ETUDE DES RELATIONS PECHE - CLIMAT EN AFRIQUE DE L'OUEST

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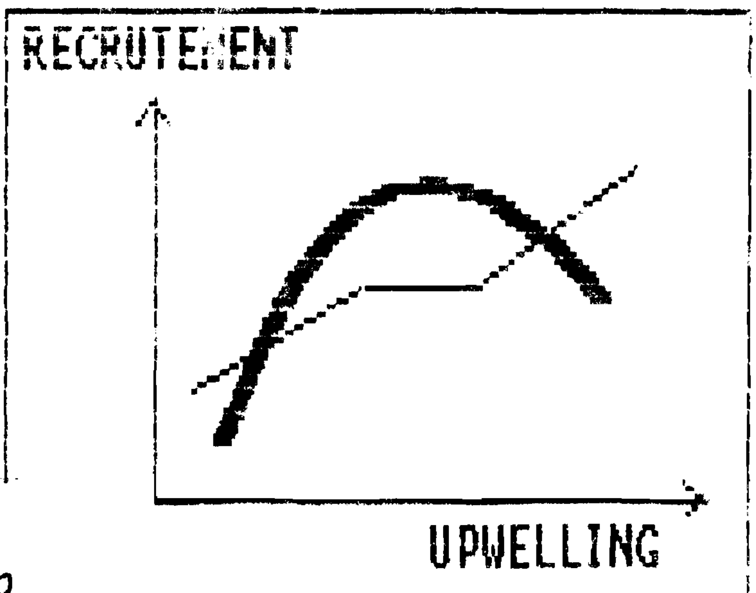

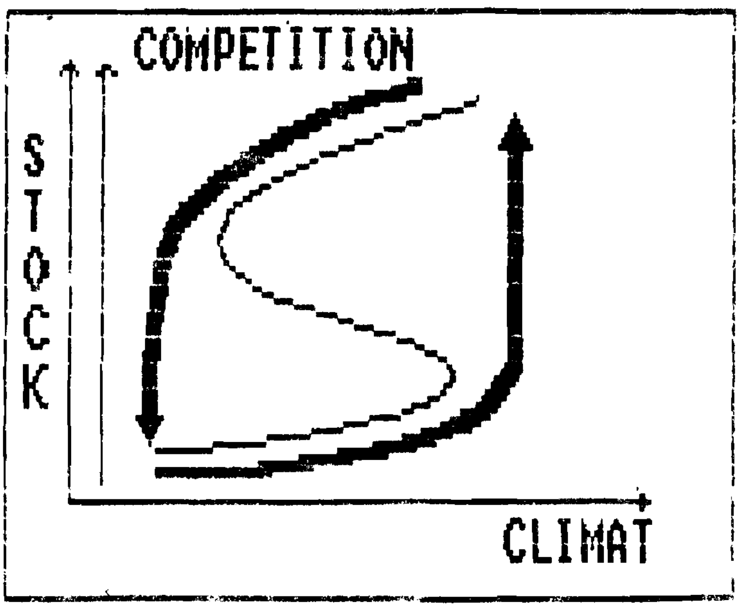

ETUDE DES RELATIONS PECHE-CLIMAT

EN AFRIQUE DE L'OUEST

par

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Depuis 1984, un groupe de recherches sur les relations pêche-climat en Afrique de l'Ouest s'est constitué à l'initiative et au sein du Centre de Recherche Océanographique de Dakar-Thiaroye (CRODT-ISRA). Ce groupe de recherches est composé de plusieurs océanographes physiciens et biologistes expatriés et nationaux. Un projet de recherches se réalise actuellement et regroupe l'ensemble des pays Ouest-africains (Maroc, Mauritanie, Sénégal, Côte d'Ivoire, Ghana et Congo). Ce projet, financé en 1988 par le FAC (650 KF), se propose d'étudier l'impact de la variabilité des zones d'upwelling sur la dynamique des clupéidés. Il regroupe environ une vingtaine de chercheurs (dont des chercheurs américains) qui travaillent sur les aspects méthodologiques et la comparaison des résultats obtenus dans les différentes zones étudiées. Philippe Cury est le coordinateur de ce programme. Un livre regroupant les différentes publications qui seront réalisées pendant cette étude sera publié au début 1989 et sera constitué d'une trentaine d'articles. Les relations pêche-climat sur le stock de thonidés de l'Atlantique Tropical Est sont également abordées.

Nous fournissons dans ce document les résumés des publications dont nous sommes les auteurs. Depuis 4 ans, seize publications ont été rédigées :

- 6 d'entre elles sont déjà publiées (ou accéptées) dans des revues internationales de classe A,
- 2 articles ont été publiés par l'ICCAT,
- 2 communications ont été présentées à des symposiums,
- 2 notes ont été publiées dans TOAN,
- 4 articles sont soumis à des revues internationales.

Ce document est destiné à faire un bilan des travaux réalisés depuis quatre ans au CRODT et à faire le point sur les capacités que le CRODT et l'ORSTOM ont acquis dans le domaine des relations pêche-climat. Nous tenons également à souligner la qualité exceptionnelle des données biologiques et d'environnement récoltées par l'ORSTOM depuis les années soixantes. Cela nous permet d'envisager l'étude sur le court, moyen et long terme des relations pêche-climat. De plus, nous faisons un effort théorique pour renouveler les méthodes d'analyse et d'approche des relations pêche-climat: ainsi l'introduction de variables climatiques dans les modèles globaux (Fréon, 1986), l'analyse multivariée des séries temporelles (Mendelssohn-Roy, 1985; Mendelssohn-Cury, 1987), l'application de la théorie des catastrophes (Cury, 1988), l'introduction des résultats de la biologie évolutive dans le domaine de la dynamique des populations (Cury, 1988) sont nouvelles dans ce type d'étude. L'approche classique des relations pêche-climat qui se réduisait à la juxtaposition de cartes de pêche et de cartes de température a été abandonnée au profit d'une approche dynamique intégrant la variabilité spatio-temporelle des écosystèmes. Ces travaux ont reçus un bon accueil au sein de la communauté scientifique internationale. L'intérêt de chercheurs confirmés et de renom pour les études que nous menons et avec lesquels nous échangeons régulièrement nos points de vue en témoignent (Prof. Margalef, Sinclair, Allen, May, Dr. Barbault, Bakun, Parrish, Herbland, ...).

Nous espérons que la diffusion de ce document permettra de faire connaître les travaux du CRODT dans le domaine des relations pêche-climat et de nouer des contacts au sein de l'ORSTOM et de la communauté scientifique internationale.

RESUME

De novembre à mai, le littoral sénégalais est le siège d'un fort enrichissement dû à un upwelling côtier. L'apparition, au niveau de la côte nord du Sénégal, du stock migrant de thiof (*Epinephelus aeneus*) est liée à la présence de cet upwelling. Les effets de l'upwelling sur les migrations dans cette zone sont étudiés. Des arguments sont ensuite avancés pour comprendre les raisons de cette migration saisonnière depuis la Mauritanie jusqu'au Sénégal.

Les données de pêche de 1974 à 1985 sont analysées en relation avec des données côtières de température de surface. Les prises par unité d'effort de la pêche artisanale sénégalaise sont calculées à partir des données récoltées à Kayar et Saint-Louis, les deux principaux centres de débarquement de la côte nord sénégalaise. Les prises par unité d'effort (prises par sortie), calculées durant la saison de pêche fournissent un indice de l'abondance apparente locale. L'intensité de l'upwelling, à l'échelle saisonnière, est calculée à partir des données de température de surface relevées quotidiennement à la côte.

La relation entre le déclenchement de l'upwelling et l'apparition des thiofs à Kayar est étudiée. Un délai d'environ un mois apparaît entre le début de l'upwelling et l'arrivée du thiof à Kayar. A l'échelle de la saison de pêche la relation entre les prises par unité d'effort ou les captures et l'intensité de l'upwelling n'est pas linéaire mais semble plutôt en forme de dôme. Les fortes anomalies de température, qu'elles soient positives ou négatives, se traduisent par une baisse de la prise par unité d'effort et des captures.

La migration du thiof des côtes mauritaniennes vers le Sénégal ne semble pas seulement due au déclenchement de l'upwelling le long des côtes sénégalaises, la relaxation simultanée de l'upwelling nord mauritanien pourrait être un facteur important favorisant ces déplacements. Ces deux phénomènes synchrones illustrent la stratégie de cette espèce à occcuper les niches écologiques les plus productives.

mots clés : Sénégal, Mauritanie, *Epinephelus aeneus*, migration, upwelling.

PROCEEDINGS OF THE ICCAT CONFERENCE ON THE INTERNATIONAL SKIPJACK YEAR PROGRAM

COMPTES-RENDUS DE LA CONFERENCE ICCAT SUR LE PROGRAMME DE L'ANNEE INTERNATIONALE DU LISTAO

ACTAS DE LA CONFERENCIA ICCAT SOBRE EL PROGRAMA DEL AÑO INTERNACIONAL DEL LISTADO

Ed.

P.E.K. Symons

P.M. Miyake

&

G.T. Sakagawa

International Commission for the Conservation of Atlantic Tunas
Commission Internationale pour la Conservation des Thonidés de l'Atlantique
Comisión Internacional para la Conservación del Atún Atlántico

Madrid, 1986

Articles publiés dans :

"RECUEILS DE DOCUMENTS SCIENTIFIQUES DE L'ICCAT"

SCRS/85/74/REV.

VARIABILITÉ DES RENDEMENTS EN ALBACORE (*THUNNUS ALBACARES*) ET LISTAO (*KATSUWONUS PELAMIS*) EN RELATION AVEC LES ANOMALIES INTERANNUELLES DE LA TEMPÉRATURE DE SURFACE

(NOTE PRÉLIMINAIRE)

par

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R E S U M E

Les relations entre la variabilité inter-annuelle de la température de surface et les rendements en albacore (*Thunnus albacares*) et listao (*Katsuwonus pelamis*) de la flottille FISM (France, Côte d'Ivoire, Sénégal et Maroc) opérant dans l'Atlantique tropical Est sont étudiés ici. Deux strates spatio-temporelles ont été retenues (Sénégal et Côte d'Ivoire), toutes deux caractérisées par le développement saisonnier d'un upwelling et d'une période de pêche intensive. On montre que la distribution des PUE de yellowfin,en fonction des anomalies de température de surface, de 1969 à 1981, est aléatoire , exceptée pour les fortes anomalies thermiques qui semblent toujours se traduire par une baisse sensible des PUE.Une interprétation, basée sur l'impact de l'environnement sur le comportement et la capturabilité de l'albacore est proposée.

