests a distinctly different approach to interpretations of year classes as compared to seasonal or 'event' spawners such as salmonids, herrings or osmerids.

Santander *et al.* (1983) provide estimates of reproduction of *Engraulis species* for the Peruvian and South African systems, respectively. Parrish *et al.* (1986) describe the changes in interannual growth, spawning and related reproductive parameters for northern anchovy off California. Pauly and Palomares (1989) estimate mortality from several predators species and the fishery mortality separately for the Peruvian fishery from 1953 to 1982, and also show seasonal and interannual growth vary considerably. The interpretations in these studies put to rest any myth of constant M, or the simplistic concept of fecundity for iteroparous species.

Spawning activity of pelagic fishes is usually a function of food availability and temperatures across the habitat. Spawning is induced in response to the physiological stresses associated with temperature induced increases in respiration rates. Overall, warming temperatures decrease ecological efficiencies across the biomass spectrum, resulting in higher turnover rates, and smaller individuals overall, although numbers of individuals may be larger (cf. Ulanowicz 1986, regarding his definition of system ascendency). Even though primary production may actually be relatively high, the biomass can become sequestered in many more, but smaller individuals, and more energy dissipated due to their inherently higher respiration rates. Given a strong primary production basis, and that growth rates may be significantly enhanced, onset of reproduction is induced at smaller sizes, and younger ages, again resulting in lower ultimate sizes, as per Pauly (1984). Ambient cooling has opposite effects.

The concepts of hormesis, the enhancement of physiological performance due to environmental stress (Stebbing, 1981, 1982; Stebbing and Heath, 1984), provides insights into both the apparent increased growth rates, changing efficiencies, and the subsequent early onset of reproduction, as a stress induced consequence.

Once any individual from any species has been 'switched' over from somatic growth to gonadal development, there are dramatic irreversible changes in the handling of lipids storage, and the gonad is favored at any time physiological stress is encountered. This is a readily interpreted, and general evolutionary imperative that ensures that species will invest available energy optimally into reproduction, rather than continued growth in threatening environmental conditions.

The massive spawnings and decreased physiological condition of anchovies (or other species) during warm ENSO events is the confirming 'symptom' of this common set of processes. The continued growth, and later maturity of individuals during cool ENSO events, or at the cooler ends of habitat gradients is also well known, indicating the opposite consequences of lower ambient temperatures. There are other implications of this behavior. Table 1 provides the generic responses by most biological systems to shifting environmental temperatures.

Observed/Expected developmental patterns for most aquatic species (and many others) tend toward the following scenarios in response to temperature patterns and contexts:

A. Ambient mid-thermal range; typical seasonal climate; low competition for resources. This is the 'usual' local pattern, where the seasonal cycle dominates the development, reproduction, and emergence of sequential generations of each species. Although often mistakenly labeled 'average' conditions, these are neither optimal for the individual species, nor all that common in nature due to the continuum of climate variability. In pelagic contexts, 'average conditions' are usually least likely to occur.

B. Ambient cool end of thermal range of species; typical seasonal climate; low competition for resources. This is one extreme of the 'optimal' situation for most populations, in that this pattern promotes slow but continuous growth, to very large size, and late reproduction. Gametes from these populations tend to be optimized, in quality and numbers per individual, for survival through periods of relative deprivation, hence more young tend to survive to older stages and ages, for larger subsequent generations. This condition characterizes growth phases for many pelagic populations.

C. Ambient upper thermal range of species; typical seasonal patterns, usual rates of competition for resources. This is the upper extreme of the 'optimal' situation for most populations. Although rapid growth is characteristic, early onset of reproduction due to physiological stress limits the adults to small size. Most of the energy consumed goes toward respiration. Reproduction rates tend to be highest, although gamete quality and survival rates tend to be low. Depending mostly upon predator abundances and food availability, this can be either a bloom, or bust period for a population.

D. 'Hot House' ambient, in which all life history stages are enhanced by increased energy throughput. Reproduction is early, and life span often shortened, or compacted such that several 'cycles' can be induced within the usual seasonal cycle. This is the ENSO warm event analogy, in which many individuals are in physiological stress, growth rates are inhibited or even reversed, and 'reproductive imperative' is induced, in which all somatic energy is shunted to the gonads for a last effort toward the production of another generation.

Table 1: Generic individual, population and ecosystem responses to changes in ambient thermal patterns.

3. NEW APPROACHES TO OLD FISHERIES QUESTIONS

Elbert H. Ahlstrom (1943, 1959, 1966) and David K. Arthur (1956, 1976) were pioneers in the field of early life stage identification and feeding requirements and paved the road for all that followed. The California Cooperative Fisheries Research Program (CalCOFI, Anon., 1950) was initiated to study the declining California sardine fishery issues through the combined efforts of many, but O. Sette (1960) was the true believer, and genuine hero of this long, ongoing study of ecosystem dynamics in response to physical forcing.

I would like to pay my respects to several other strong individual contributors in the recent decades whose efforts brought to the marine resource sciences a modicum of field-testable hypotheses. More importantly, they all emphasized the concept that there is no single dominant factor that will explain day-to-day, or year-to-year population variability. This fact is too often ignored by recruitment researchers whose studies encompass small variable sets.

First will be J.H.S. Blaxter, for rekindling the interests in laboratory studies of early life history survival requirements (Blaxter, 1965). Underlying much of the progress in La Jolla at the Southwest Fisheries Center during the late 1960s and 1970s was the series of fish energetic studies by Lasker *et al.*, (1970), and John Hunter (1972, 1976). Hunter, along with a steady stream of students whose tenures in the all-important fish rearing facility of the Southwest Fisheries Center, produced many insights (Hunter and Thomas, 1974), made this 'Golden Age' of fishery research possible.

There is at least one unsung hero in this entire venture, Roger Leong, whose incredible dedication to the smooth functioning of the fish rearing facilities can only be termed 'legendary'. Leong's knowledge of fish, nutrition, and sea water systems grew with his experience (Leong and O'Connell, 1969). Over the years, his seven day, twenty four hour vigilance was renown. The numbers of manuscripts and thesis research projects that only could have occurred with his support is certainly notable.

Beyond fish rearing, the introduction of reading daily otolith marks for very small fishes opened the door for great progress in the interpretation of growth for at-sea sampling studies. The rediscovery of iteroparity, and daily aging were the keystones for the eventual emergence of the egg production method for estimation of spawning stock abundance (Hunter and Goldberg, 1980). Aging and staging of early life history stages of anchovy, along with Charles O'Connell's histological studies of the consequences of nutritional state (O'Connell and Raymond, 1970; O'Connell, 1976), in turn, stimulated more rigor in the interpretation of at-sea samples of first feeding anchovy larvae in regard to starvation induced mortality rather than simple predation.

In the background of these programs has been a continuous need for clever means for sampling the dynamic ocean and planktonic patterns. Again, Paul Smith, whose passion for obtaining answers to challenging questions about the ocean and its inhabitants, has provided research tools, means and logic for rigorous at-sea sampling (Smith and Lasker, 1978). Earlier, under the combined influences of Lasker and Smith, William Vlymen (1974, 1977) introduced a series of approaches and estimation procedures based on hydrodynamic principles that account for combined feeding energetics and swimming costs, which remain benchmarks in the integration of empirical fish behavioral studies and physical sciences.

By the mid 1970s Reuben Lasker and Gail Theilacker had emerged as the champions of at-sea bioassays of feeding stimuli, and along with enhanced methods for assaying nutritional status of anchovy, providing the bases for the Lasker Starvation Hypothesis. Lasker's Starvation Hypothesis at once stimulated great debate across the larger fish recruitment research community (Lasker, 1975, 1978, 1988). Lasker and Zweifel (1978) summarized an enormous effort to standardize treatments, and tried valiantly to cope with descriptions of results of many of these diverse experiments.

During this same period, Jan Beyer, a systems engineer, began his synthetic studies of the progression of early life history stages of fish, from first feeding on to their ultimate recruitment into fisheries, identifying the critical processes from the perspective of individual fish larvae (Beyer, 1976a, 1976b, 1981). Beyer was invited to give a lecture series at the University of Washington in 1977, and lectures at La Jolla, which emerged as Aquatic Ecosystems - An operational research approach (Beyer, 1981). This was another benchmark idea: a population is comprised of individuals.

Sharp (1981) brought together theorists and field scientists to discuss the dynamics of climate-forced upper ocean mixing, on a local to regional scales to debate not only the relative importance of Lasker's Starvation Hypothesis, but to also help identify unifying concepts in an effort help organize global fish recruitment research into focal topics about natural limiting factors. We could not but wonder at the problems of comparing larval fish rearing studies (Theilacker and Dorsey, 1981), given the usual near absence of contextual information provided, or measured by each investigator. Owen (1981) pointed out that the ocean is dynamically structured on several time and space scales, suggesting that understanding each scale is limited to matching appropriate structures with appropriate population questions.

In one sense, this seminal 1980 meeting gave root to the ongoing CEOS approach, as Bakun *et al.* (1981) described the similarities of the pelagic fish faunas of the major upwelling systems, within the contexts of the recruitment questions. These and several follow-up discussions led to further exploration and the eventual synthesis of conclusions from then recent recruitment research and environmental processes, as understood by Bakun *et al.* (1981), from which others took direction. The IOC Sardine, and Anchovy Recruitment Program (SARP) was born.

Just as quickly, SARP died a bureaucratic death, as a result of funding crises induced by new U.S. legislation mandates to fund a more complex fisheries management structure, including a series of regional Fisheries Management Councils. The Councils simply used up all available discretionary and most research funds of NOAA's National Marine Fisheries Service. This was the beginning of the end of the CalCOFI program as well. In fact, it was the beginning of the collapse of rational fisheries management in the USA, as politics overwhelmed facts, and general fishery data collection declined, leaving more room for legal debate than for research.

The issues of larval fish starvation and other empirical information relevant to Lasker's Starvation Hypothesis are described in two seminal studies that prove that early stage larval fish starvation related to low phytoplankton densities does occur in nature, with some samples comprising up to 65% starving larvae (Theilacker, 1986) To address the parallel issues of predation on fish larvae, Theilacker *et al.* (1993) have developed an immune-assay technique for identifying stomach contents at micro-scale on organisms ranging from euphausids to fish.

Tools and relevant questions abound, yet funding for applied fisheries research has simply evaporated in recent years, as the substitution of empirical information via mathematical modeling and assumptions about how various factors are related has been adopted in fisheries management strategies. Clearly, this has been quite unsuccessful; for reasons I and others have discussed elsewhere (Walters and Collie, 1988; Cury and Roy, 1989; Cury *et al.*, 1995; FAO, 1992; Hilborn, 1992; Sharp, 1988, 1992; Vetter, 1988.)

Another critical component of present day understanding was the early development and sitting of the Pacific (Fisheries) Environmental Group by James Johnson and other supporters, providing a means for accessing global environmental data for fishery applications. Also in the late 1960s, Joseph Fletcher, and his colleagues at the University of Colorado began collating the Comprehensive Ocean and Atmosphere Data Set (COADS), which forms the nucleus for the present stage in CEOS research. Records of physical and ecological variabilities of the habitats over time, and the consequential patterns of variation of species distributions and abundances provide the bases for defining the causalities, and provides the most hope for development of predictive capabilities. Were it not for many of these people, we would likely not have ever gotten to CEOS.

The issue is loss of contextual information, and direct knowledge of fishing activities in response to short and long-term environmental processes.

4. CONTEXT, CONTEXT, CONTEXT!

There have been seminal works on the short- and long-term consequences of climatic processes, weather events, and their fisheries manifestations, (Uda, 1927, 1957; Hela and Laevastu, 1971; Southward, 1974a, 1974b; Southward *et al.*, 1975; Parrish and MacCall, 1978; Sharp, 1978, 1979; Pauly and Navaluna, 1983; Cushing, 1969; Parrish *et al.*, 1983; Rose and Leggett, 1988). However, the problem of identification of connecting mechanisms at all time and space scales remains a major task. There has since been general acceptance of the importance of environmental forcing in fisheries analyses. Although hypotheses abound, data sets are rare.

Cury and Roy (1989), and Cury *et al.* (1995) provided a new set of analytical tools, to work with available environmental and recruitment time series. Their 'discovery' that 'moderate is good' is in complete agreement with what physiological ecologists such as Priede (1977), and many others have been saying for years, from studies of individual fish in the laboratory, or in nature. The trick is to sort the causal properties from the correlates.

Surely, wind speed and direction are important driving variables in local contexts, although the fish are safely sequestered from their immediate, direct influence. On the other hand, the upper ocean is quite responsive, and a suite of processes ensues as wind speeds change, persist, or shift in direction over time. All of the known secondary responses have direct influence on the physiology, and the behaviors of affected fishes.

These local wind-driven consequences include:
1) upwelling of cool, often poorly oxygenated water;
2) advection; convergence and associated downwelling;
3) long-shore or other structured current changes that affect individuals on a short-term, dial basis.

Regional consequences include:
1) production shifts;
2) predator displacements, and changes in locale due to shifting production patterns;
3) blooms and declines of entire fauna assemblages on event scales, e.g. warm events El Niño, or cool events; and
4) ecosystem responses on seasonal population reproduction time scales.

At regional to ocean basin scales, we have many examples of climate related fisheries variation collated from fisheries literature, and these are discussed within various forums. In spite of the general agreement of the importance of climate, the subject remains poorly incorporated into resource management strategies. The necessary steps have been documented by Csirke and Sharp (1983), and more recently the U.S. National Academy of Science (Ocean Studies Board, 1994) has encouraged their incorporation. Until there are retirements within the management systems, little progress is likely. The issue at hand is that of converting a series of empirical relations into a set of causal relations, a task no less daunting than explaining any other statistical relations. The advantage that CEOS provides is its basis for comparative studies of several distinctly different physical systems, that provide contexts for the requirements of a common species composition, namely *Sardinops*, *Engraulis*, *Scomber*, *Trachurus*, *Sarda*, and *Merluccius species* (Bakun *et al.*, 1981).

5. CLIMATE CHANGE, SEA SURFACE TEMPERATURE, WIND SPEED AND DIRECTION: SO WHAT?

Moser *et al.* (1987), and Smith and Moser (1988) from CalCOFI data and showed that during the 1951-1960 period of known climatic transition there were distinct fauna shifts, amongst all species, not just the commercially important ones. There are several lessons from the recent decade that need to be integrated into the general picture of comparative studies. Among these are the basic hints from the long coastline including Ecuador, Peru, and northern Chile, from Chiloe in the south, to perhaps the Gulf of Guayaquil in the north. The observations for each region have been kept separately, and only on occasion treated as a whole. IFOP (1985) documents the fauna responses to the 1982-83 ENSO warm event along the Chilean coastline. Also, on greater spatial and temporal scales, Avaria (1985), showed that the fish production center moved from southern Peru into northern Chile as the anchoveta collapsed onshore into coastal refuge, and sardines moved onshore and southward in response to the larger system changes. Similarly, to the south in central Chile, a small sprat, *Strongomera bentickii*, locally called sardina comun, collapsed from its northerly extension from about Valparaiso, southward along the coast into Bahia Concepcíon, the Rio Bio Bio outlet.

Loeb and Rojas (1988), in a compelling study, examined the ichthyoplankton samples collected along Chile and found that during the late 1960s, it was not merely a north to south collapse of habitat, but a general decline occurred in coastal upwelling-associated fishes, distributions changed, and an increase occurred in abundance for an oceanic fauna assemblage, including sardines.

The key point in both these studies was the fact that the anchoveta did not change its distribution during the entire period of fauna changes. Anchoveta merely collapsed into coastal refuge, which are indicated along the west coast of South America by coastal promontories with northward facing bays, or substantive embayments such as the Gulf of Arauco, Coquimbo, or Iquique. The common denominator was an upstream gyre that forms whenever there is substantive northward, along shore water motion, inducing upwelling and primary production. Because this coastline is over 2 400 nm in length, and there are so many distinctive forcing patterns as a function of the El Niño-Southern Oscillation and shorter seasonal patterns, this coastline provides several dozen independent production centers, some of which happen to provide opportunities for fishing ports and fish processing facilities.

The entire coastal upwelling region of South America has actually never been exposed to simultaneous fishing pressure, and, in fact, what one can discern from the anchoveta and sardine catch patterns is that travel beyond a sailing day from any processing port was very rare, simply because these vessels were not refrigerated. The impact of offshore movements of the sardines during the recent decade has not been fully appreciated, although the similar, but even grander scale distribution of the jack mackerel, *Trachurus murphyii*, (Serra, this vol.) has recently caused a stir amongst entrepreneurs who wished that there were some economical means to capitalize on the recent bloom of that population into the offshore waters, and along the west wind drift into the Tasman Sea (Keith Sainsbury, pers. comm.).

As one means of stratifying fishing records to compare with environmental records, the South American coast provides a near-linear north-south latitudinal gradient, without the added burden of a series of major surface temperature gradients. On the other hand, the absence of fishing over the entire onshore-offshore gradient, or at distances far beyond about a 150 nm radius from each processing port can cause some distortions of the historical catch signals, as the seasonal and epochal changes perturb the centers of production, and the areas where fish graze. As the Chilean sardine fishery collapsed in recent years, distances traveled offshore and away from ports increased, but not dramatically until recently, as refrigerated holds have been adopted.

Similar concern can be voiced for the California coast, particularly north of Enseñada, where there is significant SST gradiential variation, and a complicating series of topographic forcing features. The contrast between the Gulf of California, and the Pacific coast of the California is, again, a complex issue, in that there is strong seasonal forcing from the tropical ocean within the Gulf of Mexico, that manifests quite differently north of Cabo Colnett, Baja California. The complex hydrography of the Gulf of California can confound simplistic evaluations, as the variances of combined tidal forcing and wind events on a daily basis can be as great as anywhere in the world, and needs to be dealt with in a careful fashion (Hunter and Sharp, 1983).