A B S T R A C T

This paper gives an analysis of the relationship between inter-annual sea surface temperature variability and the yellowfin (*Thunnus albacares*) and skipjack (*Katsuwonus pelamis)* yield (CPUE) for the FISM fleet (France, Ivory Coast, Senegal and Morocco) operating in the eastern tropical Atlantic. Two time-area strata have been used (Senegal and Ivory Coast) both characterized by the seasonnal occurence of an upwelling and an intensive fishing period. It is shown that the yellowfin CPUE distribution as a function of sea surface temperature anomalies , from 1969 to 1981, is random, except for strong thermal anomalies which always seem to cause significant decrease in the CPUE. An interprétation based on the behaviour and the catchability of the yellowfin is proposed.

Doc. SCRS/86/77

PECHE THONIERE ET ANOMALIES CLIMATIQUES DE L'ENVIRONNEMENT DANS L'ATLANTIQUE TROPICAL CENTRE EST EN 1984

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RESUME

Cet article analyse l'importante anomalie climatique qui s'est développée dans le Sud-est du Golfe de Guinée durant l'été 1984. Sont ainsi décrites dans la zone du Cap Lopez -importante et classique zone de pêche thonière- l'absence exceptionnelle de zone frontale, la présence en subsurface d'eaux de salinité élevée et l'existence d'un fort excédent de pluviométrie. L'analyse de la pêche thonière dans le secteur montre par contre que la saison de pêche a été dans la zone tout à fait classique quand à son calendrier et à sa localisation. Des captures exceptionnellement fortes de listao ont été notées, les rendements en albacores étant moyens.

Cette forte anomalie de l'environnement, sans effets négatifs sur les rendements de la pêche thonière, conduit à réviser la classique hypothèse d'une stricte association entre la zone frontale du Cap Lopez et l'abondance des thons dans la zone. De nouvelles recherches sont nécessaires pour mieux comprendre les relations complexes qui existent entre les prises thonières et l'environnement.

SUMMARY

This paper analyses the strong environmental anomaly observed in the south eastern Gulf of Guinea during 1984. The study describes in the area of Cap Lopez -an important tuna fishing area- several significant anomalies : an absence of surface thermal front, an excess of sub-surface salted waters and a dramatic excess of rainfalls. The analysis of the tuna fisheries in the area shows that the fishing season was very typical for both the calendar of the fishing season and for the fishing areas. The yellowfin catch rates were average, and skipjack cpue were very high.

The fact that a strong environmental anomaly did not produced any significant effect on the tuna fishery suggests that the standard paradigm of "tunas associated with Cape Lopez front" needs to be revised. New research is necessary to understand the relationship between tuna catches and the environment.

Communications à des conférences

Symposium international sur :

"LONG TERM CHANGES IN MARINE FISH POPULATIONS"

Institudo de Investigaciones Pesqueras de Vigo
Vigo, Espagne, 18-21 novembre 1986.

MIGRATION OF THIOF (EPINEPHELUS AENEUS) AND NORTH WESTERN AFRICAN UPWELLING

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ABSTRACT

In this paper the seasonal migration of thiof (Epinephelus aeneus) and the dynamic of the upwelling in Senegal and Mauritania are investigated. From 1974 to 1985, fishery data from Kayar (Senegal) are analyzed in relation with coastal sea surface temperatures at the same location and Ekman transport off Senegal and Mauritania. First, the relaxation of the north mauritanian upwelling combined with the onset of the senegalese upwelling is analyzed to understand the seasonal migration from Mauritania to Senegal. Then, the time delay between the senegalese upwelling onset and the availability of thiof off Kayar is studied. Further investigations are made using multivariate time series analysis. Finally, interannual changes of catch and local abundance and their relationship with the upwelling intensity in Senegal are analyzed. The comprehension of the mechanism of these migrations appears to be absolutely necessary to understand the long term fluctuations of this species.

Symposium sur :

"VERTICAL MOTION IN THE EQUATORIAL UPPER OCEAN AND ITS EFFECTS UPON LIVING RESSOURCES AND THE ATMOSPHERE"

Unesco, Paris, 6-10 mars 1985

SMALL PELAGICS FISH ABUNDANCE AND UPWELLING IN IVORY COAST

Philippe Cury and Claude Roy

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ABSTRACT

A model using fishing effort and a measure of upwelling intensity is proposed to analyze fluctuations in abundance of Ivory Coast coastal pelagic fish species. It has been proposed by Freon (in press).

It is shown that fishing effort alone is not able to explain observed variations of abundance. The fit of the model to the observed CPUE is better when it includes a measure of the upwelling intensity at both the time the fishes are caught but also for the previos year, so as to take into account reproduction and recruitment. Using annual upwelling index at year i and i-1 and fishing effort, the model explains 75% of the variance of the abundance index.

1. INTRODUCTION

The coastal pelagic species off Ivory Coast are exploited by purse seiners based in Abidjan. The area of investigation is shown in Fig 1. Sardinella maderensis, Sardinella aurita, Scomber japonicus and Brachydeuterus auritus form the dominant part of the catch (Anonymous, 1976). Species composition and landings show a wide interannual fluctuation ; from 1966 to 1979, the total catch varied from 9.146 to 34.457 tonnes.

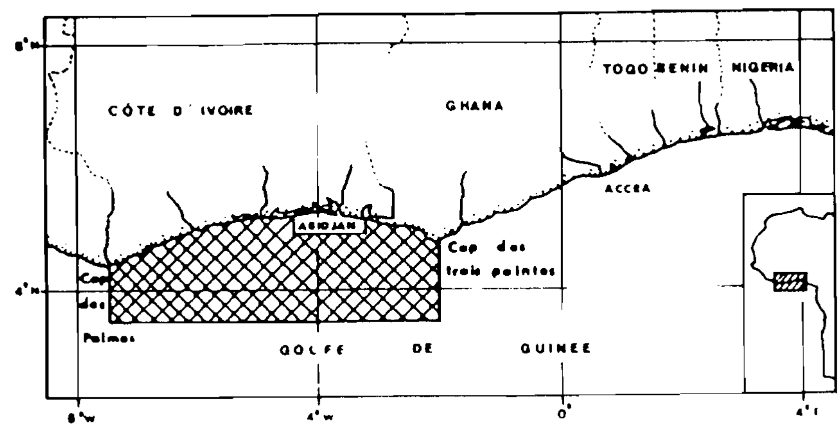

Fig. 1 : Area of investigation.

The oceanographic environment of the Gulf of Guinea is well known (Morliere, 1970 ; Picaut, 1983) and from 1966 to 1979, a number of major climatic events occurred. These climatic events induced strong variations in the productivity of the ecosystem and in the availability of food. Because of vulnerability of fishes and recruitment are strongly dependent on food availability, a model which integrates fishing effort and an index of the productivity is used to study abundance fluctuations of Ivory Coast small pelagic fishes. Similar class of model was applied by Freon (1983) to the pelagic fishery off Senegal.

2. DATA

2.1 BIOLOGICAL DATA

The catches by species and the yearly catches are presented in Tab. 1. From 1966 to 1972, the average catch was around 27000 metric tons. In 1973 the catches suddenly decreased to 9146 tonnes and stayed at a low level until 1975. From 1976 to 1979, the mean catch was about 19.000 tonnes.

ANNEES	1966	1967	1968	1969	1970	197	1972	1973	1974	1975	1976	1977	1978	1979
PRISES TOTALES	23468	34457	29100	23652	26886	28743	28564	9146	11095	11568	17434	24605	20826	18301
Prises S. maderensis	9346	12253	14012	6382	5991	9227	11518	5539	7610	8637	12407	18335	11598	15566
Prises S. aurita	5258	7506	4296	6732	10908	4932	8381	181	268	10	1506	1046	3795	455
Prises B. auritus	3662	6712	5225	2769	3603	2789	3086	1395	1859	1860	2582	3635	1480	1356
Prises S.japonicus	341	2356	582	1064	2652	5241	3513	217	61	1	11	0	6	0
Prises Divers	4816	5631	4985	6706	3733	6554	2066	1813	1296	1060	926	1483	947	924
EFFORT	3420	3746	4073	3616	5716	5484	3930	2483	2024	1768	1824	2003	2200	2681
PUE TOTALE	7.73	10.13	7.34	5.59	4.78	5.14	6.69	3.20	4.94	8.11	11.40	13.07	10.18	6.85

Tab. 1 : evolution of catches (metric tons), fishing effort (24h of searching) and CPUE (tons by 24h of searching) of the Ivory Coast pelagic species exploited by the seiners based in Abidjan, from 1966 to 1979.

Catch per unit of effort (CPUE) is used as an index of abundance. Time spent fishing is assumed to give a reasonable estimate of effort. CPUE is calculated by fortnight for each fishing area. A CPUE by fortnight for the whole area is given by the mean of CPUE of all squares fished. An annual density index for the total area studied is calculated by taking the mean of the preceding calculated CPUE. The resulting yearly average CPUE and effort are presented in Tab. 1.

2.2 ENVIRONMENTAL DATA

The annual signal of sea surface temperature off Ivory Coast is characterized by the occurrence of two upwelling seasons, the main one from July to September and a second small one from January to February.

For an upwelling area, biological productivity is dependent on upwelling intensity and off the Ivory Coast, the productivity of the coastal area is also related to river discharge (Binet, 1983). The relative intensity of the two upwellings is assumed to give a reasonable indication of the annual productivity.

Sea surface temperature data from historical merchant ships observations were kindly provided by J. Picaut and J. Servain. Monthly anomalies of sea surface temperature were calculated for the two upwelling seasons and averaged over the entire area. These anomalies are used as an upwelling index to estimate the biological productivity level . The time-series of this upwelling index from 1966 to 1979 is presented in Fig. 2. A positive upwelling index corresponds to a positive sea surface temperature departure and to a weak upwelling. Figure 2 reveals the occurrence of three main cold periods (1969, 1970 to 1972 and 1976) and two main warm periods (1968 to 1969 and 1973).