The 'sea breezes' that characterize the Mediterranean coastlines of eastern boundary current systems — with their deserts and dunes — induce upwelling, and summer stratus clouds over much of the coastal pelagic habitat. Oceanographic studies suggest the general nature of upper-ocean forcing in response to low cloud cover. Among the relevant probable consequences of clear-sky induced upper ocean mixing for species that require plankton concentrations for survival is the question of the role of stratus clouds and fogs on nocturnal upper ocean mixing that is normal under clear sky conditions. Alternatives discussed by Sharp (1981), along with the Lasker Hypothesis, suggest that larval anchovies in eastern boundary currents would more likely encounter phytoplankton concentrations in seasons when stratus clouds prevail because the clouds would suppress cooling associated with night time long-wave back radiation, and its consequent upper ocean mixing. It will also be interesting to study the seasonal spawning successes of these fishes as a function of cloud cover, cloud type, and fog, where records have been routinely collected. One suspects that this would presently only be possible in regions where major airports exist near the coastal regions. However, airports are only rarely sited in such regions because of the consequences of low clouds and fog.

The issues of which specific variables are important at various spatial scales, and when, cannot be ignored. The affects of cloud cover, and type, on night-time back radiation, and nocturnal upper ocean turbulence processes are at least as relevant as wind-driven turbulence. It is not a moot point that cloud cover patterns are related to wind speed and direction.

6. TURBULENCE, FOOD ENCOUNTER RATES AND OPTIMAL ENVIRONMENTAL WINDOWS

MacKenzie and Leggett (1991, 1993) and MacKenzie *et al.* (1990) provide discussions and reviews of the microturbulence related to feeding of relatively immobile larval fishes, pointing out that feeding rates are enhanced as wind speeds increase from low speeds (i.e., 2 ms^{-1}) to higher speeds (i.e., 6 ms^{-1}), until 'storm' level winds of 10 ms^{-1}, or more cause the entire upper water column to homogenize. This is consistent with the Optimal Environmental Window concept of Cury and Roy (1989). It was not clear, except perhaps for mathematical convenience, why the examples MacKenzie and Leggett (1991) started from a homogeneous, but low density of food organisms, unless their point was to show that fish larvae would somehow benefit from enhanced turbulence at lower food densities. However, the important dynamics of feeding patterns, strike rates and other behaviors (Vlymen, 1977) got put aside, simply because of the problem of not having empirical data.

The scenario that I and others have envisioned over the last decades is that during low wind mixing, the plankters serving as larval fish feed tended to aggregate, and if larval fishes were naturally programmed to move up and down vertically, then they would have a far greater chance of encountering high enough densities to stimulate feeding responses (Hunter, 1972; Lasker, 1975). Coming out of a well-mixed situation, such as following a storm event, there is a natural resetting of the system to one of aggregations, or new colonies of prey species as a general response to the mixing of new nutrients into the upper ocean, hence new production, and new feeding opportunities. At issue is not that theses mixing events occur, but whether their effects last long enough to cause significant starvation mortality. That starving larvae have been observed in nature is not irrelevant. Nor is the fact that many other larval fish species have not yet been observed in this state.

Although I also follow the argument that microturbulence can give increased encounter rates, my own mental image is one of having not only more targets appear per unit time, but that the targets would be moving at considerably faster relative speeds, hence there would be an increasing requirement for the larvae to sight these moving prey, respond, and react appropriately.

The difference between these several scenarios is perhaps best explained by analogy. In one case, a hungry individual finds a density of food stuff, lets say a vegetable market, where it is possible to identify large, esculent clusters, and stay in one place to feed in a leisurely fashion. In a second set of scenarios, the market is gone, and the individual is now on a continuously moving escalator, and some lesser proportion of all the individual food items are being slowly or maybe not so slowly tossed near enough to be identified, and snatched one at a time, if one is vigilant. Now increase the speed of the escalator, and the frequency of encounters to a point where the effort required to feed exceeds the value of the encountered food stuff, and we have another extreme of the myriad possibilities. Too little and too much can also define these limits (Priede, 1977; Cury *et al.*, 1995).

The problem, as I see it, is where in the spectrum that the energy balance becomes negative, or worse, where does either perception or response time fail to serve the larvae? First feeding fish larvae in particular are relatively naive. Hunter (1972) and Hunter and Thomas (1974) described fairly complex sequences of behaviors for *Engaulis mordax* that would not be well suited to a very rapid increase of relative contrary motions between predator and prey, given the timing that was necessary for each particle to be within the field of view, for repositioning and coiling of the fish larva in response, and then to strike successfully. One must wonder at the consequences of not only changes in encounter rate but also the speeds at which these two-body interactions must occur. Once mobility and full sensory capabilities are developed, and sufficient learning by trial and error has occurred, a healthy larva should be able to successfully handle a broadening spectrum of turbulence, and related feeding encounters as they progress to larger sizes, and more complex behaviors.

7. COMPARISON AND CONTRAST OF ENVIRONMENTAL CONTEXTS: INFORMATION FOR WHOM?

Comparing and contrasting coastal dynamics has mostly been anecdotal, to date, and will remain anecdotal until there is a systematic development of an ocean-observing system. What to measure and monitor is certainly a primary question needing answers. Careful reasoning of where to place monitoring systems will also be required. At issue is which questions about what problems should be emphasized. The Sardine and Anchovy Recruitment Program (SARP) was an attempt to organize the local scale sampling strategies that might provide answers about local, individual responses to environmental forcing, and subsequent survival. In their attempts to obtain insights, Leggett *et al.*, (1984) and colleagues have directed their efforts at local population responses, and bridged the scales to regional systems (Carscadden, 1983; Rose and Leggett, 1988; Carscadden *et al.*, 1989). These are important inquiries.

The CEOS comparative approach was initially designed to examine population responses to regional and subregional scales of local and regional mosaic populations. This is an integrated view, from available time series that were by necessity limited in scale, and representation due to data limitations. Because the example data sets tend to represent mostly only one bloom and recession cycle, there is the distinct possibility that the empirical relations that emerge from the CEOS analyses might be analogous to those described in Sharp and McLain (1993a) in which the data from a single cycle will not be coherent with similar previous, or subsequent cycles. The Stock-Recruitment 'loop' is a good example. Theory is not met as one observes that the declines in recruitment do not retrace the ascendant pathway(s). Kondo (1980), Kawasaki (1983), and Sharp (1981, 1987 and 1992), and Sharp and McLain (1993a, 1993b) have taken the larger view, in which systems and their decadal scale patterns of variation are examined to better understand the shorter time scale processes and events, nested within this larger context.

Clearly, combination of these approaches would be best, although not yet within grasp, primarily due to the differences in national resource management policies. Also, data limitations impose restrictions on both scientifically credible forecasting and hindcasts based on catch and effort statistics. Although the former is required for rational resource management, the latter is preferred because it is cheap, although mostly ineffective as more than providing post-mortem perspectives. The more integrated approaches are data-hungry, and presume constant monitoring of both the environment, and the fisheries. The environmental monitoring systems required are not in place. This is also a question of agency responsibilities, and national priorities.

Whether a global ocean observing system should focus on weather forecasting efforts, or climate issues, or natural resource and agricultural issues are not simple, readily resolved issues. A major insight into how to resolve these issues might be provided by the ocean resources managers and agricultural industries, by pointing out that beyond extreme events, there are more subtle variations that can have more economic impact, over longer term, than only a classic 'storm warning' system offers. More to the point, it is not only storms or El Niño events that need to be tracked, but the full spectrum of climate-driven ocean processes, until a full understanding is in hand, and a more appropriate monitoring scheme might be devised that will service natural resource management, as well as agricultural and urban societal needs.

By convention, fisheries have been treated as renewable resources. Due to the near economic collapse of many fisheries over the recent decades (FAO, 1992), these resources are only now being recognized as having the potential to shift to non-renewable status. One would think that the experience with whales, dodo birds, and forests would have sufficed to quell this governance 'Pollyanna' before now. Clearly, a renewed effort to reorganize resource management, and requisite monitoring is due.

A major issue to be overcome, and put within a 'food security' framework, is the dominance of recent climate observing system design for El Niño forecasting and climate change research. If these systems were set up to answer pragmatic management problems such as coastal ocean system dynamics within the global and ocean basin contexts, then we could be well on our way toward a rational fisheries and agriculture forecasting system.

As these climate and ocean monitoring programs are presently constituted, they provide little useful information to anyone except a few ocean modelers, who are principally involved in generating a credible 'event' forecast. They have as yet have failed to clearly identify the 'event' in terms that anyone else might use.

Ocean model products of greatest direct utility such as changes in thermal structure and local turbulence dynamics could be produced along with the SST and wind speed and direction data. The point here being that major changes in the focus of these environmental monitoring activities will be required before such pragmatic, global human food security issues will ever be made truly manageable.

8. AFTER A GOOD BEGINNING, WHERE TO NEXT?

CEOS has already begun a revolution by compiling in useful formats the COADS, for general access by researchers at their desk tops. The combined efforts of the CEOS network has focused on one of the largest single classes of foodstuff dynamics known, that of the world's coastal pelagic fisheries, and their epochal variations. It is moot that these several systems produce over twenty percent of the world's protein from the sea during their peak combined production periods. What is problematic is the periods when these production systems bottom out, and the important catches are no longer made.

Having done everything wrong, first, or too late when it was a right thing to do, California's sardine management story has provided grand examples of what not to do (Radovich, 1981; Ueber and MacCall, 1992). My own suggestion is that we take the responsibility to correct the distorted vision imposed by studying highly smoothed catch statistics and mean values from various measuring devices, by applying the half century of experimental observations on responses of aquatic species to known habitat changes during the next revision of the CEOS approach. Forecasting by analogy is the first order of business, now that at least one, and sometimes several cycles has occurred. The next obvious step is to apply what we already know about phsyiological ecology of organisms, and begin to integrate real-time environmental information into the forecast process. I am not so sure that ecosystem management is as difficult as some would like to suggest. Certainly it cannot be less protective than what has passed for fisheries management over recent decades.

REFERENCES CITED

Ahlstrom E.H. 1943. Studies of the Pacific pilchard or sardine (*Sardinops caerulea*). Influence of temperature on the rate of development of pilchard eggs in nature. *U.S. Fish and Wildl. Serv., Spec. Sci. Rep.*, 23:1-23.

Ahlstrom E.H. 1959. Vertical distribution of pelagic fish eggs and larvae off California and Baja California. *U.S. Fish and Wildl. Serv., Fish. Bull.*, 60:107-146.

Ahlstrom E.H. 1966. Distribution and abundance of sardine and anchovy larvae in the California Current region off California and Baja California. *U.S. Fish and Wildl. Serv., Spec. Sci. Rep.*, 534, 71p.

Anon. 1950. *Progress Report 1950*, California Cooperative Sardine Research Program. State of California Dept. of Natural Resources, Marine Research Committee, 54p.

Arthur D.K. 1956. *The particulate food and food resources of the larvae of three pelagic fishes, especially the Pacific sardine, Sardinops caerulea*. Ph.D. Thesis, University of California, Scripps Institution of Oceanography, 231p.

Arthur D.K. 1976. Food and feeding of the larvae of three fishes, in the California Current, *Sardinops caerulea*, *Engraulis mordax*, and *Trachurus symmetricus*. *Fish. Bull.* U.S., 74:517-530.

Anderson R.Y. 1989. *Solar-cycle modulation of ENSO: a mechanism for Pacific and global change.* Presented at the Sixth Annual Pacific Climate (PACLIM) Workshop, Asilomar, CA, March 5-8, 1989.

Avaria S. 1985. Efectos de El Niño en las pesquerias del Pacifico Sureste. *Invest. Pesq.* (Chile), 32:101-116.

Bakun A. 1990. Global climate change and intensification of coastal upwelling. *Science*, U.S., 247:198-201.

Bakun A., C. Nelson and R.H. Parrish. 1981. Environmental inputs to fisheries models for eastern boundary current. *In*: G.D. Sharp (ed.). Workshop on the effects of environmental variation and the survival of larval pelagic fishes. Paris. *IOC Workshop Rep.* 28: 67-104.

Baumgartner T.R., J. Michaelsen, L.G. Thompson, G.T. Shen, A. Soutar and R.E. Casey. 1989. The recording of interannual climatic change by high-resolution natural systems: tree-rings, coral bands, glacial ice layers, and marine varves. *In*: D. Peterson (ed.). Aspects of climate variability in the Pacific and western Americas, *AGU Geophysical Monog.*, 55:1-15.

Beyer J. 1976a. Fish I - Survival of fish larvae - A single queue approach. J. 3.15 IMSOR, 985: 1-242

Beyer J. 1976b. Fish II -- Survival of fish larvae - A single queue approach. J. 8.20 IMSOR, 985:1-68.

Beyer J. 1981. *Aquatic ecosystems - An operational research approach*. Univ. Washington Press, Seattle and London, 315p.

Blaxter J.H.S. 1965. Feeding success of herring larvae and their ecology in relation to feeding. *Calif. Coop. Oceanic Fish. Invest. Rep.*, 10:79-88.

Carscadden J.S. 1983. Population dynamics and factors affecting the abundance of capelin (*Mallotus villosus*) in the northwest Atlantic. *In*: G.D. Sharp and J. Csirke (eds.). Proceedings of the Expert Consultation to Examine Changes in Abundance and Species Composition of Neritic Fish Resources. *FAO Fish. Rep.*, 291 (3): 789-812.

Carscadden J.S., K.T. Frank and D.S. Miller. 1989. Capelin (*Mallotus villosus*) spawning on the southeast shoal: influence of physical factors past and present. *J. Can. Fish. Aq. Sci.*, 43(10):1743-1754.

Csirke J. and G.D. Sharp (eds.). 1983. Reports of the Expert Consultation to Examine Changes in Abundance and Species Composition of Neritic Fish Resources. San Jose, Costa Rica, April 1983. *FAO Fish. Rep.*, 291(3):1-102.

Cury P. and C. Roy. 1989. Optimal environmental window and pelagic fish recruitment success in upwelling areas. *J. Can. Fish. Aq Sci.*, 46(4):670-680.

Cury P., C. Roy, R. Mendelssohn, A. Bakun, D.H. Husby and R.H. Parrish. 1995. Moderate is better: exploring nonlinear climatic effects on the Californian anchovy (*Engraulis mordax*) *In*: R.J. Beamish (ed.). Climate change and northern fish populations. *Can. Spec. Publ. Fish. Aquat. Sci.*, 121: 417-424.

Cushing D.H. 1969. Upwelling and fish production. *FAO Fish. Tech. Pap.*, 84, 40p.

Deevey E.S. 1947. Life tables for natural populations of animals. *Quat. Rev. Biol.*, 22: 283-314.

FAO Fisheries Department. 1992. Marine fisheries and the law of the sea: a decade of change. *FAO Fisheries Circular*, 853, 69p.

Fasham M.J.H. 1983. *Flows of energy and materials in marine ecosystems*. Plenum, London.

Fry F. 1947. Effects of the environment on animal activity. Pub. Ontario Fish. Lab. No. 68U. Toronto Studies, Biol. Ser. 55: 1-52.

Hela I. and T. Laevastu. 1971. *Fisheries oceanography*. Blackwell, Fishing News, London.

Hilborn R. 1992. Current and future trends in stock assessment and management. *S. Afr. J. mar. Sci.*, 12:975-988.

Hjort J. 1914. The fluctuations in the great fisheries of northern Europe viewed in the light of biological research. *Rapp. P-v. Réun. Cons. int. Explor. Mer.*, 20:1-228.

Hjort J. 1926. Fluctuations in year classes of important food fishes. *J. Cons.*, Cons. int. Expl. Mer, 1(1):5-38.

Hunter J.R. 1972. Swimming and feeding behavior of larval anchovy *Engraulis mordax*. *Fish. Bull.* U.S., 70(3):821-838.

Hunter J.R. 1976. Culture and growth of northern anchovy, *Engraulis mordax*, larvae. *Calif. Coop. Oceanic Fish. Invest. Rep.*, 19:138-146.

Hunter J.R. and G.L. Thomas. 1974. Effect of prey distribution and density on the searching and feeding behavior of larval anchovy, *Engraulis mordax* Girard. *In*: J.H.S. Blaxter (ed.). *The early life history of fish*. Springer-Verlag, Berlin: 559-574

Hunter J.R. and S.R. Goldberg. 1980. Spawning incidence and batch fecundity in northern anchovy (*Engraulis mordax*). *Fish. Bull.*, U.S., 77:641-652.

Hunter J. and G.D. Sharp. 1983. Physics and fish populations: shelf sea fronts and fisheries. *In*: G.D. Sharp and J. Csirke (eds.). Proceedings of the Expert Consultation to Examine Changes in Abundance and Species Composition of Neritic Fish Resources. San José, Costa Rica, April 1983. *FAO Fish. Rep.*, 291(2): 659-682.

IFOP. 1985. Taller nacional: fenomeno El Niño 1982-83. *Invest. Pesq.* (Chile), 32 Numero especial, 256p.

IPCC. 1990. *Impacts assessment of climate change*. The policymaker's summary of the Report of Working Group II to the Intergovernmental Panel on Climate Change. WMO/UNEP. Australian Government Publishing Service. Canberra.

Kawasaki T. 1984. Why do some fishes have wide fluctuations in their number? - A biological basis of fluctuation from the viewpoint of evolutionary ecology. *In*: G.D. Sharp and J. Csirke (eds.). Proceedings of the Expert Consultation to Examine Changes in Abundance and Species Composition of Neritic Fish Resources. *FAO Fish. Rep.*, 291(3): 1065-1080.

Kinne O. 1970. Marine ecology, environmental factors. Wiley-Interscience, New York, 1(1): 1-681

Kinne O. 1971. Marine ecology, environmental factors. Wiley-Interscience, New York. 1(2): 682-1244.

Kondo. K. 1980. The recovery of the Japanese sardine - the biology basis of stock size fluctuations. *Rapp. P.-v. Réun. Cons. int. Explor. Mer*, 177:332-352.

Lasker R. 1975. Field criteria for survival of anchovy larvae: the relation between chlorophyll layers and successful first feeding. *Fish. Bull.* U.S., 73:453-462.

Lasker R. 1978. The relation between oceanographic conditions and larval anchovy food in the California Current: factors leading to recruitment failure. *Rapp. P.-v. Réun. Cons. int. Explor. Mer*, 173:212-230.