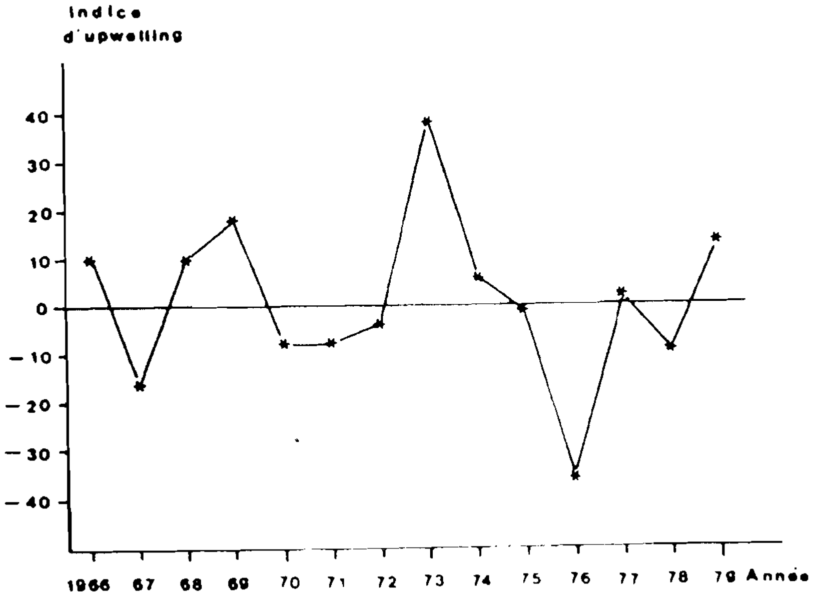

Fig. 2 : Annual upwelling index from 1966 to 1979

3. RELATIONS BETWEEN UPWELLING INTENSITY AND CPUE

Before going further into the analysis, the first step is to identify the relation between the environment and fluctuations in the catch.

The quantity of food available to the stock depends on the primary production which in turn is related to upwelling intensity. One could also assume that mortality and growth are influenced by the quantity of food available to the fishes. A strong upwelling can increase the biomass of the stock, either by increasing the growth rate or by decreasing the natural mortality rate. Vulnerability of the fishes to the fishing gear is also controlled by availability of food (Binet, 1982).

Recruitment, which occurs one year after reproduction, is also strongly dependent on the environment. Survival and abundance of larvae have been shown to be dependent on upwelling intensity (FAO, 1980).

The relation between upwelling intensity and total CPUE is presented in Fig. 3. It is clear that a low upwelling (high upwelling index) corresponds to a low CPUE and vice versa. Three groups of points do not follow this relationship. All three are related to unusual environmental or fishing conditions. From 1970 to 1972, effort was high and the stocks were close to being overfished. The low CPUE of 1974 seems to be related to a bad recruitment : in 1973, the upwelling intensity was weak and could affect survival and growth of larvae. On the other hand, the high CPUE of 1977 followed the strong upwelling of 1976 which offered good conditions for the success of reproduction and later recruitment of the 1976 year class.

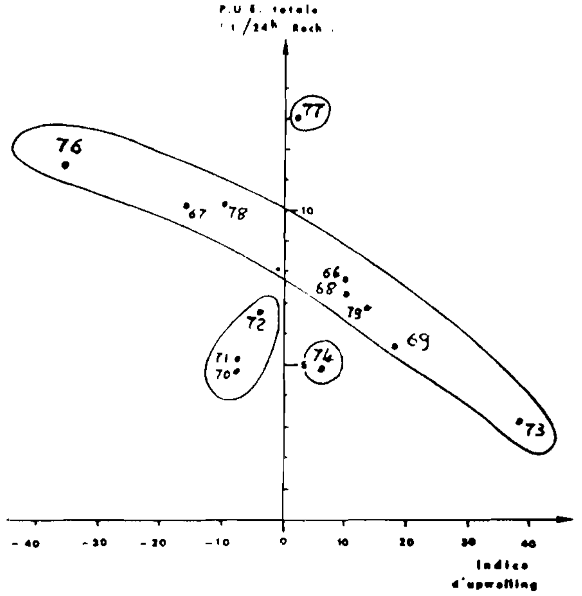

Fig. 3 : annual upwelling index and total CPUE from 1966 to 1979.

This shows that yearly CPUE thus depends on both the environment during the year of catch year as well as on the environment of the previous year.

4. DESCRIPTIONS OF THE MODEL

Taking into account the above results, the model uses fishing effort and the environmental conditions at year i and at year i-1 to describe the yearly CPUE. An exponential model (Fox, 1970) is used because it seems to be more biologically reasonable for a multi-species fishery than a Schaefer type model. The equation is of the form :

$$CPUE_i = \exp(-A_0 f_i) \cdot (A + B \cdot CLIM_i + C \cdot CLIM_{i-1})$$

with :
- CPUE = catch per unit of effort
- f = fishing effort
- CLIM = upwelling index
- i = year
- Ao, A, B, C = constants

A detailed discussion of this model can be found in Cury and Roy (1985).

5. RESULTS

In order to investigate the relative importance of each variable of the model in predicting CPUE, different situations are analyzed.

First, the model was run with only effort data as independant variable (Fig 4.1). Effort, by itself, is not able to explain variations of abundance. The observed values differed widely from the prediction.

Another run of the model was made using effort plus the upwelling index measured simultaneously to the catches (Fig. 4.2). The predicted data approximated the observed data better than in the preceding case. 46% of the total variance is explained. The residual were high in 1974 and 1977, which correspond to years where the relation between CPUE and upwelling index is poor(Fig. 3). In a preceding section, we saw that the low level of CPUE in 1974 is related to the weak upwelling of 1973 and that the high level of CPUE in 1977 to the strong upwelling in 1976. For these two years, yield was not influenced as much by the existing environmental conditions, as by recruitment.

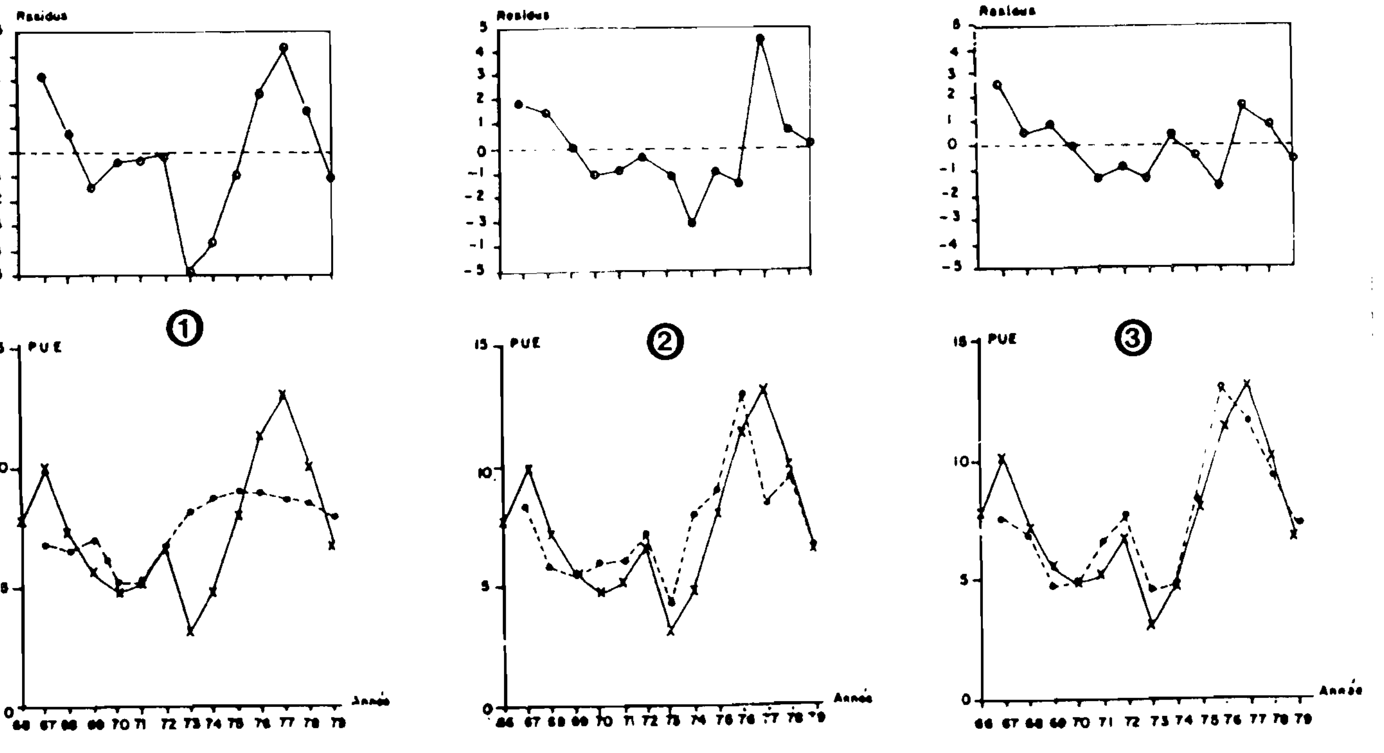

Fig. 4 : observed and adjusted CPUE from 1966 to 1969. model using : 1 - effort only
2 - effort and upwelling index at year i
3 - effort and upwelling index at year i and i-1

To take into account recruitment which is influenced by the environmental conditions that prevailed one year before the catches, the model was run with effort, upwelling index at year i and upwelling index at year i-1. The result of using these three variables is presented in Fig. 4.3. 75% of the total variance is explained. The residuals in 1974 and 1977 are low. The model integrated the influence of recruitment which was the dominant contribution in 1974 and 1977.

These results show that the coastal pelagic fishery off Ivory Coast is controlled by three different processes :

- effort
- the increase of the biomass and the vulnerability which are influenced by the environmental conditions that prevail the year the fishes are caught.
- recruitment and success of reproduction which are estimated by the environmental conditions existing one year before the fishes are caught.

6. CONCLUSION

CPUE of the small pelagic fishery off Ivory Coast is shown to be strongly dependent on complex processes involving upwelling intensity. A measure of upwelling intensity was used as an index of the productivity level. As no direct measurement of productivity over all the area is available, the use of a physical parameter (sea surface temperature) seems to give a reasonable estimate of the global productivity of the ecosystem.

The complex relations between productivity, success of reproduction and availability of food need to be further investigated because they are crucial to understanding how the ecosystem works.

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Notes parues dans :

Tropical Ocean-Atmosphere Newsletter

tropical ocean-atmosphere newsletter

Number 26 July 1984

On the Weakening of the Equatorial Undercurrent During the 1982-83 ENSO Event

A virtual disappearance or partial reversal of the Pacific Equatorial Undercurrent (EUC) was reported during the 1982-83 El Niño event both in the central Pacific at 159°W, in September 1982 when strong westerly winds replaced the usual southeast trade winds (Firing *et al.*, 1983; Lukas and Firing, 1983; Firing and Lukas, 1983), and in the eastern Pacific, at 110°W in January 1983, in spite of southeast trade winds (Halpern, 1983). This latter observation is very unusual and amazing due to its far eastern location. The disappearance at 159°W, which developed in a 120 m thick homogeneous layer (see Figure 1 in Firing *et al.*, 1983), calls to mind changes in the vertical current structure at the equator in the western Pacific when the northwest monsoon has replaced the southeast trades (Hisard *et al.*, 1970; Bubnov *et al.*, 1975; Bubnov *et al.*, 1982). The EUC in the western Pacific (at 170°E and farther west) is characterized by a double core eastward flow during northern summer. The upper core, in the 120 m thick homogeneous upper layer, is surrounded by the westward South Equatorial Current; the lower core, in the thermocline layer with its maximum speed at about 220 m depth, is connected with, but clearly distinct from, the eastward North Equatorial Countercurrent. When the northwest monsoon prevails, the lower core, which is in geostrophic equilibrium, is observed as a permanent but somewhat weakened feature; however, dramatic changes occur in the homogeneous layer. An eastward surface jet replaces the South Equatorial Current, which splits into two branches, one on each side of the equator. In addition, a subsurface westward equatorial undercurrent develops between the eastward surface flow and the permanent lower core of the EUC. The high sensitivity of this current structure to a wind change was clearly documented at 170°E during April 1967, when bursts of northwest monsoon winds alternated with southeast trade winds (Hisard *et al.*, 1970; Donguy *et al.*, 1984). The Northern Hemisphere winter structure of the equatorial current in the western Pacific is described in Figure 1 and Table 1.

In some exceptional circumstances, the current structure typical of the Northern Hemisphere winter was observed in summer, as at 163 and 174°E in summer 1976, when northwesterly winds were recorded at the equator by the R/V *Coriolis* and at Tarawa Island (1°21'N, 172°55'E) (Oudot, 1978).

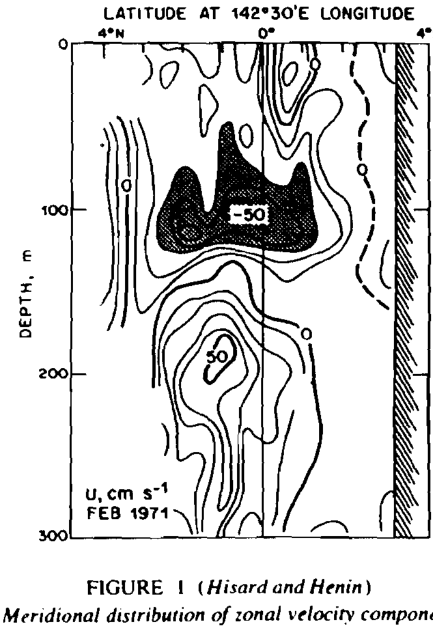

FIGURE 1 (*Hisard and Henin*)
Meridional distribution of zonal velocity component (cm s⁻¹; positive eastward) relative to 800 m depth at 142.5°E in the western equatorial Pacific Ocean north of New Guinea, measured from the Coriolis (FOC 1) in February 1971 during the northwest monsoon. In the shaded region the flow is westward with speeds greater than 30 cm s⁻¹

CONTENTS

construct seasonal thickness series for 1950 to date. Figure 1 shows these series for each season for the 850-500 mb layer.

The tropical thickness series for each season were subjected to linear regressions against the Tahiti minus Darwin mean sea level pressure index of the Southern Oscillation with a selection of time lags. It was found that the Northern Hemisphere winter, spring, and autumn thicknesses were best related to the Southern Oscillation Index two seasons earlier (in agreement wih Angell, 1981), but in Northern Hemisphere summer the optimal lag was only one season. For 850-500 mb the regressions were

$$\begin{aligned} y_{WI} &= -3.68x_{SU} - 3.10, \quad r = -0.74 \\ y_{SP} &= -2.45x_{AU} - 0.35, \quad r = -0.66 \\ y_{SU} &= -2.81x_{SP} - 0.29, \quad r = -0.58 \\ y_{AU} &= -1.98x_{SP} - 0.60, \quad r = -0.52 \end{aligned} \qquad (1)$$

where y denotes 850-500 mb thickness (gpm), x denotes Southern Oscillation Index (mb), suffixes *WI, SP, SU, AU* denote the winter, spring, summer, and autumn seasons, and r denotes the correlation coefficient. The period covered was 1951-80 for the Southern Oscillation Index.

Similar regressions for 500-200 mb were

$$\begin{aligned} y_{WI} &= -7.65x_{SU} + 0.18, \quad r = -0.68 \\ y_{SP} &= -4.91x_{AU} - 0.50, \quad r = -0.58 \\ y_{SU} &= -6.82x_{SP} + 7.93, \quad r = -0.66 \\ y_{AU} &= -5.08x_{SP} + 3.04, \quad r = -0.52 \end{aligned} \qquad (2)$$

The results in equations (1) and (2) agree with Arkin (1982), Hastenrath and Wu (1982), and Horel and Wallace (1981) in indicating that a warm tropical troposphere occurs shortly after the time of minimum Southern Oscillation Index.

Seasonal residuals of thickness computed from the regressions in equations (1) and (2) are shown in Figure 2 as a single time series for each layer. In both layers the residuals for almost a year after the March 1963 eruption of Agung were warmer than those in the year pre-

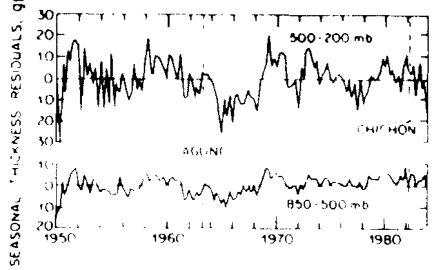

FIGURE 2 (*Parker*)

Seasonal residuals of thickness for the 20°N-20°S region computed from linear regression with optimally lagged Southern Oscillation Index. The lag was one season for summer thicknesses, otherwise two seasons. Tick marks denote Northern Hemisphere winter (December-February)

ceding the eruption. The coldest residuals were about two years after the eruption, but in the lower layer these were only about 0.1°C (1°C ≡ 15.6 gpm) colder than in late 1961 and much of 1962. A slightly greater cooling may be deduced for 500-200 mb (where 0.1°C ≡ 26.6 gpm). At 850-500 mb the cooling in 1961 was much more dramatic than that following Agung's eruption. Figure 2 could imply either that Agung resulted in a temporary warming in an otherwise cold period (1961-68) or, more likely, that the effects of Agung, if any, were indistinguishable from background variability even after compensation for the Southern Oscillation.

Figure 2 shows no cooling between the April 1982 eruption of El Chichón and the end of 1983. A cooling in Northern Hemisphere winter 1983-84 was no more marked than the coolings in 1961 and 1971, which had no antecedent eruptions, so the 1984 cooling cannot readily be connected with El Chichón. Detailed examination of the winter 1983-84 data shows that the actual cooling (*i.e.*, uncompensated for the Southern Oscillation) was most marked in equatorial regions in the Eastern Hemisphere and over the Atlantic, whereas there was slight warming near 20°N and 20°S in these longitudes. There were enhanced easterly winds in the upper troposphere from Indonesia to the Atlantic, in accord with this pattern of cooling and warming. The overall tropical cooling, relative to expectation given the Southern Oscillation Index, may have been a consequence of dynamical changes following the anomalous El Niño Southern Oscillation event of 1982-83.

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Remote Forcing of Sea Surface Temperature and Tuna Fishery Variations in the Gulf of Guinea

The seasonal cycle of sea surface temperature (SST) along the coast of the Gulf of Guinea is characterized by two upwelling seasons, the main season occurring from June to September while the second upwelling season, of smaller amplitude, occurs in December and January. Because of these two upwelling seasons, SST data in the Gulf of Guinea exhibit a strong semiannual cycle in addition to the annual cycle. The theory of remote forcing for this region (Moore *et al.*, 1978), as well as direct observations in the Gulf (Picaut, 1983), suggests that the SST fluctuation associated with the main upwelling season propagates poleward along the east and north coasts of Africa. During the smaller second upwelling season, the SST fluctuation has also been observed to propagate toward the west along the north coast from Ghana to the Ivory Coast. As it is commonly believed that upwelling areas are favorable for concentrating tuna, these results on the propagation of SST in the Gulf suggest that it would be of interest to study the relationships between the temporal and spatial variations of SST with those of the tuna fishery in the eastern tropical Atlantic Ocean. The main emphasis of the study is to examine the dynamical relations between the two, not only at the time and place where tuna are caught but also as each variable varies over time and space over the entire region. Thus, our analysis is concerned equally with where and why tuna are not caught as with the areas where they are caught.

Tuna fishing and tuna fishing success in any area are measured by catch-per-unit-effort

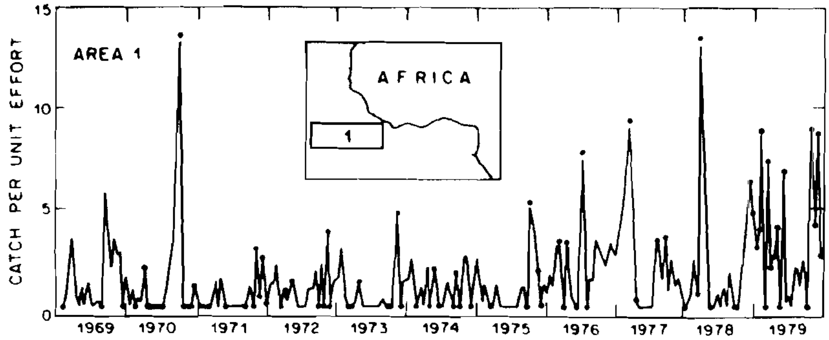

FIGURE 1 (*Mendelssohn and Roy*)
Observed (closed circles) and model predicted (solid line) yellowfin CPUE for area 1 shown in the insert

(CPUE), which is calculated by dividing the catch of a species by the number of hours spent fishing. CPUE represents a normalized rate of fishing success, and it is usually assumed in fisheries modes (though with little real evidence to support the assumption) that CPUE is proportional to the relative abundance of the species in that location. The actual data used are the catch and effort data for yellowfin and skipjack tuna from the French, Senegalese, Moroccan, and Ivory Coast purse seine fleets operating in the Gulf of Guinea during 1969 to 1979. The ocean environment is characterized by SST data and the two

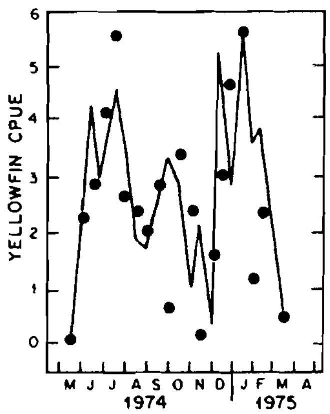

FIGURE 2 (*Mendelssohn and Roy*)
Solid line is the model estimate of yellowfin CPUE, from the second fortnight of May 1974 to the first fortnight of February 1975, when the observed data for this period were removed before fitting the model. Actual data points are indicated by circles.