Lasker R. 1988. Food chains and fisheries: an assessment after 20 years. *In*: B.J. Rothschild (ed.). Toward a theory of biological-physical interactions in the world ocean: 173-182.

Lasker R., H.M. Feder, G.H. Theilacker and R.C. May. 1970. Feeding, growth and survival of *Engraulis mordax* larvae reared in the laboratory. *Mar. Biol.*, 5:345-353.

Lasker R. and J.R. Zweifel. 1978. Growth and survival of first feeding northern anchovy larvae (*Engraulis mordax*) in patches containing different proportions of large and small prey. *In*: J.H. Steele (ed.). Spatial patterns in plankton communities. Cambridge University Press: 329-354.

Leggett W.C., K.T. Frank and J.E. Carscadden. 1984. Meteorological and hydrographic regulation of year-class strength in capelin (*Mallotus villosus*). *Can. J. Fish. Aq. Sci.*, 41:1193-1201.

Leong R.J.H. and C.P. O'Connell. 1969. A laboratory study of particulate and filter feeding of the northern anchovy (*Engraulis mordax*). *J. Fish. Res. Bd. Canada*, 26:557-582.

Loeb V. and O. Rojas. 1988. Interannual variation of ichthyoplankton composition and abundance relations off northern Chile. *Fish. Bull.*, U.S., 86(1):1-24.

Longhurst A., S. Sathyendranath, T. Platt and C. Caverhill. 1995. An estimation of global primary production in the ocean from satellite radiometer data. *J. Plankton Res.*, 17(6):1245-1271.

MacCall A.D. 1990. *Dynamic geography of marine fish populations*. Washington Sea Grant. University of Washington Press, Seattle.

MacKenzie B.R. and W.C. Leggett. 1991. Quantifying the contribution of small-scale turbulence to the encounter rates between larval fish and their zooplankton prey: the effects of wind and tide. *Mar. Ecol. Prog. Ser.*, 73:149-160.

MacKenzie B.R. and W.C. Leggett. 1993. Wind-based models for estimating the dissipation rates of turbulent energy in aquatic environments: empirical comparisons. *Mar. Ecol. Prog. Ser.*, 94:207-216.

MacKenzie B.R., W.C. Leggett and R.H. Peters. 1990. Estimating larval fish ingestion rates: can laboratory derived values be reliably extrapolated to the wild? *Mar. Ecol. Prog. Ser.*, 67:209-225.

Moser H.G., P.E. Smith and L.E. Eber. 1987. Larval fish assemblages in the California Current, 1951-1960, a period of dynamic environmental change. *CalCOFI Rep.*, 28:97-127.

Neill W.H., J.M. Miller, H.W. Van der Veer and K.O. Winemiller. 1994. Ecophysiology of marine fish recruitment: a conceptual framework for understanding interannual variability. *Netherlands J. Sea Res.*, 32(2):135-152.

Ocean Studies Board. 1994. *Improving the management of U.S. marine fisheries*. National Research Council, National Academy Press, Washington, D.C. 62p.

O'Connell C.P. 1976. Histological criteria for diagnosing the starvation condition in early post yolk sac larvae of northern anchovy, *Engraulis mordax* Girard. *J. Exp. Mar. Biol. Ecol.*, 25:285-312.

O'Connell C.P. and L.P. Raymond. 1970. The effect of food density on survival and growth of early post-larvae of northern anchovy (*Engraulis mordax* Girard) in the laboratory. *J. Exp. Mar. Biol. Ecol.*, 5:187-197.

Owen R.W. 1981. Patterning of flow and organisms in the larval anchovy environment. *In:* G.D. Sharp, conv. (ed.). Report and Documentation of the Workshop on the Effects of Environmental Variation on the Survival of Larval Pelagic Fishes. *IOC Workshop Rep. Ser.,* Unesco, Paris, 28: 167-200.

Parrish R.H. and A.D. MacCall. 1978. Climatic variation and exploitation in the Pacific mackerel fishery. *Calif. Dep. Fish. Game Fish. Bull.*, 167, 109p.

Parrish R.H., A. Bakun, D.M. Husby and C.S. Nelson. 1983. Comparative climatology of selected processes in relation to eastern boundary current pelagic fish reproduction. *In*: G.D. Sharp and J. Csirke (eds.). Proceedings of the Expert Consultation to Examine Changes in Abundance and Species Composition of Neritic Fish Resources. *FAO Fish Rep.,* 291(3): 731-778.

Parrish R.H., D.L. Mallicoate and R.A. Klingbeil. 1986. Age dependent fecundity, number of spawnings per year, sex ratio, and maturation stages in northern anchovy, *Engraulis mordax*, *Fishery Bull.*, US., 84(3):503-517.

Pauly D. 1984. A mechanism for juvenile-to-adult transition in fishes. *J. Cons.*, Cons. int. Explor. Mer, 41: 280-284.

Pauly D. and N.A. Navaluna. 1983. Monsoon-induced seasonality in the recruitment of Philippine fishes. *In*: G.D. Sharp and J. Csirke (eds.). Proceedings of the Expert Consultation to Examine Changes in Abundance and Species Composition of Neritic Fish Resources. San Jose, Costa Rica, April 1983. *FAO Fish. Rep.*, 291(2): 823-835.

Pauly D. and M.L. Palomares. 1989. New estimates of monthly biomass, recruitment and related statistics of anchovela (*Engraulis ringens*) off Peru (4-14°S), 1953-1985, p. 189-204. *In*: D. Pauly, P. Muck, J. Mendo and I. Tsukayama (eds.). The Peruvian Upwelling Ecosystem: Dynamics and Interactions. ICLARM Conf. Proc. 18.

Platt T. (ed.). 1981. Physiological bases of phytoplankton ecology *Can. Bull. Fish. Aq. Sci.*, 210, 346p.

Priede I.G. 1977. Natural selection for energetic efficiency and the relationship between activity level and mortality. *Nature*, 267(5612): 610-611.

Radovich J. 1981. The collapse of the California sardine fishery: what have we learned. *In*: Glantz M. (ed.). Resource management and environmental uncertainty. Wiley 11: 107-136.

Rose G.A. and W.C. Leggett. 1988. Atmosphere-ocean coupling and Atlantic cod migrations: effects on wind-forced variations in sea temperatures and currents on nearshore variations in catch rates of *Gadus morhua*. *Can. J. Fish. Aquat. Sci.,* 45:1234-1243.

Santander H., J. Alheit, A.D. MacCall and A. Alamo. 1983. Egg mortality of the Peruvian anchovy (*Engraulis ringens*) caused by cannibalism and predation by sardines (*Sardinops sagax*). Proceedings of the expert consultation to examine changes in abundance and species composition of neritic fish resources. San José, Costa Rica, 18-29 Ap. 1983. FAO Fisheries Rep. 291, 3: 1011-1026.

Sears M. and D. Mérriman (eds.). 1980. *Oceanography - The past.* 3rd International Congress on the History of Oceanography, Woods Hole, Massachusetts. Springer-Verlag, New York, 812p.

Sette O. E. 1960. The long-term historical record of meteorological, oceanographic and biological data. *Calif. Coop. Oceanic Fish. Invest. Rep.*, 7: 181-194.

Sharp G.D. 1976. Vulnerability of tunas as a function of environmental profiles. *In*: *Proceedings of the Tuna Fishery Research Conference*. Far Seas Fisheries Research Laboratory, Shimizu, Japan: 124-133.

Sharp G.D. 1978. Behavioral and physiological properties of tunas and their effects on vulnerability to fishing gear. *In*: G.D. Sharp and A.E. Dizon (eds.). The physiological ecology of tunas. San Francisco, Academic Press: 397-449

Sharp G.D. (ed.) conv. 1981. Workshop on the Effects of Environmental Variation and the Survival of Larval Pelagic Fishes, *IOC Workshop Rep.*, 28, 323p. IOC Paris.

Sharp, G.D. 1987. Climate and fisheries: cause and effect or managing the long and short of it all. *In*: A.I.L. Payne, J.A. Gulland and K.H. Brink (eds.). The Benguela and comparable ecosystems. *S. Afr. J. mar. Sci.*, 5: 811-838.

Sharp G.D. 1988. Neritic systems and fisheries: their perturbations, natural and man induced. H. Postma and J.J. Zijlstra (eds.). *In*: Ecosystems of the world: Part 27. Continental shelves. Elseviers Scientific Publishing Co., Amsterdam, 155-202

Sharp G.D. 1992. Pieces of the puzzle: anecdotes, time series, and Insights. *In*: A.I.L. Payne, K.H. Brink, K.H. Mann and R. Hilborn (eds.). Benguela trophic functioning. *S. Afr. J. mar. Sci.* 12: 1079-1092.

Sharp G.D. and J. Csirke (eds.). 1984. Proceedings of the Expert Consultation to Examine the Changes in Abundance and Species Composition of Neritic Fish Resources, San Jose, Costa Rica, 18-29 April 1983. *FAO Fish Rep.*, 291, (2-3), 1294p.

Sharp G.D. and D.R. McLain. 1993a. Comments on the global ocean observing capabilities, indicator species as climate proxies, and the need for timely ocean monitoring. *Oceanography*, 5(3):163-168.

Sharp G.D. and D.R. McLain. 1993b. Fisheries, El Niño-Southern Oscillation and upper ocean temperature records: An eastern Pacific example. *Oceanography*, 6(1):13-22.

Smith P.E. and R. Lasker. 1978. Position of larval fish in an ecosystem. *Rapp. P.-v. Réun. int. Explor. Mer.,* 173:77-84.

Smith P.E. and G.H. Moser. 1988. CalCOFI time series: an overview of fishes. *CalCOFI Rep.*, 29: 66-90.

Soutar A. and P.A. Crill. 1977. Sedimentation and climatic patterns in the Santa Barbara Basin during the 19th and 20th centuries. *Bull. Geol. Soc. of America*, 88:1161-1172.

Soutar A. and J.D. Isaacs. 1969. History of fish populations inferred from fish scales in anaerobic sediments off California. *CalCOFI Rep.*, 13: 63-70.

Soutar A. and J.D. Isaacs. 1974. Abundance of pelagic fish during the 19th and 20th centuries as recorded in anaerobic sediments of the Californias. *Fish. Bull.*, U.S., 72:257-273.

Southward A.J. 1974a. Changes in the plankton community in the western English Channel. *Nature*, 259:5433.

Southward A.J. 1974b. Long-term changes in abundance of eggs in the Cornish pilchard (*Sardina pilchardus* Walbaum) off Plymouth. *J. Mar. Biol. Assoc.* UK NS, 47: 81-95.

Southward A.J., E.I. Butler and L. Pennycuick. 1975. Recent cyclic changes in climate and abundance of marine life. *Nature*, 253:714-717.

Stebbing A.R.D. 1981. The kinetics of growth control in a colonial hydroid. *Journal of the Marine Biological Association of the United Kingdom*, 61:35-63.

Stebbing A.R.D. 1982. Hormesis - the stimulation of growth by low levels of inhibitors. *Science of the Total Environment*, 22:213-234.

Stebbing A.R.D. and G.W. Heath. 1984. Is growth controlled by a hierarchical system? *Zoological Journal of the Linnean Society*. 80:345-367.

Theilacker G.H. 1986. Starvation-induced mortality of young sea-caught jack mackerel, *Trachurus symmetricus*, determined with histological and morphological methods. *Fish. Bull.*, U.S., 84:1-17.

Theilacker G.H. and K.T. Dorsey. 1981. Larval fish diversity, a summary of laboratory and field research. *In*: G.D. Sharp, conv. (ed.). Workshop on the Effects of Environmental Variation and the Survival of Larval Pelagic Fishes. *IOC Workshop Rep.*, 28: 105-142. IOC, Paris.

Theilacker, G.H., N.C.H. Lo and A.W. Townsend. 1993. An immunochemical approach to quantifying predation by euphausiids on the early stages of anchovy. *Mar. Ecol. Prog. Ser.*, 92:35-50.

Uda M. 1927. Relation between the daily catch statistical studies in the influence of cyclone upon the fishing. *J. Imper. Fish. Inst.*, 23(3):80-88.

Uda M. 1957. On the relation of the important fisheries conditions and the oceanographical conditions in the adjacent water of Japan. *J. Tokyo Univ. Fish.*, 38(3):363-369.

Ueber E. and A. MacCall. 1992. The rise and fall of the California sardine empire. *In*: Glantz M. (ed.). Climate Variability, climate change and fisheries. Cambridge Univ. Press. 31-48.

Ulanowicz R.E. 1986. *Growth and development: ecosystem phenomenology*. Springer-Verlag, New York, 203p.

Vetter E.F. 1988. Estimation of natural mortality in fish stocks: a review. *Fish. Bull.*, U.S., 86(1): 25-35.

Vlymen W.J., III, 1974. Swimming energetics of larval anchovy, *Engraulis mordax*. *Fish. Bull.* U.S., 72:885-899.

Vlymen W.J., III. 1977. A mathematical model of the relationship between larval anchovy (*Engraulis mordax*), growth, prey microdistribution and larval behavior. *Envir. Biol. Fishes*, 2:211-233.

Walters C.J. and J.S. Collie. 1988. Is research on environmental factors useful to fisheries management? *Can. J. Fish Aquat. Sci.*, 45: 1848-1854.

Life History Strategies for Marine Fishes in the Late Holocene

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ABSTRACT

Things change. Organisms flourish or flounder in response. This little essay is an attempt to utilize the rudiments of population biology acquired in three decades experience as a fisheries biologist to assess the likely patterns of response of a highly diverse taxa to the introduction of a single exotic species. Or, more directly, how will the marine fishes which survived the turbulence of the Pleistocene respond to ten thousand years of interaction with a marine primate ?

RÉSUMÉ

Les choses changent. En réponse les organismes prospèrent ou disparaissent. Ce petit essai constitue une tentative pour utiliser les rudiments en biologie des populations que j'ai acquis au cours de trois décennies d'expérience en tant que biologiste des pêches et qui ont été consacrées à évaluer les patterns probables de la réponse d'un taxon à l'introduction d'une seule espèce exotique. Ou, de façon plus explicite, comment les poissons marins qui ont survécu les turbulences du Pleistocène répondront à dix mille ans d'interaction avec un primate marin ?

INTRODUCTION

It is well known that fishes are the ancestors of all terrestrial vertebrates; however, it is not generally realized that mammals arose 80 million years before teleosts and that the teleosts which dominate today's seas evolved along with the modern mammals and birds following the massive extinction that brought the Cretaceous to a close about 65 million years ago (Table 1). Mass extinctions are followed by very extended periods with a depauperate fauna during which new forms evolve. Hobson (1994) has suggested that following the last mass extinction of marine fishes, at the end of the Cretaceous, the depauperate period lasted for about 10 million years (i.e., the Paleocene) and he notes that most forms of modern acanthopterygii arose during the Eocene.

Era	MYBP	Period	MYBP	Event
	-0.001	Late Holocene		Massive extinction
	0.0001	First modern fishing vessels		—
		Early Holocene		
	0.01			
		Pleistocene		
	1.8			Arctic glaciation begins
		Pliocene	3	Bering Sea opens to Arctic
	5			Isthmus of Panama closes
Cenozoic		Miocene		
	22			
		Oligocene	30	Most modern teleost families present
	35			
		Eocene		Rapid diversification of teleosts, mammals and birds
	55		55	
		Paleocene		
	65			Massive extinction
		Cretaceous	110	First diatoms
	140		145	First teleosts and birds
Mesozoic		Jurassic		
	210		225	Early mammals
		Triassic	245	First dinosaurs
	250			Massive extinction
		Permian		
	290		305	Early mammal-like reptiles
		Carboniferous	330	First reptiles
	360			
Paleozoic		Devonian	375	First sharks
	410		415	First bony fishes
		Silurian	425	First jawed fishes
	440			
		Ordovician		
	500		505	First agnatha
		Cambrian		
	590			

Table 1: The Evolution of Fishes. (MYBP= million years before present).

The descendants of the teleost fauna which evolved in the warm seas of the Paleocene and Eocene, when alligators were found north of the Arctic Circle (Dawson *et al.*, 1976) and temperatures at the bottom of the ocean were near 13°C (Crowley, 1983), today dominate the tropical and subtropical ocean. The largest component of today's marine fish fauna is the tropical Indo-Pacific fauna which is descendent from the Tethys fauna. The other two major faunas, i.e., the North Pacific and North Atlantic cold-temperate faunas, are descendant from the high latitude fauna of Panthalassa. These cold-temperate faunas were undoubtedly displaced from high latitudes to the mid-latitudes by the climatic deterioration which started with the build up of Antarctic glaciation in the Miocene (Berger, 1982), and accelerated in the late Pliocene and Pleistocene. Polar seas and deepwater regions are depauperate in marine fishes due to the small amount of time which has been available for fishes to evolve to the very cold marine climatic conditions which developed with the onset of extensive northern hemisphere glaciation about 2.4 million years ago (Shackleton *et al.*, 1984; Frakes *et al.*, 1993).

The recent or Holocene period started at the end of the last ice age, about 10 thousand years ago, and for the purposes of this paper I have divided it into the early Holocene and the late Holocene. The early Holocene - late Holocene boundary utilized in the paper coincides with the invention of the internal combustion engine. This boundary will, in the future, be easily noted in the increased lead and trace metal contents of estuarine and marine sediments. It is very clear that the early Holocene period was a period of mass extinction of large terrestrial vertebrates; however, there is no evidence of mass extinctions in marine vertebrates during this period. In fact, one of the major differences between the early and late Holocene is that humans had little effect on the marine environment in the early Holocene. The exception to this occurred near the end of the early Holocene when destructive land use practices resulted in massive sedimentation in the Mediterranean. The results can be seen at ancient sea ports such as Ostia in Italy and Utica in Tunisia which are now miles from the sea.