Cartesian components of the wind vector, which were extracted from the meteorological files of the U.S. National Climatic Center. In order to increase the spatial coverage of the environmental data, SST data extracted from the hydrological files of the French Bureau National des Donnes Océanographiques were merged with the other environmental data.

The Gulf of Guinea was divided into eleven areas, each corresponding to a typical catch or environmental process. For each area the mean CPUE for yellowfin and skipjack tuna and the mean of the three environmental variables were all calculated per fortnight. (The catch and effort data are only available to us by fortnight, hence fortnight is used as the basic time unit of the analysis.) Each of the resulting series contained at least some missing data; the CPUE series contained a missing data point in an area whenever there was no fishing in the area, even though it is possible that there were fish in the area.

Missing data were estimated for each area by fitting a local autoregressive model of order 2 in each area using a technique that gives maximum likelihood parameter estimates and minimum mean square error data estimates when there are data missing in the original series (Shumway and Stoffer, 1982). These local models have as their variables the two CPUE series, the SST data, and the two components of the wind speed. The estimates produced by these local models were evaluated by comparing the model estimates for the known data points, by examining qualitative properties of the estimates where no data were available, and finally by artificially removing data from a series and then reestimating the model to see how well the known values were estimated. Figure 1 gives an example of the fit of the model to the yellowfin CPUE data from area 1. As can be seen, the model estimates are very close to the observed values except at the extremely high peaks. Moreover, the estimates of the missing data points are consistent with what is known about the fishery.

In area 1 the local model predicts seasonally positive values of CPUE over a long time period during which there is no available fishing data (Figure 1). These estimates agree with data from more recent years (not used in our analysis) in areas into which the fishery extended and the levels of CPUE were found to be consistent with those predicted by our model and to occur during the same part of the year as predicted by the local models. Figure 2 shows the result of estimating one of the local models after artificially removing ten months of data. The estimated data are very close to the observed values, giving us further confidence in the validity of our techniques. A more detailed discussion of this issue and of the other techniques discussed in this article can be found in Mendelssohn and Roy (1983).

A detailed analysis of the importance of each of the variables in estimating the missing CPUE data shows that the evolution of the environmental parameters rather than persistence of CPUE is the most important predictor of the CPUE data. That the models appear to be able to predict accurately CPUE values even in areas where there has been little fishing is strong evidence that the success of this tuna fishery is influenced by the ocean environment. In some of the areas the "scenario" postulated by the local models for relatively high CPUE values is consistent with observations, which suggest that tuna concentrations are most likely to be found where the water is relatively colder one month before fishing takes place, followed by the warmer waters with which tuna appear to be associated. Thus, warm water *per se* is not sufficient to ensure large concentrations of tuna.

The completed data sets were then Fourier transformed and spectral density matrices were calculated by direct smoothing of the periodogram. Principal components in the frequency domain (PCFD) (Brillinger, 1981) were then calculated for each of the spectral density matrices in order to examine simultaneously the spatial and temporal evolution of the CPUE and the environmental data. When the CPUE data are analyzed by themselves at the annual and semiannual frequencies, the space-time dynamics appear to reflect most closely the dynamics of the fishing fleet rather than some relative measure of abundance. These results suggest that some caution needs to be used when interpreting results using CPUE data as an index of abundance.

When the SST data are analyzed, at both

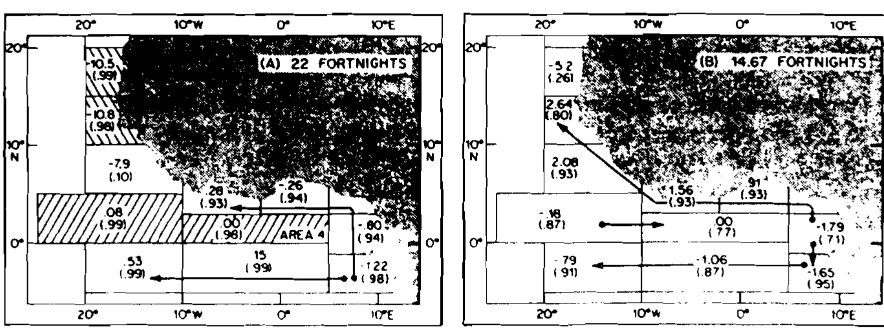

FIGURE 3 (*Mendelssohn and Roy*)
Phase and coherence (in parentheses) of the first component of the SST eigenanalysis among the eleven areas at (A) 22 and (B) 14.67 fortnights. Phases are in units of fortnights. Arrows represent our interpretation of the phase lag progression. Areas in phase are hatched.

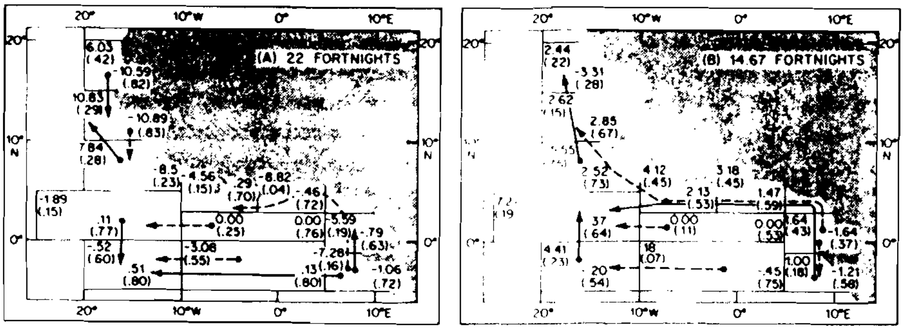

FIGURE 4 (*Mendelssohn and Roy*)
Phase and coherence of yellowfin CPUE (upper left corner) and SST (lower right corner) among the eleven areas at (A) 22 and (B) 11 fortnights for the first component of the canonical analysis. Phases are noted in fortnights. Arrows represent our interpretation of the phase lag progression for yellowfin (solid line) and for SST (dashed line).

the annual and semiannual frequencies, the phase lag between the areas shows a clear propagation poleward along the north coast (Figure 3). The propagation speed is roughly 1.5 m s^{-1}, which is consistent with the speed of an internal Kelvin wave generated by remote wind forcing (Picaut, 1983). In a similar analysis extending as far south as 15°S, we found that the annual and semiannual SST fluctuations propagate along the equator and then poleward in both directions at about 1.5 m s^{-1} also.

The SST and CPUE data were analyzed together by calculating canonical correlations in the frequency domain (Brillinger, 1981). Unlike the PCFD method, which tries to find the linear combination of the variable across space that contains the most variance at any frequency, this analysis tries to find the linear combination of each variable at a given frequency with the highest coherence, *i.e.*, we find at each frequency the most predictable part of the CPUE data as well as the part of the SST data that yields this best prediction. Figure 4 shows the phase lag and coherence between each of the original series and the CPUE or SST series. Each component series arbitrarily has been assigned a phase of zero in area 4.

The most obvious feature of Figure 4 is that the annual and semiannual SST fluctuations exhibit the same propagation as when the SST is analyzed independently of the CPUE data, indicating that the part of the SST data most coherent with CPUE is the dominant characteristic of the SST field at these frequencies. At the annual frequency, the CPUE has a propagation along the coast similar to SST, and at a similar rate of movement. A relationship between SST propagation and the movement of tuna is not surprising, since this region has two upwelling seasons which are related to the propagation of SST and which are associated with conditions such as thermal fronts and the aggregation of nutrients and food sources for the tuna which are favorable for the concentration of tuna.

Both the availability and vulnerability of the tuna population in the Gulf of Guinea are shown to be dependent on the ocean environment. Moreover, and most importantly, fishing success is seen to be dependent not only on the environmental conditions at the time and place where the tuna are caught, but also on complex biological and physical processes such as upwelling, which bring about favorable conditions for the aggregation of tuna and for their catch

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El Niño and Sea Surface Temperature Variability off Central California

Sea surface temperature (SST) measurements with accuracy of ±0.2°C have been recorded daily at 0800 local time since March 1971 at a coastal station (Granite Canyon: 36.4°N, 121.9°W) located 11 km north of Pt. Sur and about 25 km south of Monterey in central California. This site is close to the deep ocean because of the very narrow (6 km width) continental shelf.

Figure 1 shows a smoothed version of the daily SST time series produced with a 101-weight cosine filter. Surface water warmer than normal can easily be identified with each El Niño episode occurring during the past thirteen years (*i.e.*, 1972-73, 1976-77, 1982-83), except for the relatively weak 1979-80 El Niño episode. El Niño influence on coastal SST is mainly seasonal. The higher than average SSTs associated with El Niño episodes tend to occur during autumn and winter, consistent with intensified poleward flow in the California Countercurrent. An abrupt decrease in temperature in 1973, 1977, 1980, and 1981 corresponds to the spring transition to coastal upwelling. The spring transition, which is a major oceanographic feature off California and Oregon, signals the seasonal change from warm, non-upwelling to cold, upwelling conditions. While this transition is not always distinct because of its short time scale (*ca.* one week) it appears to be most intense following El Niño episodes. Beginning in 1979 the water was warmer during the seasonal upwelling periods. In 1983 the SST signature of coastal upwelling was less intense than usual because of the accumulation of warm water near the coast associated with the 1982-83 El Niño and because upwelling favorable coastal winds

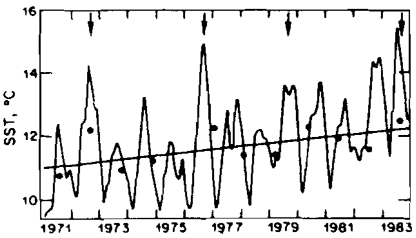

FIGURE 1 (*Breaker et al.*)
Sea surface temperatures at Granite Canyon smoothed with a 101-weight cosine filter. Arrows identify El Niño episodes. Dots represent annual mean values computed from March through February. Dashed line is a least-squares fit; see text for equation.

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Long–term Trends and a Major Climate Anomaly in the Tropical Pacific Wind-field

Introduction

Data from winds in the Pacific were subjectively analyzed. These data are from Florida State University (FSU), and cover the period 1961-1983. They strongly suggest that the central and eastern Pacific trade winds, both north and south of the equator, have undergone a zonal strengthening of the order of 1 ms⁻¹ over that time. To validate this major change in the tropical atmospheric circulation, a subset of the ship-wind data of the UK Meteorological Office was used. This information provided monthly averages and observations, by five-degree squares, for the period 1920-1983 in the region (120°E - 75°W; 30°S - 30°N). Some quality control produced these monthly averages. We omitted those observations lacking either speed or direction and those which were deemed physically unreasonable *[Editor's Note: This is unexplained]*. These data were not smoothed, and hence squares with no observations were flagged *[Editor's Note: This is unexplained]*.

We present the preliminary results of a study of these data. During the period of overlap with wind data from FSU, the two data sets showed good agreement. In particular, the intensification of the tropical easterlies east of about 160°W was traceable back to 1946, and in some areas back to the 1920s. The year 1946 is important in other respects. It forms the abrupt end of a strong, decade-long westerly anomaly in the tropical circulation. During that year, we also observe a permanent increase of approximately 1 ms⁻¹ in the strength of the western extension of the NE trades. Within this region of the western Pacific, both before and after the prolonged warm anomaly, there is little evidence for a gradual strengthening. In the SW Pacific, there appears to be little change in the circulation, apart from the anomaly during the 1940s, over the 64 years of records.

Analysis and Discussion

In Figure 1, a longitude-time plot of zonal velocity anomalies, averaged annually from 5°S to 5°N, is presented. The anomalies are shown with respect to a 64-year climatological record; years containing no data have been indicated by a cross-barred box. The shaded regions of positive, or westerly, anomalies highlight several features that we wish to indicate. One is the persistent, basin-wide westerly anomaly of the late 1930s to the mid 1940s. As the peak of this disturbance is from 1940 to 1945, it can be suggested that the decade-long climate anomaly is due to less-reliable observations made during the Second World War. The quality control during this period drastically reduces the ratio of the number of observations used, as opposed to those available. However, examination of those that remain, and of regions such as the central North Pacific that retain the pre-war number of observations, consistently shows the anomaly. The classification by Quinn *et al.*, (1978) of El Niño events includes the periods 1939-1941, 1943-1944, and 1946. These periods should be viewed as major climate anomalies rather than as a succession of El Niño events.

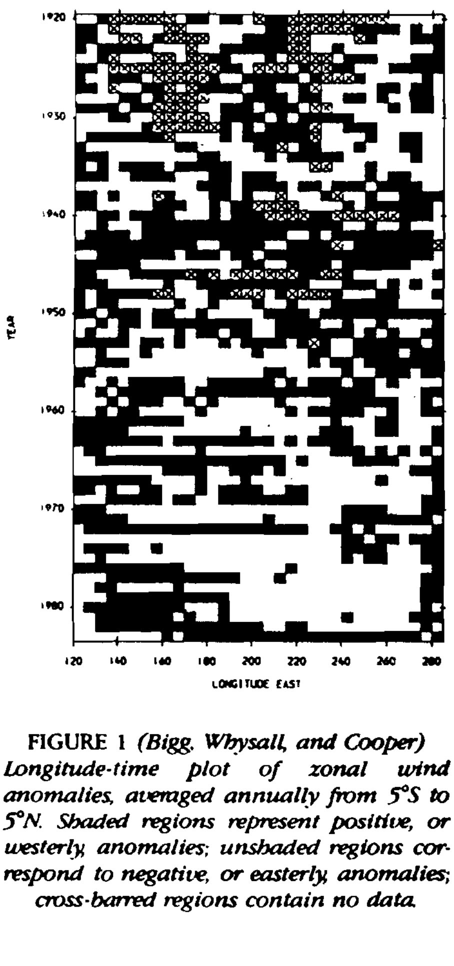

FIGURE 1 *(Bigg, Whysall, and Cooper) Longitude-time plot of zonal wind anomalies, averaged annually from 5°S to 5°N. Shaded regions represent positive, or westerly, anomalies; unshaded regions correspond to negative, or easterly, anomalies; cross-barred regions contain no data.*

The other feature recognizable in Figure 1 is the trend towards more easterly winds as the present day is approached, particularly in the central and eastern Pacific. This is seen by the large space-time area of negative, or easterly, anomalies following the persistent westerly anomaly during the 1940s.

To give a view of these features distant from the equatorial region, we present Figures 2 and 3 as time-series of 12-month running means of winds averaged over regions of the North and South Pacific trade winds, respectively. The two regions (5°-25°N, 180°-160°W and 0°-20°S, 130°-110°W) correspond to the central areas of Barnett's (1977) first empirical orthogonal function of the two trade-wind belts. The individual monthly values were calculated by averaging those 5° squares that contain data. In those months with inadequate data, the climatological average wind was used to avoid aliasing effects. The horizontal sections of Figure 3 in the late 1930s therefore mean that there were few or no observations at that time.

Both figures show the trend towards stronger easterlies after the mid 1940s, with the South Pacific (Figure 3) showing the slow increase and the North Pacific (Figure

Impact of the Northwest African Upwelling on the Migration of the *Thiof (Epinephelus aeneus)* (Pisces: family Serranidae)

The appearance of the migrant stock of the grouper fish, known as *thiof (Epinephelus aeneus)* (Pisces: family Serranidae) along the north coast of Senegal (Figure 1) is related to the onset of coastal upwelling. We analyzed the fishery data, from 1974 to 1985, in relation to coastal sea surface temperature (SST) and Ekman transport. First, the impact of this upwelling on the dynamics (migration intensity) of the *thiof* is analyzed. Then, some hypotheses are presented to explain the seasonal migration from Mauritania to Senegal.

The Senegalese coast, the northwest boundary of the African continent, is one of the most productive maritime areas of the world. The trade winds blow seasonally from the north and parallel to the coast during the winter and spring. From October through June, the resulting Ekman transport is mainly offshore and brings to the surface cold, rich subsurface waters (Wooster *et al.*, 1976). During the summer, tropical warm waters advected by surface currents from the south replace the cold and rich upwelled waters. A strong seasonal temperature cycle along the coast results from the alternation of these two contrasting water masses. The thermal amplitude of this seasonal cycle may be as large as 15°C.

Saharan fish species, occurring from July to October in the permanent cold upwelled water between 20°N and 30°N, begin to migrate toward the south in November (Champagnat and Domain, 1978). They reach the Senegalese coast around November, and occupy this area until June when the cold upwelled waters are replaced by the warm tropical waters.

From 1974 to 1985, 14–day temperature anomalies are calculated from daily, coastal sea–surface temperatures collected in Kayar, the main fishing landing point on the north Senegalese coast. From these data, an annual upwelling index is calculated by adding the 14–day temperature anomalies from October through June (Table 1). We define the beginning of the upwelling season as the maximum difference between the temperature of two consecutive 14–day periods. Fourteen–day mean seasonal offshore Ekman transport, using daily wind–speed data from 1974 to 1984, is calculated for two locations at Yoff (15°N) and at Nouadhibou (20°N).

From 1974 to 1985, catch per unit of effort of the Senegalese small–scale fishery was calculated from the fishery data collected in Kayar. Catch per unit of effort (catch per trip) and catch calculated during the fishing season (October to June) gives a measure of apparent and local abundance (Figure 2). The beginning of the fishing season is identified from the fishery data by the sharp increase of catch per unit of effort that appears when the fish arrive in Kayar.

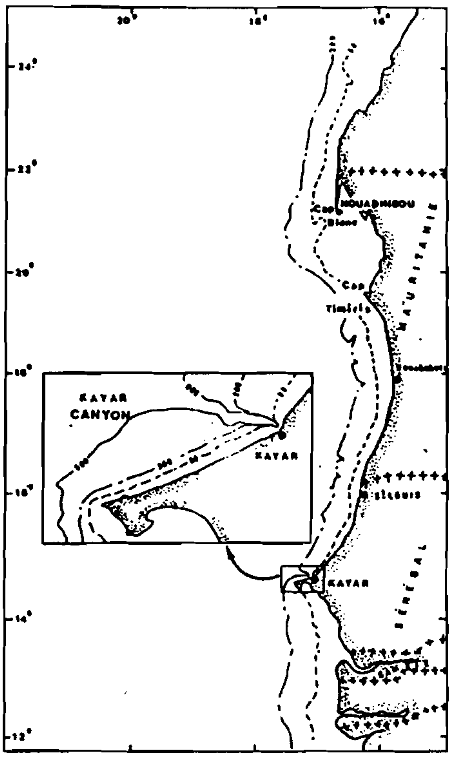

FIGURE 1 *(Cury and Roy)*
Topography of the continental margin off Sénégal and Mauritania.

TABLE 1 *(Cury and Roy)*
Annual upwelling index from 1975 to 1985 at Kayar.

Year	Upwelling Index
75	-4.58
76	-11.96
77	-3.34
78	-1.36
79	3.40
80	2.09
81	....
82	6.53
83	9.30
84	6.17
85	-7.87

The relationship between the onset of upwelling and the occurrence of *thiof* at Kayar is investigated. A mean lag of about one month (between one and three 14–day periods) is found between the onset of upwelling and the occurrence of the *thiof* at this location (Figure 3). There is no apparent relationship between the temperature measured in Kayar when the fish arrived nor one or two 14–day periods before their arrival (the temperature varies between 18 and 24°C. This agrees with the concept that the onset of the migration is due more to an ecological process (enrichment level) than to a particular thermal preferendum.

The upwelling off Mauritania is permanent between 20°N and 25°W (Wooster *et al.*, 1976). It is surprising that, if the conditions off north Mauritania are favorable all the year, the *thiof* migrates seasonally southward. In fact, the onset of the Senegalese upwelling appears simultaneously with a reduction of the upwelling off north Mauritania (Figure 4). The upwelled water in the Senegalese upwelling is composed mainly of South Atlantic Central Water, which is more rich than the North Atlantic Central Water upwelled north of 20°N. We measured the intensity of these two upwellings using the Ekman transport as an index. However, due to the different types of the upwelled water masses, we note that the enrichment is more important in the Senegalese upwelling than in the area farther north (Voituriez and Herbland, 1982). The *thiof* migrates from northern Mauritania, which is productive during all the year (but with variable intensities), to the north Senegalese coast, which is more productive during the upwelling season. This migration strategy illustrates the ability of the *thiof* to colonize the most productive areas.