The late Holocene period can be characterized by the presence of modern fishing vessels employing a diverse array of technological improvements which greatly increase their capacity to harvest fishes. Synthetic twines for nets, hydraulic power sources and technological advances in net design have fostered the development of specialized purse-seines, high-rise bottom trawls, midwater trawls, and huge gillnets. A wide range of electronic devices are used to increase fish catching efficiency (i.e., radio, radar, loran, depth recorders, sonar, lidar, satellite navigation and net mounted telemetry). Airplanes and helicopters are used to locate fish schools, sidescan and multibeam sonars are used to precisely map bottom topography, and remote sensing from aircraft and satellites is used to identify environmental conditions which relate to fishing success (i.e., location of fronts, real time sea surface temperatures and ocean color). This increase in fishing technology has allowed the world's marine catch to increase from a minimum estimate of about 18.10^6 t in 1948 to a peak of $86.3.10^6$ t in 1989. Estimates of the world's marine fish catch prior to the invention of the internal combustion engine are unavailable but probably did not exceed 3.10^6 t. The great increase in the world's catch during this century has primarily been due to the expansion of fishing to species, stocks and geographical areas which were previously unexploited or lightly exploited. Although the technology has continued to improve, the world's marine catch has declined since 1989. It is clear that in many regions fishery yields have approached, or even exceeded, levels that will be sustainable. Pauly and Christensen (1995) recently calculated that the percentage of the annual primary production required to support existing fisheries and bycatch has already reached 25% in the world's upwelling ecosystems and 35% in the world's non-tropical shelf ecosystems. The potential for fisheries expansion in the future appears to be limited primarily to oceanic regions.

The premise of the present paper is that humans have caused and will continue to cause large alterations in the populations and diversity of marine fishes in the late Holocene. Most projections of the effects of human exploitation of the sea deal with a time scale of less than a decade and are primarily concerned with population fluctuations. I am not evaluating what will happen if current trends are projected for the next decade or even the next century, when the human population may be more than four times today's value. Instead, I am addressing what will happen over the next small increment of time on a geological time scale (i.e., the next ten thousand years). At this time scale, the effect of humans on marine fishes will be both direct (fishing, sedimentation, pollution, and the filling of estuaries), and indirect (changes in food webs and interactions between natural climatic changes and the direct effects) and it will primarily be expressed not in population fluctuations but in extinctions.

The purpose of the present paper is to examine the life history strategies for marine fishes which were successful in the Pleistocene and early Holocene and to compare them with strategies which would appear to be advantageous or disadvantageous in the late Holocene. The major assumption made is that global human population will not be markedly smaller than it was at the start of the late Holocene.

1. SUCCESSFUL VERTEBRATE LIFE HISTORY STRATEGIES OF THE LATE PLEISTOCENE

At the end of the Pleistocene there were a number of similarities between the successful life history strategies of marine and terrestrial vertebrates. One of the most conspicuous strategies was the reduction of mortality by acquisition of large size. This strategy has been utilized by a wide range of pelagic fishes (tunas, billfishes, sharks, molas, and some jacks), demersal fishes (halibuts, groupers and some scianids and skates) and marine mammals (whales, sea lions and porpoises). Terrestrial examples are best seen in the wildlife parks of Africa, in the Paleolithic cave paintings of France and in the La Brea tar pits of California. A second strategy, aggregation to reduce predation, was utilized by mobile, highly social, often migratory, lower trophic level animals. Species with this life-history strategy (i.e., terrestrial herding herbivores, flocking waterfowl, and marine schooling planktivores) dominated the vertebrate biomass of terrestrial and marine environments at the end of the Pleistocene. Two other strategies, (i.e., those utilized by small generalists and small specialists) were utilized by a large number of highly diverse species. Fishes with these strategies are often territorial and they generally do not achieve large population sizes.

The primary difference in the community structures of Pleistocene terrestrial and marine vertebrates is that the bulk of terrestrial vertebrates are herbivores whereas only a small component of marine vertebrates subsist on plants. Marine food chains therefore tend to be longer and more complex than terrestrial food chains and the marine fauna is more dominated by predatory forms than is the terrestrial fauna. Another major difference is that the majority of marine fishes have reproductive strategies which include high to very high fecundity, very small larval stages and no parental care. The consequence of the above is that most marine fishes have very high mortality rates during their early life history.

1.1. Life history strategies at risk in the late Holocene

There are a number of life history strategies which will be particularly at risk in the late Holocene (Table 2). The marine fishes which are most likely to disappear quickly are high trophic level predators which have suddenly themselves become prey to modern fishing vessels. These predators have the dual problem that they are now experiencing mortality rates greatly in excess of those which occurred prior to their exploitation by humans and in addition their prey is now greatly reduced by the same predator that is preying on them. The most susceptible of the predaceous fishes are those which have relied on the king-of-the-reef strategy (i.e., large territorial fishes such as many of the serranids, lutjanids and lethrinids, and some of the sciaenids, sparids and scorpaenids). These fishes often have considerable longevity, a delayed age at maturity and their recruitment is often small in relation to population biomass.

Large to moderate sized, predaceous, territorial reef fishes and rockfishes which have late age at maturity, very low natural mortality rates and low recruitment rates vs. adult stock size:

Snappers	Lutianids
Sea Basses	Serranids
Scavengers	Lethrinids
Rockfishes	Scorpaenids
Sea Bream	Sparids

Large to moderate sized shelf dwelling, soft bottom predators which are susceptible to bottom trawling:

Cods	Gadids
Flounders	Pleuronectids
Soles	Bothids
Rockfishes	Scorpaenids
Croakers	Sciaenids
Skates	Rajids

Large to moderate sized schooling midwater fishes susceptible to midwater trawling:

Hakes	Merluccids
Rockfishes	Scorpaenids
Armorheads	Pentacerolids
Roughyes	Trachichthyids

Shelf dwelling, pelagic, estuarine dependent or anadromous fishes which home to restricted spawning grounds or have low fecundity:

Herrings, shads	Clupeids
Capelin, eulachon	Osmerids
Salmon	Salmonids
Sharks	Carcharhinids, Squalids

Large to moderate sized shelf dwelling, schooling, pelagic fishes:

Bonitos, sierras	Scombrids
Jacks, trevallies	Carangids
Corvina, weakfish	Sciaenids
Barracudas	Sphyraenids
Salmon	Salmonids

Any species with exceptionally high monetary value:

Bluefin tuna
Halibuts
Aquarium fishes
Red snappers
Groupers
Medicinal fishes
Salmon
Red mullets
Billfishes

Table 2: Obvious losers.

Fishes susceptible to capture by bottom trawls (such as the shelf dwelling gadids, pleuronectids, bothids, sparids and scorpaenids) are likely to have high extinction rates. Many of these species have a delayed age at maturity which is associated with their large size. In addition to the delayed maturity problem, skates and demersal sharks will be particularly at risk due to their low fecundity. Many of the smaller species which are presently not targeted by bottom trawl fisheries, but whose habitat is subject to trawling, are likely to face increased exploitation as the primary trawl species become less abundant and they also face increased mortality through incidental capture and decreased productivity through alterations in habitat caused by many centuries of trawling. Schooling midwater or epibenthic species which are susceptible to midwater trawling, such as hakes, armorheads, roughies and some scorpaenids, will also be at risk.

Pelagic, schooling fishes are particularly susceptible to capture by modern purse-seines and gillnets. Prior to exploitation by fisheries, small and mid-sized pelagic fishes (sardines, anchovies, herrings, mackerels and jack mackerels) achieved real reductions in mortality by aggregating in dense schools. This behavioral pattern, which was highly successful in the early Holocene, now results in greatly increased mortality when these species are targeted by a fishing fleet using modern fishing technology. Aggregation of fishes into dense schools allows a modern purse-seiner to kill all, or nearly all, of the fish in a school in a single set. While schooling is likely to be a very poor strategy for the late Holocene; shoaling (i.e., when numerous fish schools are in close proximity) is even worse. When shoaling occurs in some species (i.e., clupeids and engraulids) a modern fishing fleet can kill several hundred thousand tons (i.e., more than 10 billion fish) in just a few days. In most small pelagic fishes the survivors from one day of fishing re-aggregate in schools which are less numerous but essentially of the same size as the original schools. This behavioral trait is particularly mal-adapted for the late Holocene as it results in a situation where mortality rates due to fishing do not decrease as the population size decreases. The behavioral traits which allowed many small schooling fishes to reduce their mortality rates from predation in the early Holocene now often result in greatly increased mortality rates from modern fishing fleets. On the positive side, there will be a reduction in predation rates for many of the small pelagic fishes as fishing will reduce the numbers and diversity of their predators. The trade-off between increased fishing mortality and decreased predation mortality may allow some small pelagics to increase both their ranges and population sizes while others will be at risk of extinction (Beverton, 1990). Generally the tropical small pelagics will be the most likely to have population and range increases as pre-exploitation predation rates tended to be higher in the tropics due to the highly diverse tropical fauna. Also tropical species are more likely mature at an early age and to be indeterminate spawners, which may allow them to maintain or even increase their fecundity under the altered physical environments, species composition and age structures of the late Holocene. Cold-temperate and subpolar small pelagics are the most likely to be at risk as they have higher ages at maturity and tend to spawn only once per year at established locations.

The mid-sized and larger coastal, pelagic predators such as the barracudas, bonitos, Spanish mackerels, salmons, and carangids which aggregate in schools are also at risk during the late Holocene. Many of these species have fast absolute growth rates and delayed ages at maturity, which makes them susceptible to recruitment overfishing.

Some fishes will be at risk of extinction in the late Holocene simply due to the fact that they have exceptionally high value to fishers. Examples include bluefin tuna, red snappers, groupers and aquarium fishes.

How will extinctions actually occur? Many species will simply fade away as a result of a life history strategy which does not produce enough new adults to replace those lost in the altered environments that will occur in the future. Many of those lost will be species which were relatively uncommon even before the rapid increase in exploitation by fisheries. It is likely that the changes in the populations of fishes will lead to large alterations in the invertebrate marine fauna and some fishes will disappear due to changes in the species composition of invertebrates which result in the destruction of their niches. Direct loss of habitat as well as physical or chemical alteration of habitats will remove some species, particularly fishes which utilize freshwater or estuarine habitats as part of their life history. Shallow reef and rocky bottom ecosystems, which contained the most complex and diverse marine fish communities in the Pleistocene, are likely to be highly altered by fishing, reef destruction, and sedimentation. The simple increase in mortality rates due to fishing will cause some species to go extinct. This is not likely in the next few decades; however, the effects of centuries of increased mortality will eventually take its toll. Many species will be stressed, but still viable under present climatic conditions but many of these will be lost during periods with different climatic conditions.

1.2. Life history strategies likely to be successful in the late Holocene

The late Holocene ocean will differ from that of the early Holocene in two major ways: a great reduction in the abundance of large and moderate-sized predators, caused by the increase and diversification in fishing power and an extensive physical, chemical and biological alteration of estuarine and nearshore environments. Many species will have greatly reduced population size and distribution and many stocks will eventually go extinct. Changes which will cause many stocks to decline and disappear will allow other types of fishes to increase both their ranges and populations (Table 3). A number of life history characteristics which occur in the present marine fish fauna appear to be particularly advantageous for the environment that is developing in the late Holocene (Table 4). Factors which will be of importance in determining which species will be favored include population rates, behavioral traits, genetic stock structures and habitat preferences. Obviously, avoidance of fishing mortality will be of high importance in the determination of which species will be successful in the late Holocene.

Population dynamics factors will be critical in the determination of which species will be successful during the late Holocene. Fishes which have low absolute growth rates (i.e., small maximum size) but high relative growth rates (i.e., they reach adult size quickly) will be favored. Fishes with an early age at maturity, high fecundity rates, and a high recruit to adult ratio will be favored. Fishes which have a relatively plastic age at maturity and/or indeterminate spawning (factors which allow excess energy to be readily used to increase annual fecundity) will have an advantage over those with a set age at maturity and set annual fecundity. Fishes able to persist under high mortality rates (i.e., those with a low natural mortality rate relative to their age at maturity or to their recruit-adult ratio) will also be favored. Fishes whose population size and or range has been limited by large or schooling predators could have great increases in their distribution and abundance as the abundance and distribution of predators is reduced.

Behavioral traits which will be favored in the late Holocene include nearly any trait which spreads out the population or makes it difficult for fishers to locate or harvest them. For example, it will be advantageous to be solitary or to live in small groups, to have an age-dependent habitat distribution, to be non-territorial, to be nomadic but to have little seasonal pattern in migrations.

Some habitats will be less affected by fishing and environmental alteration than others. Oceanic fishes will be less at risk than estuarine and neritic fishes; mesopelagic and bathypelagic fishes will be less at risk than epipelagic, benthic, and reef fishes.

It is possible that certain stock structure types will be favored. A species with a widely dispersed but relatively viscous stock structure (i.e., a stock which intermixes on a time scale of more than a decade) would be favored over a species with geographically restricted multiple genetic stocks each with fluid stock structure. The reason is that geographically restricted, multiple stocks can be decimated one by one whereas a single viscous stock can constantly recolonize areas from which it has disappeared. A fishery which only occurs over part of a stocks' range can drive a highly fluid stock to commercial extinction where a highly viscous stock would be maintained in the unexploited or less exploited part of its range.

Marine fishes have a broad spectrum of life history and behavioral characteristics some will be advantageous and others disadvantageous in the late Holocene. Species which have many characteristics which place them at risk may survive or even be abundant if the net effect of their life history strategy is favorable. The yellowfin tuna, *Thunnus albacares*, is a good example of a species with a mixture of favorable and unfavorable characteristics. On the negative side they are large, juveniles and young adults aggregate in schools which are susceptible to purse-seines, and they have a high value as food. They have a very high absolute growth rate and a low growth rate in relation to either their size at maturity or maximum size. The majority of yellowfin do not reach maturity until they are more than 120 cm; however, some reach maturity at 90 cm when they are about three years old. They are heavily exploited before they reach maturity and thereafter. Yellowfin tuna also have a number of characteristics which are favorable. They are oceanic and have a single, highly viscous genetic stock which is dispersed over the entire tropical ocean. The larger adults are too fast to be caught by trawls, too deep and too dispersed to be heavily exploited by purse-seines, and their catch rates appears to be directly density dependent. In addition they are indeterminate spawners with very high fecundity and they appear to be rather plastic in their age at maturity.

POPULATION RATES

- Low absolute growth rate.
- Small maximum size.
- High relative growth rate (vs. asymptote or maximum size).

- Small size at maturity.
- Early age at maturity.
- Indeterminate spawning.
- High recruit: adult ratio.
- Compensatory spawner-recruit relationship.

- Low natural mortality rate (relative to the von Bertalanffy parameter K).
- Ability to sustain a high natural mortality rate.

BEHAVIOR

- Solitary (as opposed to schooling).
- Mobile (as opposed to sedentary).
- Little pattern to movement (i.e. no set migrations)
- Non-territorial
- Age dependent habitat distribution.
- Avoidance of spawning concentrations

STOCK STRUCTURE

- Single widely dispersed genetic stock.
- Viscous stock (a fluid stock is available to more fishers).

HABITAT

- Oceanic (as opposed to coastal)
- Meso-pelagic
- Bathy-pelagic
- Neustonic
- Abyssal
- Non-benthic

BEST STRATEGY

- Be small, bony, ugly and unpalatable to primates

Table 3: Advantageous life-history strategies for the late Holocene.

Small offshore, non-schooling, meso-pelagic or epipelagic fishes:		
	Lanternfishes	Myctophids
	Cyclothone	Gonostomatids
	Deepsea smelts	Bathylagids
	Flying fish	Exocoetids
Small, solitary, ugly, shore fishes:		
	Blennies	Blennids
	Sculpins	Cottids
	Poachers	Agonids
	Prickbacks	Stichaeids
	Kelpfish	Clinids
Small unpalatable, reef and slope bottomfishes:		
	Lizardfish	Synodontids
	Sandlance	Ammodytids
	Gobies	Gobiids
	Leatherjackets	Balistids
	Toadfish	Batrachoidids
Small, reef and slope dwelling generalists:		
	Cardinalfish	Apogonids
	Damselfish	Pomacentrids
	Soldierfish	Holocentrids
	Wrasses	Coridids
	Butterflyfish	Chaetodontids
Small, early maturing pelagics with indeterminate spawning:		
	Tropical anchovies	Engraulids
	Tropical herrings	Clupeids
	Round herrings	Dussumierids
	Scads, Jacks	Carangids
	Frigate mackerel	Auxis

Table 4: Obvious winners.

2. DISCUSSION

It is relatively easy to pick out life-history and behavioral characteristics which will place marine fishes at risk of extinction over the next several thousand years; anyone with local fisheries knowledge could add their favorite candidates to the lists of obvious winners and losers. However, it should be recognized that we have little real knowledge of the interactions between species, little information on crucial environmental interactions, and little ability to predict what will happen when the species composition of an ecosystem is highly altered. Some species which have a number of life-history and behavioral characteristics which put them at risk may become dominant species due to other of their characteristics which give them an advantage in the altered ecosystems of the future. In contrast some species which have life history characteristics which would appear to be advantageous in the late Holocene will become extinct due to alterations in food webs or interactions with species which have suddenly become abundant or scarce.

It is possible that some ecosystems will have more biomass of fishes than they have at present while others may become dominated by invertebrates. Rapid increases and decreases in the abundance and distribution of species should be expected as the marine biota reacts to anthropogenic alterations of their habitat. This type of occurrence may have already happened in several ecosystems; for example the 'gadoid outburst' in the North Sea, the sparid outbreak off of northwest Africa, the gobid outbreak in the Benguela current. The best - excuse me: the worst - example is the present situation in the Black Sea (See Daskalov *et al.*, this vol.) where environmental alteration has resulted in an incredible change of the community structure.

3. FISHERIES MANAGEMENT

One of the early fisheries science concepts is that prior to exploitation there was some sort of an equilibrium state and that the fisheries would be able to achieve an equilibrium maximum, or 'optimum', yield from a population if we could just get fishing mortality at the right level (Roedel, 1975). In many areas of the world we currently have the knowledge to tell when stocks are over harvested and depleted; but very few areas of the world have political regimes capable of managing a stock at a fishing mortality rate which would even approach 'optimum' levels.

The political and fisheries regimes that I am most familiar with, those of the USA, are examples of fisheries management at the beginning of the late Holocene. Both the Pacific and Atlantic coasts of the USA have bellwether fisheries which have been exploited for several centuries, have great economic and cultural importance, many decades of well funded multidisciplinary research and extensive state-of-the-art fishery management regimes. The bellwether fishery on the Atlantic Coast is the George's Bank groundfish fishery and on the Pacific Coast it is the salmon fishery. The fisheries regimes for both fisheries are based on the concept of achieving the 'optimum yield' of the individual regulated species. The groundfish fishery harvests a mixture of marine fishes whereas the salmon fishery harvests just a couple of anadromous species but each species has/had many isolated genetic stocks. Evidence was available for each fishery which clearly showed that the principal stocks were being overharvested and that the populations were in an extended state of decline. The management regimes in each of these fisheries can only be credited with overseeing the collapse of its fishery. In discussing the collapse of the George's Bank fishery, Apollonio (1995) suggested that part of the problem was that "we don't know in fact how to control fishing mortality in multi-species groundfish fisheries". He even questioned the very concept that the management regime was based on "what is optimum yield (OY) anyway?" The situation with the Pacific Coast salmon fishery of the Washington to California region has had equally bad success in reducing mortality; which in this case includes extensive alteration of the river systems utilized for reproduction and early life history. This fishery is now only maintained by fish hatcheries, a large number of genetic stocks have already been driven to extinction and many more are endangered (Nehlsen *et al.*, 1991).

Most current fisheries management regimes operate on concepts based on equilibrium states. John Issacs has suggested that the marine fauna is never at equilibrium and that it is constantly recovering from environmental perturbations on a wide range of time scales (Behrman, 1992). If one takes Issacs' view and includes anthropogenic impacts (i.e., increasing fishing pressure and environmental alteration), one is led to the conclusion that the expected pattern which will occur over the next few thousand years in most fisheries ecosystems is a series of extensive but unpredictable changes.

It is possible that a fisheries management regime based on long-term preservation of species diversity will someday prevail. Fishery management regimes are of course primarily dependent upon political regimes which, history teaches us, are very ephemeral. One should therefore not be led to the conclusion that any fishery management regime will last longer than the political regime it was based on. In my opinion a strategy of reliance on fisheries management appears to be inferior to one based on being a small, quick growing, early maturing, non-schooling, offshore fish which is unpalatable to primates.

I would place my bet that the late Holocene will be a myctophid heaven.

REFERENCES CITED

Apollonio S. 1995. Northeast groundfish: assigning blame won't improve management; asking questions will. *National Fisherman*, 76 (2).

Behrman D. 1992. *John Isaacs and his oceans*. American Geophysical Union, ICSU Press, Washington D.C., 230 p.

Berger W.R. 1982. Climate steps in ocean history - Lessons from the Pleistocene. *In*: *Climate in earth history*. National Academy Press, 44-54.

Beverton R.J.H. 1990. Small marine pelagic fish and the threat of fishing. Are they endangered? *J. Fish. Biol.*, 37: 5-16.

Crowley T.J. 1983. The geological record of climate change. *Rev. Geophys. and Space Phys.*, 21(4): 828-877.

Dawson M.R., R.M. West, W. Langston and J.H. Hutchinson. 1976. Paleogene terrestrial vertebrates: northernmost occurrence, Ellesmere Island, Canada, *Science*, 192: 781-782.

Frakes L.A., J.E. Francis and J.I. Syktus. 1993. *Climate modes of the Phanerozoic: the history of the earth's climate over the past 600 million years*. Cambridge University Press, 271 p.

Hobson E.S. 1994. Ecological relations in the evolution of acanthopterygian fishes in warm-temperate communities of the Northeastern Pacific. *Environmental Biology of fishes*, 40(1): 49-90.

Nehlsen W., J.E. Willians and J. A. Lichatowich. 1991. Pacific salmon at the crossroads: stocks at risk from California, Oregon, Idaho, and Washington. *Fisheries*, 16(2): 4-21.

Pauly D. and V. Christensen. 1995. Primary production required to sustain global fisheries. *Nature*, 374(6519): 255-257.

Roedel P.M. 1975. A summary and critique of the Symposium on Optimum Sustainable Yield. *In:* P.R. Roedel (ed.). Optimum sustainable yield as a concept in fisheries management. *Amer. Fish. Soc.*, Spec. Pub., 9: 79-89.

Shackleton N.J. and 16 others. 1984. Oxygen isotope calibration of the onset of ice rafting and history of glaciation in the North Atlantic region. *Nature*, 307: 620-623.

Fisheries Resources as Diminishing Assets: Marine Diversity Threatened by Anecdotes

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ABSTRACT

Fish stock dynamics are studied using fishery statistics which do not take into account the existence of the intraspecific diversity in fish populations. Populations are generally considered to be homogeneous and management considers each stock of a given species as a global entity. However recent genetic population studies reveal unsuspected intraspecific diversity. Examples of population collapses and local extinctions are presented which, in spite of restrictive measurements (limitation of the effort, quotas...), do not come back to their former abundance level (bluefin tuna, cod, herring, marine turtles, salmon...) resulting in decreasing catches from these stocks. At first sight, reports of fluctuations of such local populations may be viewed as anecdotal. The incorporation of fisheries history (anecdotes such as local extinctions) into models used by fishery scientists would help evaluate the true rate of disappearance of resource species and the ecological cost of fisheries. We present here a qualitative approach of fish behavior, based on earlier work of the first author to explain why the extinction of local populations may affect long-term overall fish productivity. The erosion of the marine intraspecific diversity could lead to a long-term decline in the productivity of the marine resources.

RÉSUMÉ

La dynamique des populations de poisson est étudiée en utilisant des statistiques de pêches qui ne prennent pas en compte l'existence de la diversité intraspécifique. Les populations exploitées sont généralement supposées homogènes et la gestion considère les stocks comme des entités globales. Cependant de récentes études menées en génétique des populations révèlent une diversité intraspécifique inattendue. On présente des exemples d'effondrement de stocks et d'extinctions locales qui, en dépit de mesures d'aménagement (limitation de l'effort, des quotas...), ne se reconstituent pas pleinement (thon rouge, morue, hareng, les tortues marines, les saumons...) et aboutissent globalement à de moindres captures. A première vue, certaines fluctuations de populations locales peuvent être perçues comme des anecdotes. L'incorporation de l'histoire des pêches (anecdotes comme celles des extinctions locales) dans les modèles utilisés par les scientifiques pourrait aider à évaluer le réel impact de l'exploitation sur le taux de disparition de la diversité intraspécifique et son coût écologique. Nous présentons un cadre conceptuel basé sur un précédent travail du premier auteur qui permet d'expliquer pourquoi les extinctions locales peuvent conduire à long terme à un déclin des ressources marines. L'érosion de la diversité marine intraspécifique pourrait conduire à un déclin progressif de la productivité des ressources marines.

1. GLOBAL FISHERIES IN A NEW AND GLOBAL PERSPECTIVE

Almost all fish species have tiny eggs of one or a few millimeters, in diameter whatever are their adult sizes. Some life history traits of marine species have been apparently shaped by strong selective pressures. As a result, most fish populations have an enormous capacity of resilience due to the high batch fecundity and to the large populations they develop. This is part of what allows the impressive fish catches extracted from the oceans. However present global fisheries are not doing so well, not to say that fisheries are a global disaster (Pauly, 1995). The world marine fish catch have increased almost fivefold from around 19.10^6 t in 1950 to 100.10^6 t in 1992; this latter value was considered a threshold value; thus, in 1994 the FAO pointed out that 69% of the global fish stocks for which assessments are available, are either fully exploited, overfished, depleted or slowly recovering from depletion. Fisheries are in a new and global context. Will marine fish exploitation be viable under a persistent degraded ecological state? This certainly constitutes one of the most important challenge for the next decades of exploitation of renewable resources (Roberts, 1997).

Although fisheries assessment has been extensively developed over the last century, it has not hitherto considered the evolutionary consequences of fishing itself (Berry, 1995). The ever-increasing intensity of exploitation and the deterioration of fish stocks have generated an urgent need for a better understanding of evolution driven by harvesting and its implications for management (Stokes *et al.*, 1993). Intense fishing mortality could act as a new selective pressure producing genetic change, for example on heritable traits such as growth rate and age of first reproduction (Sutherland, 1990). Thus life histories of fish could be altered as a result of harvesting, inducing a risk of possible long-term decline in yields. Species are sometimes profitable at very low population levels and if a fishery targets a high-value species, it may reduce the stock to a level that leads to depletion and collapse. Fisheries-induced collapse of marine populations can have two consequences for biodiversity. First, the populations may not recover and/or re-colonize their ecological niche. Secondly, rare genes can be lost as a result of a drastic decrease in population number. To take a longer-term view and to rethink the way in which wild populations are harvested is needed.

Recently Pauly (1995) defined a 'shifting baseline syndrome' wherein a gradual accommodation of the creeping disappearance of resource species takes place due to inappropriate reference points: each generation of fisheries scientists accepts as a baseline the stock size and species composition that occurred at the beginning of their careers, and uses this to evaluate changes. Thus, Pauly (op.cit.), identified a lack of the use of fisheries history, to help us to understand and to overcome the shifting baseline syndrome and to evaluate the true social and ecological costs of fisheries. In this paper we would like to emphasize the importance of considering 'anecdotes' such as local populations extinctions for long term sustainable fisheries. Using an ecological framework, the relevance of the intraspecific level for fish stock management will then be considered.

2. HETEROGENEOUS MARINE FISH STOCKS

Field and genetic studies greatly modify any simplified view of population dynamics and structures. Hedgecock *et al.* (1989) report genetic heterogeneity within the central Californian northern anchovy stock (*Engraulis mordax*), previously regarded as a panmictic population. Thus, anchovy stocks that were thought to be homogeneous are in fact a mosaic of 'elementary' populations (Hedgecock, 1991). According to Mathisen (1989) the anchoveta stock off Peru consists of a large number of local subpopulations each of which is genetically adapted to 'home' to a different upwelling location and to spawn during a specific period of the year. European sardine populations are traditionally assigned to six different 'races'; however, further subdivisions have been made according to spawning seasons that are separated by several months and that may define sympatric populations (Wyatt *et al.*, 1991). As noted by Hedgecock (1991) for *Engraulis mordax* off California, the 'demonstration of sympatric, biologically distinct subpopulations within the main spawning area of the central stock is unexplained by current concepts of northern anchovy stock structure'. Electrophoretic analysis of stock structure in Northern Mediterranean anchovies, *Engraulis encrasicolus*, clearly illustrate the independence of anchovy stocks in the Northern Mediterranean and given a restricted level of migration, one would predict that regeneration of depleted stocks would be almost totally autochthonous (Bembo *et al.*, 1996). Recent genetic studies emphasize the fact that even high migrating fish populations are heterogeneous, even in an apparently homogeneous environment, and that this heterogeneity should play a fundamental role in population dynamics. Microsatellite DNA provide that Atlantic cod (*Gadus morhua*) overwintering in inshore Newfoundland are genetically distinguishable from cod overwintering offshore (Ruzzante *et al.*, 1996). Restriction analysis of mitochondrial DNA of swordfish (*Xiphias gladius*) revealed no differentiation among samples from three sites in the Mediterranean Sea (Greece, Italy, Spain) but a high degree of differentiation between Mediterranean samples and a sample from the Gulf of Guinea (Kotoulas *et al.*, 1995). Another study indicated that the mtDNA haplotype frequencies were significantly different among samples from the Pacific Ocean, the Atlantic Ocean and the Mediterranean Sea (Bremer *et al.*, in press). Genetic analyses are generally very sensitive to gene flow. Relatively low levels of exchange between stocks, negligible from a management perspective, may be sufficient to ensure genetic homogeneity (Bembo *et al.*, 1996). These recent genetic analyses also clearly suggest that, under such integrity, recovery from collapse would be slow.

3. DIVERSITY AND EXPLOITATION

3.1. Generalities

Probably well over half of all vertebrate species are fishes as there are in excess of 22 000 described species of fish, and vertebrates as a whole comprise around 43 000 species (Anon., 1992). Thus fishes make up the most abundant class of vertebrates, both in terms of numbers of species and of individuals. It also appears that fish typically exhibit higher levels of variation both between and within populations than in other vertebrates (Ryman and Utter, 1987). More than 13 000 species are marine species, but the fisheries industry is based on a remarkably small number of species. Thus over one million tonnes each of 12 fish species (10 marine and 2 freshwater) were caught in 1989; together this comprised $34.7.10^6$ t, or 35% of the total world catch (Anon., 1992).

Overfishing seems to be a major threat to biodiversity as it depletes resources, and thus can lead to loss of genetic integrity, local populations and even species. Moreover, the important catches of immature fish prevent the stocks from renewing themselves. In the North Sea, only 2 to 3% of cod and haddock rich maturity (60 cm, 4 years) and more than 90% of cod and 65% to 80% of grouper caught (between the Gulf of Biscay and West Scotland) are composed by juveniles. For fixed species (giant clams Tridacnidae), low densities and erratic recruitment make such populations prone to overfishing, inducing local extinctions (Lucas, 1994). Natural environment changes, and especially for species which inhabit or migrate in area in vicinity of human activity numerous causes (such as habitat degradation, anthropogenic changes, deterioration of water quality, etc.) often lead to a local disappearance of a species. In Chichiawan stream, Taiwan, the salmon cohort born in 1987 has been destroyed by the typhoon Lynn which occurred during the breeding season. Some fishing methods such as the use of dynamite, chemicals (bleach and cyanide), bottom trawling or bottom-set net can damage or destroy habitat, reducing the survival of organisms. Introduction of fishes was thought to be a solution to various problems: introduction of fast-growing fish for fish culture, introduction of predatory fishes to control fish production in ponds, 'improvement' of sport fisheries, 'control' of unwanted organisms (aquatic weed, snails, mosquitoes, etc.), to fill seemingly 'empty' ecological niches. But such introductions generally create major problems (Moreau *et al.*, 1988), through predation or competition. The introduced fishes can reduce or cause local extinction of some endemic species (Lodge and Hill, 1994).

Most examples of collapses are due to multiple causes and are the result of interaction between various factors. Generally, for marine species it is the consequence of a natural disturbance such as environmental changes, associated with intense exploitation (Beverton, 1990).

3.2. Facts and numbers

*3.2.1- Herring (*Clupea harengus*)*

Herring are known for their tendency to return to the spawning ground where they themselves have been hatched. Fecundity data show that herring hatched in the Southern North Sea and the English Channel probably are genetically distinct from those in the Central and Northern North Sea (Zijlstra, 1973).The subpopulations of each spawning site tend to maintain their integrity over the years. Thus, when several of these subpopulations were destroyed by overfishing in the 1960s, they did not re-appear after the recovery of the total North Sea stock from 75 000 t in 1975 to 1.4 $.10^6$ t in 1992. The size of the actual spawning sites hardly decreased during this period and the former spawning sites that were fished out in the 1960s were not reoccupied since (Corten, 1993). The herring stock recovered during the 1980s owing to the closure of the herring fishery in the late 1970s - early 1980s and subsequent increases in recruitment. However the spawning-stock biomass which used to range between 2 and 5.10^6 t in the 1950s, hardly reaches 1 million t in the 1990s. (Serchuk *et al.*, 1996). Generally, during their feeding migration, fish appear to follow the same route from one year to another, and like the choice of the spawning and overwintering grounds, it is probably also determined by tradition (Corten, op.cit.). Thus, it may be that the recolonization of a feeding ground requires the presence of older, experienced herring to guide new generations to the former, traditional feeding ground (Corten, op. cit.). Herring adapt their feeding ground with local conditions: for example in the 1980s, their feeding grounds during June to July changed from the Western North Sea to Northeastern North Sea, and they extended their migration and changed their vertical distribution (Corten and Van de Kamp, 1992). Another change in migration involved Baltic herring, which in 1986 changed from the Kattegat and Skagerrak into the North Sea (Anon, 1991).

Herring have been caught in Norway since time immemorial. The history of the herring fisheries can be traced back hundreds of years, but data on stock assessment are only available since the 1950s. The adult herring stock was estimated to range from 7 to 10.10^6 t in the 1950s, but declined in the 1960s and since then remained below 2.10^6 t (Hamre, 1994). The Norwegian spring-spawning herring showed a steady pattern in its feeding migration for many decades until the collapse of the stock in the late 1960s. After this local extinction, herring remained in the vicinity of the Norwegian coast throughout the year (Corten, 1993). These fishes now extend their feeding ground over the Norwegian Sea east of 5°W, but they have not yet rediscovered their old feeding grounds. In 1963 and 1964, heavy exploitation of both immature and mature herring by Norwegians in Norwegian waters led to a collapse of the overwintering stock. It is only in 1984, after the recruitment of the first strong North Sea class, that herring reappeared in the Norwegian zone.

Atlantic herring (*Clupea harengus harengus* L.) was, before its collapse in 1977 (probably due to overfishing, Moeller, 1984) supported on the Georges Bank, the largest herring fishery in the Northwest Atlantic. After almost a decade herring have reappeared. An analysis of age composition, isozyme characteristics, time of the reappearance, shows that the reappearance of this population would have resulted from resurgence of a residual Georges Bank population (Stephenson and Kornfield, 1990) rather than recolonization from other areas located nearby, i.e., Jeffreys Ledge and S.W. Nova Scotia.

Herring stocks are composed of different subpopulations adapted to local areas. Thus, a concentration of fishing effort on certain subpopulations can lead to the extinction of these components before the total stock shows signs of overfishing (Corten, 1993). This characteristic make herring stocks prone to local extinction even if, generally, they will recover; thus, the depleted British Columbia stock recovered as soon as fishing stopped (Saville, 1980). However in general, once the spawning site has been abandoned by the population, it is not easily re-occupied by later generations. Thus,there is evidence of extinction, such as that of Pacific herring, *Clupea harengus pallasii* or that of the Hokkaido-Sakhalin herring, which has disappeared since 1946 (Tanaka, 1983). Certain races have never recovered from earlier overfishing: the spring-spawning stock of Icelandic herring is now effectively extinct, though Jakobsson (1985) believes that the failure of this stock to recover may be associated with a sharp decline in the level of primary production in the area. Corten (1990) mentions the recolonization of the Aberdeen Bank spawning ground in 1983 after an absence of 15 years. Bergstad *et al.* (1991) noticed that the traditional spawning ground off Karmoy in Southern Norway has been recolonized in 1989, 30 years after the stock was depleted.