At a seasonal time scale (fishing season), the form of the relationship between catch per unit of effort (or catch) and upwelling intensity is not linear but shows a dome shape (Figure 5). Strong negative or positive anomalies of temperature appear to have a negative effect on the catch per unit of effort and catch. Similar results have been found by Cayré and Roy (1985) for Atlantic tunas and by Le Reste and Odinetz (1984) for shrimp in Casamance. One of the most important conclusions of the CINECA program was that primary productivity is affected by too weak or too strong physical processes (Barber, 1982). These results applied to the higher levels of the food chain may present an interesting hypothesis to explain the non–linearity between climate and fisheries.

The results emphasize the importance of local and remote effects on fish migrations. They also point out the necessity of considering the impact of environment on fish in terms of physical processes. This means introducing only simple values but also an analysis of the variability of physical parameters.

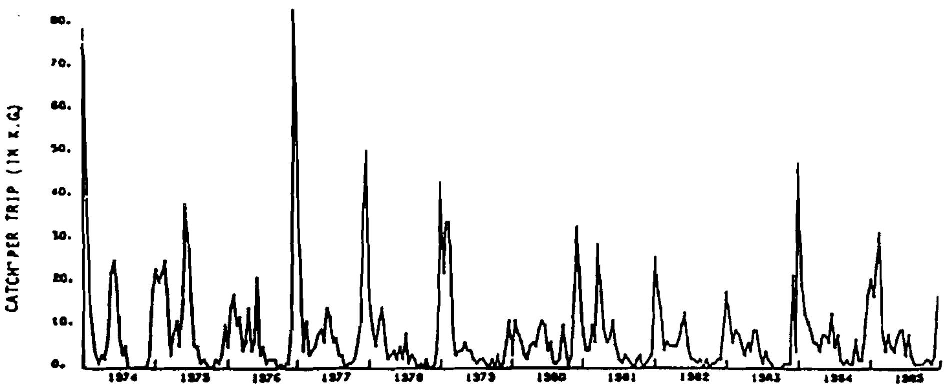

FIGURE 2 *(Cury and Roy)*
Catch per unit of effort (catch per trip) at Kayar, from 1974 to 1985.

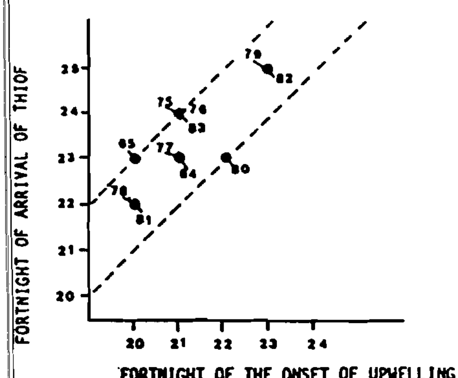

FIGURE 3 *(Cury and Roy)*
Date (fortnight = 14–day period) of the arrival of thiof *and of the upwelling onset at Kayar, from 1975 to 1985.*

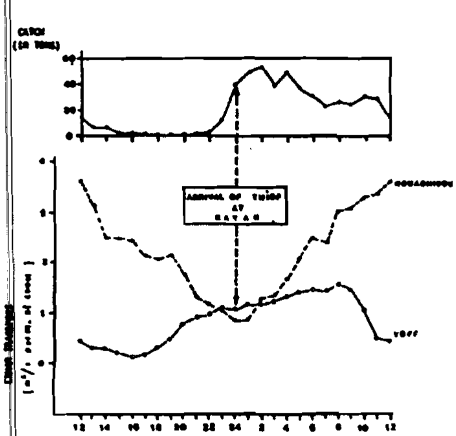

FIGURE 4 *(Cury and Roy)*
Offshore Ekman transport (m^3/s per meter of coastline), at Nouadhibou and Yoff from 1974 to 1984. Mean catch of thiof *at Kayar during the same period.*

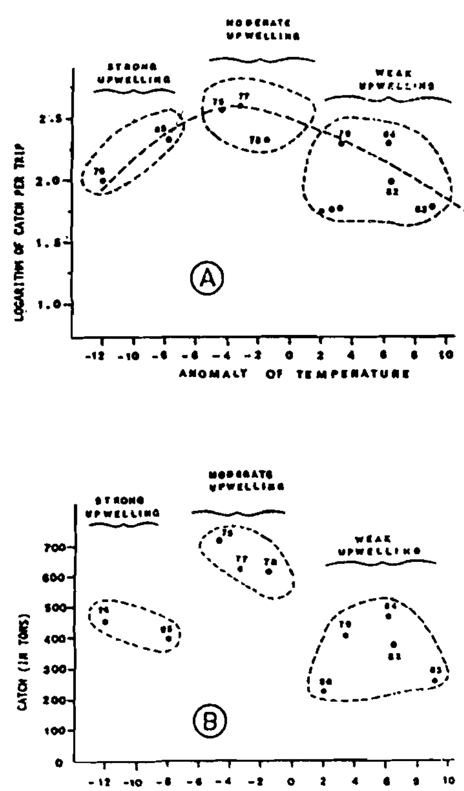

FIGURE 5 *(Cury and Roy)*
Logarithm of catch per trip (A) and catch versus temperature anomalies at Kayar (B).

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Articles soumis à des revues

NATURAL SELECTION AND CATASTROPHE-TYPE REGULATION IN PELAGIC FISH STOCKS

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Abstract

The temporary extinction of coastal pelagic marine fish stocks during unpredictable time periods is a natural phenomenon. For these short life cycle species (life span of 4 to 8 years) the appearance of quick and sustained recoveries after time periods of decades to centuries is not rare. It is difficult to identify the underlying mechanisms of these long term fluctuations when using major changes in climate or in fishery exploitation. Considering evolutionary aspects, we hypothesize that the long periods of low biomass levels are the result of strong interspecific selective pressures with only minor impacts resulting from climatic fluctuations. The recovery of depleted biomasses would be the result of an adaptive process (micro-evolution). A model using catastrophe theory is proposed to illustrate the long term regulation of these ecological systems.

Temporary extinction of stocks as a natural and unpredictable phenomenon

Three of the most important pelagic stocks in the world are unfortunately well known for their instability : the Japanese sardine (*Sardinops melanosticta*), the Pacific sardine (*Sardinops sagax*) and the Peruvian and Chilian anchoveta (*Engraulis ringens*). Recent fishery statistics (1,2,3), old literature (4), as well as paleoecological studies (5,6) show some evidence of dramatic population fluctuations in the immediate and remote past. Thus temporary extinctions of these short life cycle species (life span of 4 to 8 years) may last for decades or centuries.

Even though some authors (7,8) suggest that large scale environmental phenomena may influence fish stock dynamics, these large fluctuations exhibit no obvious patterns (9) and their relations to variations in climate or fishery exploitation rates are often questionable when analyzing long term changes (10,11,12). Thus the temporary extinction of pelagic stocks appears to be a natural and unpredictable phenomenon.

The underlying mechanisms that could lead to a better understanding of these long term changes in fish stocks are far from being identified, probably because of the complexity of the interactions between the environment and the stocks. The theories of natural regulation of stock size are not mutually exclusive, and a synthesis of several approaches may be most useful (13). Most studies of change in fish stock abundance have analyzed the quantitative impact of extrinsic factors (11) but some changes in abundance are also the result of changes in the ecological adaptability of the species (14). The purpose of this article is to study this last point, that is the qualitative aspects of fish stock changes from an evolutionary point of view.

Interspecific competition at low stock level and its implications

When two species compete and one becomes rare, it suffers dissymmetrical selective pressures (15). The dominated species has primarily interspecific contacts while the dominant species has essentially only intraspecific contacts. Thus the severity of interspecific competition would depend on fish stock size.

It is particularly difficult to analyze and show such subtleties in marine ecology. We have to refer to experimental research in terrestrial ecology (16,17) to understand the possible evolutionary implications of competition on population changes. The experiments referred to in (16,17) were as follows:

two competitive species of flies, of which one is more efficient and thus rapidly becomes more abundant at the beginning of the experiment, were placed together in an experimental cage . After several generations a competitive inversion may lead to the elimination of the more abundant species. This new equilibrium reflects the intervention of a selective process and confirms the reality of microevolution. There would thus be a modification in the behavior of the dominated species, becoming competitively superior within a few generations.

These evolutionary changes are structures or newly adopted properties which allow a new function and consequently permit the opening of a new adaptive zone (18). Subtle developmental mechanisms may have important consequences on individual survival and may lead to the expansion of a population.

The stock biomass of competitive species increased after the recent collapses of the Japanese sardine, Pacific sardine and Peruvian and Chilian anchoveta. Respectively the mackerel (*Scomber japonicus*) (19), the anchoveta (*Engraulis mordax*) (20) and the sardine (*Sardinops sagax*) and the horse mackerel (*Trachurus murphyi*) (21) have all increased stock biomass. Consequently the interspecific competition is probably severe for the depleted stocks. Are the coastal pelagic species able to exhibit evolutionary changes within their population ? In other words, do they have a high adaptive potential ?.

Adaptive potential of pelagic species

Two essential characteristics may confer a strong adaptive potential to the pelagic fish populations: biotic potential and demographic plasticity.

Pelagic species have a high biotic potential. Every female is able to lay thousands or millions of eggs several times during one year, even though the survival of only two eggs are necessary to maintain the population . The large amount of genetic variations not used in each generation represents an important selective advantage (22). Physical and biological environments fluctuate considerably in the pelagic ecosystem. It is also difficult to predict the particular combination of genes which will be of interest for the next generation. Under these circumstances the probability for certain genotypes to exhibit more optimal fitness under new conditions is high. The species would be able to adapt to a rapid environmental change or to a new way of life.

The plasticity of a trait, that is not its mean value but its variance, is also a major adaptive response (23,24). Thus the adaptive mechanisms could be the result of the intervention of the evolution of a trait or the canalization of the variability of this trait (25). Two types of plasticity can be defined (26): continuous and discrete plasticity. Continuous plasticity corresponds to gradual responses to environmental changes, while discrete plasticity, also called developmental switches (23), would produce individuals with alternative characteristics that are sometimes better adapted.