*3.2.2- Northern cod (*Gadus morhua*)*

The Sami Fjord Cod in Northern Norway is of three types, all different from the Norwegian Arctic cod, which spawns off Lofoten (Eythorsson, 1993). These three types are: The Algae-cod (in Sami: *tararunuk*) which is brown in color, never leaves the fjord. This type of cod seems to be disappearing, along with the brown algae belt that it lives in. The Fjord cod (Sami: *vuotnaguolli*), which spawns in the fjord and does not migrate out of it. It starts spawning before the migrating cod. The migrating cod (Sami: *buoiddesguolli*), which spawns in the fjord in winter, but lives in the open sea the rest of the year. Similarly, the analysis of mtDNA provided evidence that Atlantic cod overwintering in offshore Newfoundland are genetically distinguishable from cod overwintering offshore (Ruzzante *et al.*, 1996).

The commercial extinction of northern cod off Newfoundland and Labrador in 1992 was a social and economic disaster for the region. The high rates of exploitation in the late 1980s and early 1990s are thought to be responsible for the collapse of the six major cod stocks in Eastern Canada by 1993. The hypothesis that the primary cause of the collapse was environmental has been proposed (climate change, seal predation, changes in the ecosystem) (Lear and Parsons, 1993; Mann and Drinkwater, 1994). Against this speaks the fact that two declines in annual survival probabilities in the 1980s appear at the same time inshore and offshore as fishing effort increased (Hutchings and Myers, 1994). Indeed, even if an increase of natural mortality in the first half of 1991 occurred, overfishing was high enough to cause a collapse of the cod population (Myers and Cadigan, 1995b). It has also been claimed that the collapse was due to overfishing alone (Hutchings and Myers, 1994; Myers and Cadigan, 1995a,b). Results of studies on three of these stocks (Southern Labrador/North-East Newfoundland, St-Pierre Bank, and Northern Gulf of St-Lawrence) attribute the collapse of this stocks to overfishing (Myers *et al.*, 1996). Because of errors on the estimations of population abundance and fishing mortality (the first one was overestimated and the second was underestimated), quotas were too high. The over capacity of fishing fleet allowed to increase the fishing mortality and the discarding of juveniles. As a consequence, the number of fish entering the fishery was reduced and the extremely low levels of spawners inhibited the recovery of the population (Myers and Barrowman, 1994). All of this lead to a declining long-term catch rate, even under a fishing effort that switched from inshore to offshore (from areas of low to high catch rates).

3.2.3- Bluefin tuna

The bluefin tuna (*Thunnus thynnus thynnus*) has a temperate distribution. It is supposed to have a 'natal homing' strategy, which brings it back to spawn either in the South Central Mediterranean Sea or in the Gulf of Mexico (Cury *et al.*, in press). This migrant fish which has been fished in Mediterranean Sea since the 8th millennium BP (Desse and Desse-Berset, 1994) is much sought after for the quality of the flesh, or for sport fishing (mostly in the Eastern USA).

Bluefin tuna has disappeared from some areas (Norway, N-E Brazil, Black Sea, etc.) where they were feeding during the 1960s. The disappearances may have various causes: change in fishing pattern for Norway, overfishing off Brazil (Cury *et al.*, op cit.). But the hypotheses would not explain entirely the depletion of stocks of bluefin tunas. This is also true for other causes that must be taken into account such as climatic changes or variations on the main prey biomass (anchovies in the Black Sea).

Fish catch statistics may help track migration patterns and particularly reproductive migration as these fish tend to aggregate when they spawn. Bluefin tuna is certainly the tuna species that is fished in the Atlantic Ocean since most ancient times. Archeological studies reveal that 8th millennium BP age, bluefin was found in a coastal pre-ceramic Neolithic site of Cape Andres Kastros in Cyprus (Desse and Desse-Berset, 1994). It was also exploited more than 3 000 years ago by the Greeks. Then Phoenicians, and subsequently Romans, initiated active fisheries using large traps all around the Straits of Gibraltar. This exploitation was developed until the early XXth century all around the Mediterranean Sea. Since 1950, new fishing gear (hand-lines made of nylon thread, pole and line, purse seine, longline) offered possibilities of development for new coastal fisheries in the Eastern and the Western Atlantic. Bluefin tuna supplied national markets of fresh fish and a low demand market for canning. By 1960, the bluefin fisheries reached their maximal geographical extension. Then, at the end of the 1960s, two major fisheries disappeared. Bluefin tuna entirely vanished from the Brazilian area (centered on the Equator between 25 and 35°W) (Cury *et al.*, in press), a major fishing zone during the early sixties (producing 64% of the West Atlantic bluefin catch between 1963 and 1965). The North East Atlantic bluefin fishery off Norway was also a major one during the 1950s (an average 20% of the bluefin catch between 1951 and 1962); this fishery had collapsed by 1965.

3.2.4- Many others

Many more examples may extend the list of natural or human induced disappearance of marine populations. Over the last century, Pacific salmon (*Oncorhynchus* spp.) have totally or partially disappeared from about 40% of their breeding ranges in the states of Washington, Oregon, Idaho, and California (Comm. on Protection and Management of Pacific Northwest Anadromous Salmon, 1995). The European sea sturgeon (*Acipenser sturio*), once numerous along western coastal Europe and Scandinavia, has today only marginal populations in the Gironde River, France, and possibly in the Black Sea. The Adriatic sturgeon (*Acipenser dabryanus*) limited to the Yangtze River, the Adriatic sturgeon (*Acipenser naccarii*), or the Amu-Dar shovelnose sturgeon (*Psuedoscaphirhynchus kaufmanni*) of the Amu-Darya River are all in sharp decline or near extinction (Waldman, 1995). Not only fishes are subject to local extinctions. Marine turtles, coconut crabs and giant clams (long-lived and slow-growing species) are endangered in most of the South Western Pacific islands region (Zann, 1994). Not only overfishing but also the increasing pressure from rapidly rising human populations, urbanization, agricultural, industrial development, result in a significant loss of coastal habitats, pollution and eutrophication of coastal lagoons and reefs; the consequence are local extinctions of various populations. Green turtle (*Chelonia mydas*) migrate between tropical and subtropical feeding and a local specific nesting ground. The females probably return to nest at their natal rookery (Carr, 1967). For thousands of years green turtles have been fished, but in the last four centuries, increasing exploitation of green turtle marketing has driven several populations to extinction and has greatly diminished others (Parsons, 1962). Former rookeries such as Grand Cayman, Bermuda, Alto Velo, have not been re-colonized by natural recruitment (Parsons, 1962). Because of natal homing, overharvesting of nesting assemblages is not compensated by recruitment from other rookeries (Bowen *et al.*, 1992).

4. FISHERIES RESOURCES AS DIMINISHING ASSETS

Due to extension and openness of seas and oceans, the extinction through overfishing of a marine species rarely occurred until recent times. Today many fish species are known to have been brought to the verge of extension and are added to the red list by the Species Survival Commission of the World Conservation Council (IUCN) (Grain, 1995). The need to protect biodiversity has become increasingly apparent over the past two decades (Ryman *et al.*, 1995). Gould (1996) recently discussed the importance of preserving the diversity of life as the lost of one species is forever. He argued that the same arguments can not be done when considering the intraspecific diversity. Moreover, local extinctions may not be considered as important as the great majority of the stocks shows sign of recovery. It seems that populations reduced to 1/1000th or so of their peak sizes for long time periods (e.g., more than 20 years in the case of the California sardine), can form a nucleus of a revival when conditions become favorable (Beverton, 1990). In this sense, reducing intraspecific diversity does not represent the same kind of threat as species extinctions. However, reducing intraspecific diversity of marine populations could affect the long-term productivity of the fisheries. There are several reasons for that. The first one is that long-term stocks sustainability should not be taken for granted: reviewing collapse and recovery of pelagic fish stocks, Beverton (op. cit.) noted "the possibility that the collapsed population may never be able to fully regain its former status in the ecosystem"; among nine documented stocks which experienced a collapse, only one has fully regained its original size. Then, at the subpopulation scale, the extinction of one or few populations can pass unnoticed if the others have a great productivity and a subpopulation may become extinct before signs of overfishing are noticed in the total stock. Finally, even if regulation of fisheries is established, the biomass of the total stock will fluctuate at a long-term lower level. The second reason is that ecological frameworks are now being developed that can help to incorporate fisheries history (anecdotes such as the local extinction documented in this paper) into models for fisheries scientists. These models may help us evaluate the true disappearance of resource species and their ecological cost to fisheries. In ecology, it is common to consider a demographic exchangeability of individuals (two individuals are then equivalent) and this is used to define populations in most models of population and community ecology (Templeton, 1989). Recently Cury (1994) proposed a generalization of 'natal homing' within which homing is viewed as part of a continuum of reproductive strategies, all relying on imprinting. This generalization postulates that a newborn individual memorizes early environmental cues, which later determine the choice of its reproductive environment. This way of looking at fish population dynamics implies that inertia is the driving force in the functioning of natural systems. Because every individual is able to explore a specific environmental possibility and in some way to transmit it to its descendants, it makes each of these individuals unique in terms of their reproductive behavior. In other words, once a spawning site has been abandoned or fished out, it takes a long period of time to reoccupy it by later generations. As noted in the Introduction, the resilience of marine fish population is potentially enormous and allows the fisheries to be so successful. On the other hand, various behavioral mechanisms that lead to the discrete population concept thwart the renewal process in its duration and intensity dimensions (see also Parrish, this vol.). Thus, the disappearance of subpopulations can have a detrimental effect on long-term marine fish catch (Fig. 1).

The paradigm underlying most fisheries regulation is to prevent undersized fish from being caught and/or to allow a sufficient number of fishes to escape harvest to ensure a sufficient adult spawning stock, so as to maintain high recruitment levels. The two principal forms of regulation are to control the size of organisms taken and the amount of harvesting effort applied (Bohnsack and Ault, 1996). Rarely are the effects of fishing on the genetic or stocks composition considered. Management has led to an ultimate pathology of less resilient and more vulnerable ecosystems, more rigid and

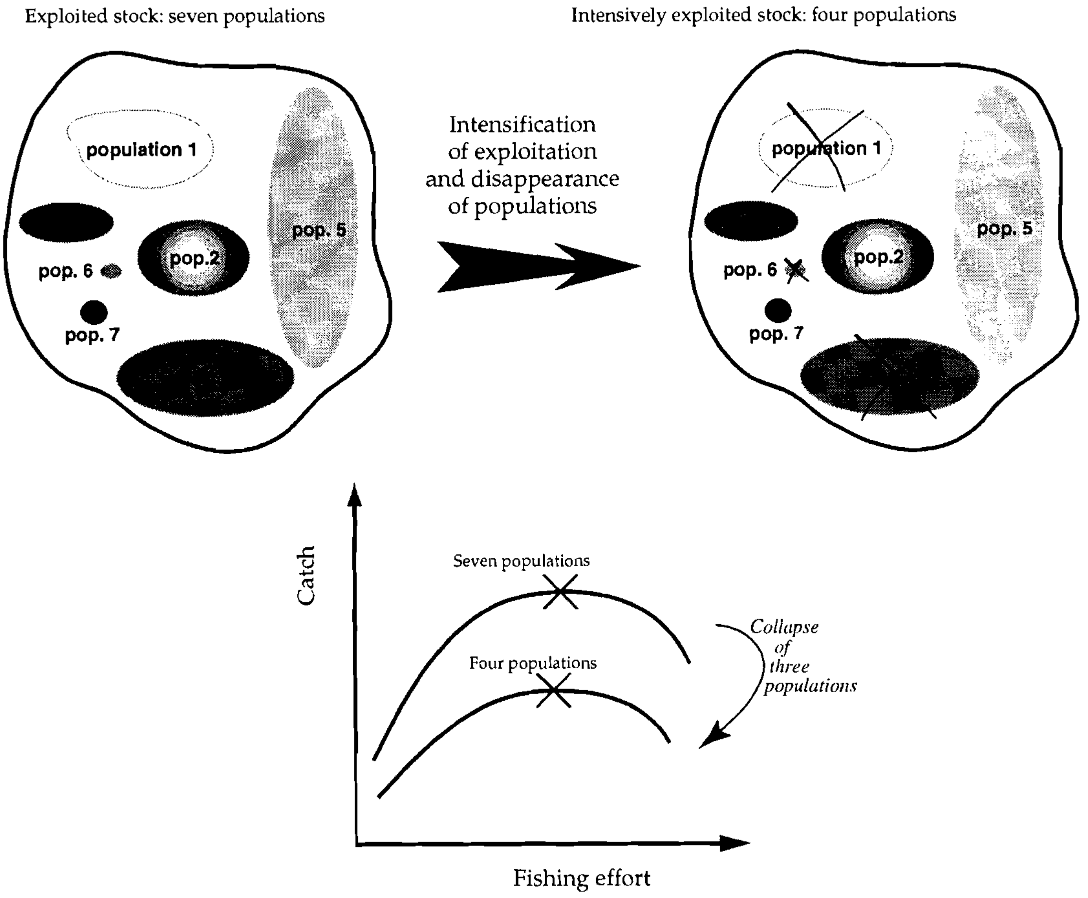

Fig. 1 : Schematic representation of how the erosion of the intraspecific diversity may affect the productivity of fisheries. The disappearance of three populations under intense exploitation can have a detrimental effect on long-term marine fish catch. Productivity declines as a result, as suggested in the catch-effort diagram where two catch levels are possible for a given fishing effort according to the composition of the two stocks.

unresponsive management agencies and more dependent societies (Gunderson *et al.*, 1995) A new objective is to change from single species management to ecosystem management aimed at protecting marine biodiversity and at promoting its viable use. This constitute a chance to integrate biodiversity into fish population dynamics and to develop frameworks to understand and promote new concepts on the functioning and the dynamics of renewable resources (Cury, 1994). As mentioned by Franck and Leggett (1994), a greater consideration of the implications of ecological and evolutionary theory could lead to significant advances in the understanding of processes of population regulation in marine fishes. Because fish are the only major food source harvested from natural populations, a knowledge of the structure of these populations is essential for proper resource management. The need for better understanding of biodiversity among fishes is particularly needed below the species level (Ryman *et al.*, 1995).

REFERENCES CITED

Anon. 1991. *Report of the Herring Assessment Working Group for the Area South of 62°N.* ICES/C.M., 1991/Assess, 15.

Anon. 1992. *Global diversity : status of the earth's living resources.* Chapman and Hall, London, 585p.

Bembo D.G., G.R. Carvalho, N. Cingolani and T.J. Pitcher. 1996. Electrophoretic analysis of stock structure in northern Mediterranean anchovies, *Engraulis encrasicolus. ICES J. Mar. Sci.*, 53: 115-128.

Berry R.J. 1995. Marine genetics- a cautionary tale with a happy ending (so far). *TREE*, 10(11), 472p.

Bergstad O.A., I. Rottingen, R. Toresen, A. Johannessen and O. Dragesund. 1991. *Return of Norwegian spring spawning herring (Clupea harengus L.) to historical spawning grounds off southwestern Norway.* ICES C.M. 1991/H:24.

Beverton R.J.H. 1990. Small marine pelagic fish and the threat of fishing; are they endangered? *J. Fish Biol.*, 37 (Supplement A): 5-16.

Bohnsack J.A. and J.S. Ault. 1996. Management strategies to conserve marine biodiversity. *Oceanography*, 9(1): 73-82.

Bowen B.W., A.B. Meylan, J.P. Ross, C.J. Limpus, G.H. Balazs and J.C. Avise. 1992. Global population structure and natural history of the green turtle (*Chelonia mydas*) in terms of matriarchal phylogeny. *Evolution*, 46(4): 865-881.

Bremer J.R.A, J. Mejuto and B. Ely. M.S. In press. Interoceanic population structure of the swordfish (*Xiphias gladius*) as revealed by DNA sequence analysis of the mitochondrial control region.

Carr A., 1967. *So excellent a fish: A natural history of sea turtles.* Scribner, N.Y., USA.

Comm. on Protection and Management of Pacific Northwest Anadromous Salmon. 1995. *Upstream: salmon and society in the Pacific northwest.* Washington-DC., USA, National Academic Press., 402p.

Corten A. 1990. Long-term trends in pelagic fish stocks of the North Sea and adjacent waters and their possible connection to hydrographic changes. *Neth.J.Sea Res.*, 25 (1-2): 227-235.

Corten A. 1993. *Learning processes in herring migrations.* ICES/ C.M., 1993/H: 18.

Corten A. and G. Van de Kamp. 1992. Natural changes in pelagic fish stocks of the North Sea in the 1980s. *ICES Mar. Sci. Symp.*, 195: 402-417.

Cury P. 1994. Obstinate nature: an ecology of individuals. Thoughts on reproductive behavior and biodiversity. *Can. J. Fish Aquat. Sci.* (Perspectives), 51 (7): 1664-1673.

Cury P., O. Anneville, F.X. Bard, A. Fonteneau and C. Roy. In press. Obstinate bluefin tuna: an evolutionary approach to analyze reproductive migrations. *ICCAT: SCRS.*

Desse J. and N. Desse-Berset. 1994. Osteometry and fishing strategies at Cape Andreas Kastros (Cyprus, 8th millennium B.P.). Fish exploitation in the past. Proceeding of the 7th Meeting of the ICAZ Fish Remains Working Group. Van Neer W (ed.) *Annales du Musée Royal de l'Afrique Centrale, Sciences Zoologiques*, Tervuren, 274: 69-79.

Eythorsson E. 1993. Sami Fjord fishermen and the state: traditional knowledge and resource management in northern Norway. *Traditional Ecological Knowledge*, 13: 133-142.

Franck K.T. and W.C. Leggett. 1994. Fisheries ecology in the context of ecological and evolutionary theory. *Annu. Rev. Ecol. Syst.*, 25: 401-422.

Gould S.J. 1996. *Comme les huit doigts de la main.* Fayard, 511p.

Grain A.R. 1995. Fishing out aquatic diversity. *Seedling*, 12 (2): 2-13.

Gunderson L.H., C.S. Holling and S.S. Light (eds.). 1995. *Barriers and bridges: to the renewal of ecosystems and institutions.* Columbia Univ. Press, New York, 593p.

Hedgecock D. 1991. Contrasting population genetic structures of pelagic clupeoids in the California current. *In*: T. Kawasaki, S. Tanaka, Y. Toba and A. Taniguchi (eds.). *Long-term variability of pelagic fish populations and their environment.* Pergamon Press, Oxford: 199-207.

Hedgecock D., E.S. Hutchinson, G. Li, F.L. Sly, and K. Nelson. 1989. Genetic and morphometric variation in the Pacific sardine, *Sardinops sagax caerulea*: comparisons and contrasts with historical data and with variability in the northern anchovy, *Engraulis mordax. Fish. Bull.* U.S., 87: 653-671.

Hamre J. 1994. Biodiversity and exploitation of the main fish stocks in the Norwegian - Barents Sea ecosystem. *Biodivers. Conserv.*, 3: 473-492.

Hutchings J.A. and R.A. Myers. 1994. What can be learned from the collapse of a renewable resource? Atlantic cod, *Gadus morhua*, of Newfoundland and Labrador. *Can. J. Fish Aquat. Sci.*, 51 (9): 2126-2146.

Jakobsson J. 1985. Monitoring and management of the Northeast Atlantic Herring Stocks. *Can. J. Fish Aquat. Sci.*, 42: 207-221.

Kotoulas G., A. Magoulas , N. Tsimenides and E. Zouros. 1995. Marked mitochondrial DNA differences between Mediterranean and Atlantic populations of the swordfish, *Xiphias gladius*. *Molecular Ecology*, 4: 473-481.

Lear W.H. and L.S. Parsons (eds.). 1993. History and management of fishery for northern cod in NAFO divisions 2J, 3K, and 3L. Perspectives on Canadian marine fisheries management. *Can. J. Fish Aquat. Sci.*, 226: 55-89.

Lodge D.M. and A.M. Hill. 1994. Factors governing species composition, population size, and productivity of cool-water crayfishes. *Nord. J. Freshwat. Res.*, 69: 111-136.

Lucas J.S. 1994. The biology, exploitation, and mariculture of giant clams (Tridacnidae). *Rev. Fish. Sci.*, 2 (3): 181-224.

Mann K.H. and K.F. Drinkwater. 1994. Environmental influences on fish and shellfish production in the Northwest Atlantic. *Environ. Rev.*, 2: 16-32.

Mathisen O.A. 1989. Adaptation of the anchoveta (*Engraulis ringens*) to the Peruvian upwelling system. *In*: D. Pauly, P. Muck, J. Mendo and I. Tsukayama (eds.). The Peruvian upwelling ecosystem: dynamics and interactions. *ICLARM Conference Proceedings*, Manila, Philippines, 18: 220-234.

Moeller H. 1984. Causes of the collapse of pelagic swarm fish stocks. *In*: H.H. Reichenbach Klinke and W. Ahne (eds.). *Contributions to Fish Parasitology and Toxicology*, 13: 187-199.

Moreau J., J. Avignon and R.A. Jubb. 1988. Introduction of foreign fishes in African inland waters: suitability and problems. *Biol. Ecol. Afr. Freshwater Fish.*, 216: 395-425.

Myers R.A. and N.J. Barrowman. 1994. *Is fish recruitment related to spawner abundance?* ICES C.M. 1994/G:37.

Myers R.A. and N.G. Cadigan. 1995a. The statistical analysis of catch-at-age data with correlated errors. *Can. J. Fish Aquat. Sci.*, 52: 1265-1273.

Myers R.A. and N.G. Cadigan. 1995b. Was an increase in natural mortality responsible for the collapse of northern cod? *Can. J. Fish Aquat. Sci.*, 52: 1274-1285.

Myers R.A., N.J. Barrowman, J.M. Hoenig and Z. Qu. 1996. The collapse of cod in eastern Canada : the evidence from tagging data. *ICES J. Mar. Sci.*, 53(3): 629-640.

Parsons J. 1962. *The Green Turtle and Man*. University of Florida Press, Gainesville, Fl, USA.

Pauly D. 1995. Anecdotes and the shifting baseline syndrome of fisheries. *TREE*, 10(10), 430p.

Roberts C.M. 1997. Ecological advice for the global fisheries crisis. *TREE*, 12 (1): 35-38.

Ruzzante D.E., C.T. Taggart, D. Cook. and S. Goddard. 1996. Genetic differentiation between inshore and offshore Atlantic cod (*Gadus morhua*) off Newfoundland: microsatellite DNA variation and antifreeze level. *Can J. Fish Aquat. Sci.*, 53: 634-645.

Ryman N. and F. Utter (eds.). 1987. *Population genetics and fishery management*. Washington Sea Grant, Seattle, 420p.

Ryman N, F. Utter and L. Laikre. 1995. Protection of intraspecific biodiversity of exploited fishes. *Reviews in Fish Biol. Fish*, 5(4): 417-446.

Saville A. (ed.). 1980. The assessment and management of pelagic fish stocks. *Rapp. P.-v. Réun. Cons. int. Expl.Mer.*, 177p.

Serchuk F.M., E. Kirkegaard and N. Daan. 1996. Status and trends of the major roundfish, flatfish, and pelagic fish stocks in the North Sea: thirty-year overview. *ICES J. Mar.Sci.*, 53: 1130-1145.

Stephenson R.L. and I. Kornfield. 1990. Reappearance of spawning Atlantic herring (*Clupea harengus harengus*) on Georges Bank: population resurgence not recolonization. *Can. J. Fish Aquat. Sci.*, 47(6): 1060-1064.

Stokes T. K. , J.M. McGlade and R. Law (eds.). 1993. The exploitation of evolving resources. *Lecture Notes in Biomathematics*. Spinger Verlag, 99, 264p.

Sutherland W.J. 1990. Evolution and fisheries. *Nature*, 344 (26 April).

Tanaka S. 1983. Variation of pelagic fish stocks in water around Japan. *In*: G.D. Sharp and J. Csirke (eds.). Proceedings of the Expert Consultation to Examine Changes in Abundance and Species of Neritic Fish Resources. *FAO Fish. Rep.*, 291.

Templeton A.R. 1989. The meaning of species and speciation : a genetic perspective. *In*: D. Otte and J.A. Endler. *Speciation and its consequences*. Sinauer Associates, Sunderland, Mass, USA: 3-27.

Waldman J.R. 1995. Sturgeons and paddlefishes : A convergence of biology, politics, and greed. *Fisheries*, 20 (9): 20-21.

Wyatt T., D.H. Cushing and S. Junquera. 1991. Stock distinctions and evolution of european sardine. *In*: T. Kawasaki, S. Tanaka, Y. Toba and A. Taniguchi (eds.). *Long-term variability of pelagic fish populations and their environment.* Pergamon Press, Oxford: 229-238.

Zann L.P. 1994. The status of coral reefs in South Western Pacific islands. *Mar. Pollut. Bull.*, 29 (1-3): 52-61.

Zijlstra J.J. 1973. Egg weight and fecundity in the North Sea herrings (*Clupea harengus*). *Neth. J. Sea Res.*, 6 (1-2): 173-204.

The CEOS Network: A Brief Summary of Experience

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ABSTRACT

The Climate and Eastern Ocean Systems Project (CEOS) 1991-1997 was implemented through an informal network which emphasized exchanges of ideas among colleagues, rather than simple exchange of data. Some of the advances that resulted from these exchanges - many of them during visits and/or workshops organized by the CEOS - are (1) confirmation of the wide applicability of the Cury/Roy hypothesis of 'dome-shaped' recruitment windows vis-à-vis wind intensity; (2) the demonstration of concurrently acting 'global' and 'local' effects on upwelling ecosystems; (3) the usefulness of time series analysis, and of mass-balance trophic models for quantifying some of the effects on (2); and (4) the usefulness of items (1-3) for identifying the causes of recent observed changes in some systems, and for predicting the impact of global change on upwelling systems in general.

RÉSUMÉ

Le projet sur le climat et les bords est des systèmes océaniques (CEOS) 1991-1997 a démarré à travers un réseau informel qui a mis l'accent sur l'échange d'idées et non sur le simple échange de données. Parmi les résultats issus de ces échanges - et réalisés à l'occasion de visites ou de groupes de tra-

vail organisés par CEOS - on peut citer : (1) la confirmation du caractère opératoire de l'hypothèse de Cury et Roy concernant la relation en forme de 'dôme' entre le recrutement et l'intensité du vent ; (2) la démonstration de l'existence de phénomènes à des échelles globale et locale agissant simultanément sur les écosystèmes d'upwelling ; (3) l'utilité des techniques d'analyse des séries temporelles ainsi que des modèles trophiques pour quantifier certains des effets mentionnés en (2) ; et (4) l'intérêt des points (1-3) pour identifier les causes des récents changements observés dans certains systèmes et plus généralement pour prédire l'impact du changement global sur les systèmes d'upwelling.

1. CEOS: A NETWORK EXPERIENCE

The idea of the CEOS network emerged in 1991, after an informal meeting where some of us had been wondering about the potential usefulness of performing comparative analyses in upwelling systems and arguing about how to initiate the required world-wide comparisons. Few months later the CEOS network started (see Bakun *et al.*, 1992).

1.1. The implicit, unstated rules of CEOS

There are usually important but unstated, implicit rules which make or break a project. Here, we make explicit some of the rules which, we believe, made CEOS the success it was.

The first one was that within the network *we worked with people and not with their data*. During the last five years, small groups of colleagues met to exchange ideas and methods to work on well identified scientific questions, relevant to global and local changes in upwelling systems. Usually, these working groups lasted for ten to fifteen days, sometimes more. Most of the time, the colleagues from developing countries had an excellent knowledge of their fisheries and their dynamics; this was not always the case for scientists working in developed countries. On the other hand, access to good libraries and to new methods was most of the time easier in developed countries. For these reasons, the CEOS network tried to play a role in helping to share field and academic experiences among the different participants. The many multi-authored articles included in this book is one result of this sharing. Our network thus succeeded at facilitating the transfer of expertise, at promoting exchanges within the scientific community, and to help to maintain links among people, which itself gave rise to new ideas and projects.

1.2. A multidisciplinary network designed as an evolving scientific framework

Interesting scientific questions nowadays often require a multidisciplinary approach, especially concerning environmental studies. However, di Castri (1986) notes that "interdisciplinarity, when it is considered and implemented as an end in itself, and not as a tool for addressing new complex problems, leads too often to verbose descriptions and non explanatory results". Thus, another rule of the CEOS research project was to focus not on the definition and the exploration of interdisciplinary linkages, but on jointly addressed questions. Disciplines such as oceanography, ecology, statistics or economy were sometimes put together and lead to new insights within the CEOS network.

Inevitably, in a group with such a diversity of participants, the question of methodology came under close scrutiny. All of us from different points of view, were addressing retrospective analyses and had questions about change. What is a change, how can it be detected and modeled at different scales? Uncertainty, causality links, evolution, scales problem, long- and short-term impacts are all common issues that are addressed by different disciplines and fruitful insights may result through exchanges of methods. However, as the disciplines become more and more technical and specialized, they frequently ignore each other; the techniques that have been developed in one field are neglected by the others. The CEOS network has allowed to share methodology between disciplines. For example this book contains statistical techniques which have been firstly developed in econometrics in order to separate long-term trend from other cyclical and seasonal variabilities and which are presently applied to oceanography. This leads to new insights and helped us to reformulate scientific objectives. Mass-balance models, commonly used to describe 'local' systems were used for inferences on global vs. local effects on upwelling systems (see section 3.2 below). Generalized additive models (Hastie and Tibshirani, 1990) which have been first developed in statistics for medicine were applied to environmental *variability* and *fish* population dynamics (see section 3.1 below). An interactive software (CLIMPROD) was used for choosing and fitting surplus production models including environmental variables (see Mendoza *et al.*, Yanez *et al.*, this vol.). Object-oriented object simulations developed in computing sciences may help to simulate fishery activity facing change (see Le Fur, this vol.).

The CEOS project was not defined as a specific program with fixed objectives and tasks but as a multidisciplinary network with scientific questions that were allowed to evolve. Everyone was able to promote new ideas, to use new methods or new data sets, and to explore and develop new objectives. The contributions in this volume illustrate the benefit that results from such freedom being available.

1.3. Data availability within and outside the CEOS network

Making raw data available to a wide range of users is difficult, and a tradition for doing so is lacking in most disciplines (Pauly, 1994). Physical oceanography is one of the few exception, and several institutes followed on the proud tradition initiated by Commodore Matthew F. Maury by compiling and making available the Comprehensive Ocean-Atmosphere Data Set (COADS) (Woodruff *et al.*, 1987). With the help of the National Center for Atmospheric Research (NCAR-USA), CEOS went one step further when we decided to distribute on CD-Rom, as a CEOS product, a full version of the COADS dataset and the accompagning microcomputer based software (see Roy and Mendelssohn, this vol., and Box 1). Data extracted from the COADS were obviously made available to all CEOS participants, and these replied in kind, making their

Box 1: How to obtain and use the COADS

The Comprehensive Ocean-Atmosphere Data set (COADS) was selected by CEOS as key source of environmental data for comparative analyses of upwelling systems.

To support this and similar future effort, CEOS also made available entire COADS, covering the years 1895 to 1990, in form of five CD-Roms, covering the oceans as follows
Vol. 1: North Atlantic Ocean;
Vol. 2: Central Atlantic Ocean;
Vol. 3: South Atlantic Ocean and Indian Ocean;
Vol. 4: Western Pacific Ocean; and
Vol. 5: Eastern Pacific Ocean.

These CD-Roms may be obtained separately or as a complete set by writing to:
- Claude Roy for the Atlantic (email: croy@orstom.fr)
- Roy Mendelssohn for the Pacific (email: rmendels@pfeg.noaa.gov)

These CD-Roms are distributed with a software program (for PC or MAC) for extracting and summarizing time series or other information, for selected area. Please specify in your order whether you use an Apple Macintosh computer or one using an Intel processor. No charge are requested.

Users of the COADS must remain conscious of the limitations of this dataset, whose variable data density and changes in measuring devices induce changes where none occurred, or mask changes which did occur (see Roy and Mendelssohn, this vol.).

local data sets available to their CEOS partners. Having become, through their publication in this book, part of the public domain, the bulk of these data may now also be obtained by the readers of this book, by contacting the first author (c/o ORSTOM), or the original author.

A related, large data set, but pertaining only to the Peruvian upwelling system, and documented in Pauly and Tsukayama (1987) and Pauly *et al.* (1989) may be obtained by contacting the last author (pauly@fisheries.com).

Also, Fishbase the computerized encyclopedia of fishes (Froese and Pauly, 1996), may be consulted for information on the biology of the fish species discussed in this volume (see Box 2).

Box 2: Availability of FishBase and Ecopath

FishBase and Ecopath are two software products developed at, and available from ICLARM, to support the research and assessment work of fisheries scientists. The former tool, FishBase, which is supported by the European Commission, began in the late 1980s as a large database on fish, covering their nomenclature (valid scientific names, synonyms, common names in various languages), their biology (growth mortality, reproduction, food and feeding habits, respiration, etc.), and their uses (through time series of fisheries catches, of recruitment, etc.). Gradually, however, the many cross-linked data sets in FishBase, and the routines created for their display have turned it from a passive data repository into to an analytic tool, allowing for establishing and/or testing relationships and hypotheses not previously documented. This process is being strengthened by extensive provisions for citing and/or otherwise acknowledging external contributions, which have has led to an increasing number of collaborators making complex data set available for inclusion in and analysis through FishBase. Presently covering over 4/5 of all extant marine and freshwater fish species (i.e., 25 000, all to be covered by the year 2000), FishBase is available on CD-Roms that are updated and reissued annually, with FishBase 97 (Froese and Pauly, 1997) as the latest release. FishBase may be obtained for US$ 95 (and US$ 50 for updates), or free of charge (for collaborators). Contact R. Froese at ICLARM (M.C.P.O.Box 2631, 0718 Makati, Philippines; r.froese@cgnet.com) for details.

The latter of the two software tools mentioned above, Ecopath, based on an approach initiated by J.J.Polovina, Hawaii in the early 1980s, became in the late 1980s an ICLARM project funded by the Danish International Development Agency (DANIDA), devoted to the further development and dissemination of a simple, generic tool for the construction and validation of mass-balance trophic model of aquatic ecosystems. Jarre-Teichmann and Christensen (this vol.) present the master equation of the Ecopath approach. Important developments of Ecopath since their contribution was completed include a Monte-Carlo resampling module for dealing with uncertainty in a Bayesian context (Ecoranger), and a module (Ecosim) which reinterprets the (linear) master equation into a system of coupled differential equations, thus allowing Ecopath files to be used as basis for dynamic simulations, and thus for predictions of the impacts of fishing on the different elements of an ecosystem. A fully documented program (Ecopath 4.0 for Windows) incorporating these and numerous other analytical features is available free of charge from Villy Christensen, ICLARM (see address above, or v.christensen@cgnet.com).

2. ENVIRONMENT AND PELAGIC FISHERIES: WHAT HAVE WE LEARNED?

Huge fluctuations and unexpected appearances or disappearances are not new to this century, and have been reported from past fisheries. During the famous 'sardine crisis', at the end of the 19th Century in France, a scientific commission was mandated by the government to investigate the causes of the fishery's collapse. In a context of almost complete ignorance of ecology and of pressure to reduce fishing effort and to ban the more productive fishing gears, all studies concluded that it was environmental and climatic factors that were responsible (Durand, 1991). Contrary to the initial hypotheses, which assumed large migrations, the scientists admitted the idea of local and regional races with short migrations. To some, it was obvious that sardine had to return where they were hatched. Having discovered that eggs do float, and that larval feeding was pelagic, the scientists conducting these early studies assumed that temperature, winds and currents should be important factors for larvae survival. It appeared that sardine needed moderate and relatively constant temperature and that this species was sensitive to great temperature fluctuations and turbulence associated with the wind. Winds were incriminated both for their deleterious effects on feeding conditions and for spreading the eggs and larvae. For Mader (1909), the main cause of appearance and disappearance of the sardine was the direction and the force of the winds. Almost one hundred years later, after decades of studies, data collection and the emergence and decline of various versions of the Theory of Fishing, the question arise: what have we really learned?

The theories which aimed to control, predict and manage fisheries are now often considered as having a poor rate of success. Doubts are justified since several of the best studied and presumably best-managed fisheries have collapsed, whereas numerous successful and productive fisheries exist, which have been neither well studied, nor are subject to modern management (Francis, 1980). Without minimizing the great scientific advances that occurred in fish population dynamics, we are forced to admit that fisheries management, as defined above, has failed. It may be argued that it is not the classical theory of fishing per se which failed, and that the stock collapses, now put at the feet of this theory, were in fact due to not strictly applying the regulations derived from that theory.

Still, the theory itself can be faulted for its implicit assumption of independence of successive observations and its inability to take into account the qualitative discontinuities and threshold phenomena that are frequently observed (Francis, 1980; Roberts, 1997). Another, perhaps even stronger criticism is that the classical theory of fishing was unabashedly single species, notwithstanding the strong trophic interactions among, e.g., the living components of upwelling system (Jarre-Teichmann and Christensen, this vol.). We have only begun to deal with this issue, which is elaborated upon in section 3.2 below. Global changes that occur at the ecosystem level appear to have a strong effect on fish population dynamics. Yañez *et al.* (this vol.) show that the anchovy and the sardine in North Chile and in Peru between 1950 and 1993 were intensively exploited and affected by global environmental changes such as the El Niño events.

Long-term changes, i.e., decadal wind increase, appear to have strong effects on fish population dynamics in the Canary Current. Kifani (this vol.) showed that a long-term increase in Moroccan coastal upwelling intensity between 1950s and mid-1970s has induced the sardine long-term fluctuation. Binet *et al.* (this vol.) showed that two periods of high abundance and southward spreading of sardines (*Sardina pilchardus*) with accompanying changes affecting others pelagic fishes, appears to be strongly linked to decadal changes in the environment. On the other hand, Pezennec and Koranteng (this vol.) suggested that for a particular and spatially well-defined environment, the strengthening of the minor upwelling appears to be the only likely cause of the drastic changes that occurred in the sardinella fisheries off Côte-d'Ivoire and Ghana during the last decades.

Both local or global environmental changes that frequently happen within an ecosystem at a scale of the last decades of observations may drastically affect fish population dynamics. The example of an anomalous migration of *Sardina pilchardus* in Senegal led Demarcq (this vol.) to hypothesize that the mean seasonal intensity or the 'precocity' of the upwelling is not sufficient to initiate an abnormal southward migration and that the seasonal transition is a key parameter in this process. Béné and Moguedet (this vol.) suggested that both a global environmental factor (the effect of Amazon River) and a local environmental factor (local river outflow) have an effect on the Guyana shrimp fishery dynamics. Daskalov *et al.* (this vol.), Prodanov *et al.* (this vol.) as well as Stergiou and Christou (this vol.) presented ecological changes that appeared in related upwelling systems and the effects of the environmental factors that are suspected to produce these changes at different scales of observation.

These and related oceanographic processes are now relatively well understood and their relationships with fish behavior better explained. Great advances also have been made to link reproductive strategies, feeding habits and fish behavior (Cury and Roy, 1991; Pauly and Tsukayama, 1987; Pauly *et al.*, 1989). Much of this knowledge is now explained by the 'triad' concept, which shows that enrichment, concentration and retention processes appear to be key factors that affect fish recruitment (Bakun, 1996). This concept also inspired many of the studies of the CEOS project presented in this volume.

3. COMBINING LOCAL AND GLOBAL RESEARCH STRATEGIES: THE CEOS ACTIVITIES

The results of CEOS research in West and South-West Africa, North and South America and in Europe are extremely valuable by themselves. Comparisons between sites is, however, a major scientific task. Drawing valid scientific inference requires multiple realizations of the process of interest, preferably over a range of differing conditions, in order to separate causality from happenstance with a reasonable degree of confidence. Marine ecosystems are hardly amenable to experimental controls. Fortunately, the comparative method represents a powerful method (Bakun, this vol.), and its use was another tacit (sometimes explicit) rule within the CEOS network.

3.1. Environmental impact on fisheries: Optimal Environmental Windows, the Climprod software and the ACE algorithm

The Optimal Environmental Window (OEW) concept relates the recruitment of the fish of upwelling systems with their environment (Cury and Roy, 1991). Previously established during a research project in West Africa, the OEW hypothesis needed corroboration from other areas. Boyd *et al.* (this vol.) and Serra *et al.* (this vol.) present corroborations of the OEW hypothesis for anchovy in South Africa and Chilean sardine, respectively, while Bakun (1996) generalized the OEW in the context of his 'triad' theory. Also Faure and Cury (this vol.) showed that a combination of several environmental factors determine the level of pelagic fish catch within upwelling system, and that winds appear to have a dome-shaped relationship to the fish production of these systems. Mendoza *et al.* (this vol.) examined the ability of environmental factors to explain the variability of catch time series from the upwelling system off eastern Venezuela using the CLIMPROD software of Fréon *et al.* (1993), which again confirmed the crucial role played by the wind.

This crucial role of the wind is, in retrospect, not surprising: fishes, in upwelling as well as elsewhere tend to have tiny eggs, in the order of one millimeter, whatever their adult sizes. Winds determine the rate at which the surface waters are mixed and transported in which these eggs hatch into larvae, and must find suitable food at high densities. Theses winds have to be 'just right' -not too weak and not too strong, and hence the importance of non-linear, dome-shaped relationships such as the OEW.

This brings us to ACE (Alternating Conditional Expectation; Hastie and Tibshirani, 1990), used by numerous contributors to this volume to 'tease out' non-linear relationships among data sets that would otherwise have seemed unrelated. Based on this experience, which confirms earlier work by Mendelssohn and Mendo (1987) and Mendelssohn (1989), we conclude that any attempt to relate biological and physical time series - and not only in the context of the OEW hypothesis - must consider non-linear techniques such as ACE or GAIM (Generalized Additive Models ; Hastie and Tibshirani, 1990), lest it will fail to identify crucial, non-linear relationships.

3.2. Capturing interspecies and ecosystem relationship through trophic mass-balance models

Living species, whether exploited or not, interact in various ways, some of them very hard to quantify. Fortunately, the strongest interactions between organisms — eating, or being eaten — belong to a class of interactions that are straightforward to quantify, notably through mass-balance models of ecosystems (Christensen and Pauly, 1992). Indeed, this approach, implemented through the ECOPATH software, is so easy to apply that to date, nearly hundred applications have been published (e.g., in Christensen and Pauly, 1993), or are in press, thus allowing comparisons among different types of ecosystems, or global analyses (Pauly and Christensen, 1995). Here the mass-balance approach was applied for comparisons among upwelling, i.e., in a context previously thought not amenable to this type of approach (Jarre-Teichmann and Christensen, this vol.).

Indeed, these comparisons, in spite of the lack of time dimension in ECOPATH model, added to the main theme of his volume — the disentangling of global vs. local impacts — a trophic perspective which the analysis of catch time series could not have contributed. Moreover, it has recently emerged that ECOPATH-type mass-balance models can be used to parameterize the differential equations of full-blown simulation models (Walters *et al.*, 1997). This allows explicit consideration of the temporal dimension, e.g., to examine the effect of fishing one component of an upwelling ecosystem, via its trophic linkages, on the other components of that same ecosystem.

Vasconcellos *et al.* (in press) present comparisons of the dynamics of various ecosystems (including the upwelling systems studied by Jarre-Teichmann and Christensen, this vol.) showing that following a disturbance (a five-fold increase, for ten years of the fishing mortality of the major species of small pelagics), the system return time is an inverse function of detritus recycling within a system. Upwelling ecosystems have a low degree of internal detritus recycling (see Jarre-Teichmann and Christensen, this vol.) and hence their food webs do not dampen well shocks due to fishing or other disturbances (Vasconcellos *et al.*, in press).

Clearly, investigations of this sort are germane to questions such as tackled by the CEOS project and network, and it is hoped that studies of this sort will be continued.

3.3. Long-term environmental changes and human responses

Decadal environmental changes are a reality. Using new state-space statistical models, Schwing *et al.* (this vol.) present evidence that environmental parameters are significantly correlated in the California Current system, in a manner consistent with increased upwelling (SST and sea level have decreased, and salinity has increased). The analysis of several temperature data set by Koranteng and Pezennec (this vol.) documents multi-decadal changes in the Côte d'Ivoire-Ghana coastal ecosystem. Mahé (this vol.) estimated the total annual yield of freshwater flowing into the Atlantic Ocean from West and Central Africa, and showed a global change between two periods, a 'wet' period before 1970 and a 'dry' period afterwards.

Human responses to changes are numerous; sometimes they appear to be similar, sometimes they do not. The Senegalese and the Ghanaian ecosystems have many ecological similarities. Comparing the strategy and tactics developed by the small-scale fishers to the variability of their environment, Ferraris *et al.* (this vol.) found flexibility and adaptability in both communities. Using an artificial intelligence model, Le Fur (this vol.) formalized the communication between actors at the local level and their collective response to changes at larger scales. Global and local changes also affect markets. Durand (this vol.) found that prices in the soybean meal market induce short-term fluctuations in the fishmeal price because of speculative effects, while fishmeal price longer trends influence soybean meal price through their impact on the demand for soybean meal. Sharp (this vol.) analyzed the constraints that appear in fisheries at different levels and scales, from the ecological to the institutional. Parrish (this vol.) hypothesized a long term view of what fisheries will lead to in terms of biodiversity. Cury and Anneville (this vol.) focused on the intraspecific diversity of fisheries based on a generalization of the natal homing hypothesis in Cury (1994). As it turns out, all of these different approaches are based on evolutionary considerations and stressed the importance of fisheries diversity, both implicit subthemes of CEOS.

4. NEW CHALLENGES

Overall, it appears that fishery science is better at dealing with the biological dimension of fisheries — including their interactions with the biotic and abiotic environment — than with the human dimension (hence the rather pessimistic account of Parrish, this vol.).

The world marine fish catch was about 20 million tonnes in the early 1950s, and about five times higher in the early 1990s - not counting a staggering discarding rate of by-catch, estimated at about 30 plus or minus 10 million tonnes (Alverson *et al.*, 1994). Whether present catches are 'sustainable' or not is a moot point: it is already obvious that these catch levels are 'sustained' at only a very high ecological (damage to demersal habitats, coral reefs, massive changes in species compositions), and economical costs (massive subsidies, Malthusian overfishing, Pauly, 1994). Moreover, it is unlikely that the soaring demand for fish and related marine products will continue to be accommodated; this is thus bound to create new tensions.

Ecosystem variability, induced by local and global changes will add to these difficulties. We hope that at least some of the concept and methods presented here will turn out useful for dealing with ecosystem variability, and to help us keep upwelling systems and other fisheries resources systems as one of the source of food that our succeeding generations will so badly need.

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REFERENCES CITED

Alverson D.L., M.H. Freeberg, S. Murawski and J.G. Pope 1994. A global assessment of fisheries bycatch and discards, *FAO Fish Tech. Pap.* (339).

Bakun, A., V. Christensen, C.Curtis, P.Cury, M.H. Durand, D. Husby, R Mendelssohn, J. Mendo, R Parrish, D. Pauly and C Roy. 1992. The Climate and Eastern Ocean Systems Project (CEOS). Naga, *the ICLARM Quartely*, 15(4): 26-30.

Bakun, A., 1996. *Patterns in the ocean: ocean processes and marine population dynamics.* Calif. Sea Grant College Syst. Univ of Calif., La Jolla. 323p.

Christensen V. and Pauly D. 1992. A guide to ECOPATH II program (version 2.1). *ICLARM sofware* 6. Manila: ICLARM. 72pp.

Christensen V. and Pauly D. 1993. Trophic Models of aquatic ecosystems. *ICLARM Conf. Proc.* 26. Manila: ICLARM 390pp.

Cury P. 1994. Obstinate nature: an ecology of individuals: thoughts on reproductive behavior and biodiversity. *Can. J. Fish. Aquat. Sci. (Perspectives).* Vol. 51 (7): 1664-1673.

Cury P. and C. Roy eds. 1991. *Pêcheries ouest-africaines. Variabilité, instabilité et changement*, Paris. ORSTOM, Paris, 525p.

Di Castri F. 1986. Commentary, in *Sustainable Development of the biosphere*, Clark W.C., Munn R.E. eds, on " The resilience of terrestrial ecosystems : local surprise and global change", Chap. 10 by C.S. Holling: 317-320.

Durand M.H., 1991. La crise sardinière française : les premières recherches scientifiques autour d'une crise économique et sociale. *In*: P. Cury et C. Roy (eds.). *Pêcheries ouest-africaines : variabilié, instabilité et changement*, ORSTOM, Paris: 26-36.

Francis R.C. 1980. Fisheries science now and in the future: a personal view. *N. Z. J. mar. freshwat. Res.*, 14(1): 95-100.

Fréon P., Mullon C. and G. Pichon. 1993. *Experimental interactive software for choosing and fitting surplus production models including environmental variables.* FAO Computerized Information series, fisheries 5.

Froese R. and D. Pauly (eds). 1997. *Fishbase 97: concepts, design and data sources.* ICLARM, Manila.

Hastie, T.J and R.J. Tibshirani, 1990. *Generalized additive models.* Chapman and Hall [ed.] London : 335 p.

Mader C. 1909. Recherches sur la sardine du Golfe de Gascogne. *Bull. de la Station biologique d'Arcachon*,XII :125-276.

Mendelssohn R. and J. Mendo 1987. Exploratory analysis of anchoveta recruitment off Peru and related environmental series. In Pauly and Tsukayama (eds.) The Peruvian Anchoveta and Its upwelling ecosystem: three decades of change. *ICLARM Studies and Reviews* 15: 294-306

Mendelssohn R. 1989. Reanalysis of recruitment estimates of the Peruvian anchoveta in relationship to other population parameters and the surrounding environment. In Pauly,. Muck, Mendo and Tsukayama (eds.) 1989. The Peruvian upwelling ecosystem: dynamics and interactions. *ICLARM Conference Proceedings* 18: 364-385.

Pauly D. and I. Tsukayama (eds.) 1987. The Peruvian anchoveta and its upwelling ecosystem: three decades of change. *ICLARM Studies and Reviews* 15, 351p.

Pauly, D., P. Muck, J. Mendo and I. Tsukayama (eds.). 1989. The Peruvian upwelling ecosystem: dynamics and interactions. *ICLARM Conf. Proc.* 18, 468p.

Pauly D. and V. Christensen. 1995. Primary production required to sustain global fisheries. Nature, 374: 255-257.

Pauly D. 1994. *On the sex of fish and the gender of scientists: A collection of essays in fisheries science.* Chapman & Hall. Fish and Fisheries Series 14. 250p.

Roberts C.M. 1997. Ecological advice for the global fisheries crisis, *TREE*, 12(1): 35-38.

Vasconcellos M., S. Mackinson, K. Sloman and D. Pauly. in press. The stability of trophic mass-balance models of marine ecosystems: a comparative analysis. Ecological Modelling.

Walters C. 1986. *Adaptive management of renewable resources.* Macmillan, New York. 374p.

Walters C., V. Christensen and D. Pauly. 1997. Structuring dynamic models of exploited ecosystems from mass-balance assessments. *Rev. Fish Biol. Fis.* 7(2): 139-172.

Woodruff S.D., R.J. Slutz, R.L. Jenne and P.M. Steurer. 1987. A Comprehensive Ocean-atmosphere Data Set. *Bull. Amer. Meteor. Soc.*, 68, 1239-1250.

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This volume brings together thirty-three contributions presented at an international conference held on 6-8 September 1994 in Monterey, California, USA under the auspices of the Climate and Eastern Ocean Systems Project (CEOS). The CEOS was a collaborative project linking a variety of research institutions and devoted to study the potential effects of global versus local changes on the pelagic marine fish resources of upwelling systems. These stocks of small pelagics, such as sardines, anchovies or mackerel, account for about one third of the world's yield of marine fish and thus are of key importance to many, especially developing countries. The dynamics of theses stocks appear to be closely related to physical oceanographic processes. The goals of this international research project were to understand the changes that affect environment and consequently the resources in upwelling areas, to desentangle the observed changes in terms of their origins and scale and to analyze the links between environment and resource. The contributions in this volume cover the most important upwelling areas of the world, and describe, compare and assess the observed changes and their impacts. Some initial scenarios already available are presented. It is hoped that these contributions will prove useful to fisheries managers, and also lead to new research ideas and projects.

Oceanography – Pelagic fisheries – Statistical models – Global change – Upwelling areas.

Cet ouvrage rassemble trente-trois contributions présentées lors d'une conférence qui s'est tenue à Monterey en Californie du 6 au 8 septembre 1994 dans le cadre du programme CEOS. Le programme de recherche CEOS a permis à un grand nombre d'institutions de divers pays d'Amérique, d'Afrique et d'Europe de collaborer pour étudier dans une perspective comparative l'impact des changements climatiques sur les ressources en espèces pélagiques dans les différentes zones d'upwelling mondiales. Il est maintenant établi que la dynamique de ces stocks dépend très étroitement de l'environnement physique et des modifications des processus océanographiques. Les recherches ont porté plus spécialement sur la manière d'évaluer et de caractériser les changements observés en distinguant l'origine et l'échelle, globale ou locale, de ces phénomènes. Les changements climatiques sont décrits, analysés et comparés, leurs impacts sur les ressources pélagiques sont évalués, quelques scénarios d'évolution dorénavant identifiés sont présentés. Cet ouvrage, qui enrichit la connaissance des relations entre environnement et ressources, pourra être utilement mis à profit par les gestionnaires des pêches. Nous espérons qu'il participera également à la production de nouvelles idées et projets de recherche.

Océanographie – Espèces pélagiques – Modèles statistiques – Changements climatiques – Zones d'upwelling.

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