Evolutionary changes and the size of the population

Another important factor which is essential to the understanding of the evolutionary mechanism is the population size. These evolutionary changes occur only in small size populations (27). An intuitive approach is to consider that with a large gene pool, the fixation and conservation of evolutionary changes is difficult because of dilution in the population. Abundant populations are inert from an evolutionary point of view (22). The occurrence of an evolutionary change would be favored within small size populations, like the depleted stocks.

Climatic impact and the size of the population

The responses of stocks to climatic changes have been studied by Skud (28) who considered competition with other species. This author shows that the reaction of the stocks to environmental changes may vary with the inversion of dominance. Stock abundance is then controlled by the abundance of the dominant species. The response to environmental factors is weakened. The thesis that climatic factors affect the abundance of a species but do not govern its absolute population density has also been supported (28).

Selective pressures and evolutionary changes as a possible mechanism for recovery

These biological and evolutionary considerations show that the response of a population to environmental and interspecific selective pressures vary with the stock level. Evolutionary changes of depleted stocks under strong selective pressures, may occur. They can appear very rapidly within a population (29), which permits observation on an ecological time scale.

We support the thesis that a low biomass level of lengthy duration would be due to strong interspecific competitive pressures and in a minor way, due to climatic changes. The recovery would be the result of an adaptive process (evolutionary change). This implies that after recovery there would be a new relationship between the population and its environment, that is a new adaptive strategy adopted by the species under different interspecific and environmental selective pressures.

To model discontinuous changes in natural phenomena , the topological theory of dynamical systems (30), now known as the catastrophe theory (31), has been developed. A model using a one-dimensional section of a cusp catastrophe is proposed to illustrate the regulation of these pelagic ecological systems (Fig. 1). It allows a representation of the discontinuities that exist between stock abundance and environment by investigating a bistable phenomenon which displays hysteresis. Thus for a prosperous stock, interspecific competition is weak and there is a strong climatic impact on stock size. The collapse appears for a weakened stock (jump phenomena on way 1 on Fig. 1). Interspecific competition is strong for a depleted stock which fluctuates only slightly under climatic fluctuations. Furthermore evolutionary changes that may appear under strong selective pressures allow recovery to a prosperous stock level (jump phenomena on way 2 on Fig. 1).

Conclusion : importance of the qualitative aspects of a population

Evolutionary changes may occur rapidly in a depleted stock, so that the evolutionary time-scale approaches the ecological time-scale. Natural selection may thus impinge upon natural regulation. The adaptationist and the mechanist points of view represent the two major approaches to understanding long term changes (26). They are not mutually exclusive but overlap and together they can contribute to a better comprehension of long term regulation in fish stocks. Thus following some authors (14), we caution the ecologist who might be tempted to seriously consider theoretical models of populations, depending on oversimplified abstractions of static animals or simple interactions between climate and stock size, when analyzing long term changes in fish stocks.

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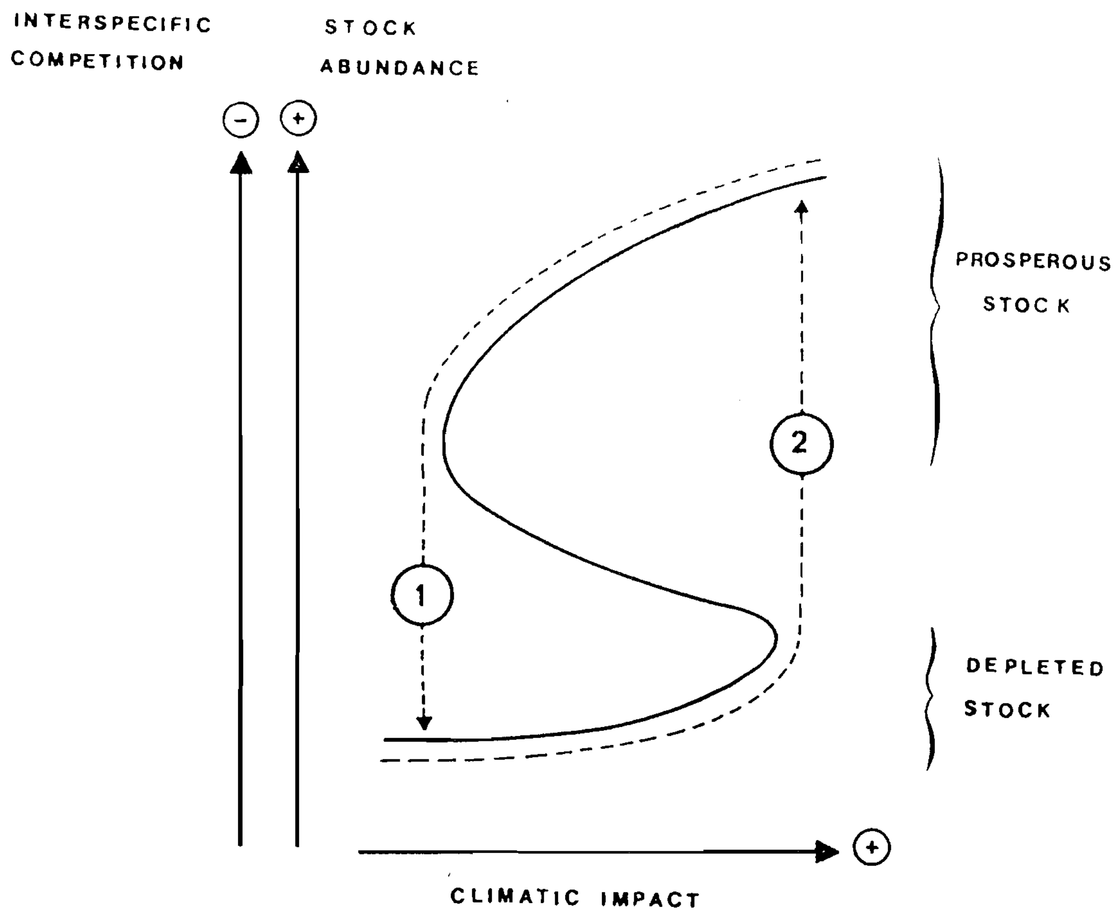

Figure 1: The catastrophe type regulation of fish stock abundance can be expressed with a one dimensional section of a cusp catastrophe. The dashed line represents the possible way on the theoretical topology (solid line). The severity of interspecific competition is correlated with stock abundance, it is weak for a prosperous stock and strong when the stock is depleted (Y-axis). The stock collapses when its level is too low under unfavorable climatic impact (way 1). The stock is able to recover to a prosperous level under favorable climatic conditions, when evolutionary changes occur under strong selective pressures (interspecific competition) (way 2).

DYNAMIQUE COMPAREE DE DEUX ESPECES DE SARDINELLES DES COTES OUEST-AFRICAINES

PREMIERE PARTIE :

APPARENCES ET REALITES DE LA COMPETITION ENTRE SARDINELLA AURITA ET SARDINELLA MADERENSIS

COMPARATIVE STUDY OF TWO SARDINELLA SPECIES DYNAMIC OF THE WEST-AFRICAN COAST

PART ONE :

APPEARANCES AND REALITIES OF THE COMPETITION BETWEEN SARDINELLA AURITA AND SARDINELLA MADERENSIS

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RESUME

Les deux espèces de sardinelles (*Sardinella aurita* et *Sardinella maderensis*) sont présentes dans les trois régions d'upwelling de l' Ouest africain (zones sénégalo-mauritanienne, ivoiro-ghanéenne et congo-angolaise). La compétition entre ces deux espèces, présentant une grande similitude de forme, à l'activité et aux régimes alimentaires très proches et occupant les mêmes zones géographiques semble effective.

Une étude approfondie montre que les stratégies d'occupation du milieu et de reproduction de ces deux espèces sont intimement liées à la dynamique des upwellings mais qu'elles divergent en de nombreux points. Une complémentarité spatio-temporelle existe entre la dynamique de ces deux espèces et rend la coexistence possible.

Même si la compétition entre deux espèces de poissons pélagiques peut souvent paraître effective en écologie marine, rares sont les exemples où elle peut être mise en évidence au niveau de l'abondance respective des stocks. Les auteurs insistent sur le fait que les mécanismes de compétition pour des espèces spécialisées comme les pélagiques doivent être précisés au niveau de certains paramètres du cycle vital de l'espèce.

L'importance de l'étude des mécanismes d'évitement dans l'analyse et la compréhension de la dynamique de ces populations apparemment en compétition directe est ainsi soulignée.

mots-clés: Sardinelles, Afrique de l'Ouest, compétition interspécifique.

DYNAMIQUE COMPAREE DE DEUX ESPECES DE SARDINELLES DES COTES OUEST-AFRICAINES

DEUXIEME PARTIE :

STRATEGIES DEMOGRAPHIQUES DE SARDINELLA AURITA ET SARDINELLA MADERENSIS ET DYNAMIQUE DES STOCKS

COMPARATIVE STUDY OF TWO SARDINELLA SPECIES DYNAMIC OF THE WEST-AFRICAN COAST

PART TWO :

LIFE-HISTORY STRATEGIES OF SARDINELLA AURITA AND SARDINELLA MADERENSIS AND STOCKS DYNAMIC

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RESUME

Les stratégies démographiques de deux espèces de sardinelles (*Sardinella aurita* et *Sardinella maderensis*) qui sont présentes dans les trois régions d'upwelling de l' Ouest africain (zones sénégalo-mauritanienne, ivoiro-ghanéenne et congo-angolaise) sont comparées. Les stratégies d'occupation et d'exploitation du milieu, de croissance et de reproduction sont pour ces deux espèces intimement liées à la dynamique des upwellings mais elles divergent en de nombreux points. *S. aurita* présente une plasticité et une adaptabilité remarquable aux fluctuations du milieu dont elle tire partie. En cela, elle semble être plus sensible aux variations climatiques que *S. maderensis* qui apparaît comme étant une espèce tolérante aux fortes pertubations de l'environnement. Ainsi une plus grande variabilité des paramètres biologiques et démographiques est observée pour la première espèce.

Dans une optique théorie des jeux, ces deux espèces ne prennent pas les mêmes risques pour survivre dans ces milieux trés perturbés que sont les zones d'upwelling. De fait, *S. aurita*, espèce opportuniste, joue le jeu de la variabilité hydroclimatique alors que *S. maderensis*, espèce rustique, possède une stratégie de tolérance aux pertubations du milieu. *S. aurita* possèdent une stratégie adaptative plus souple liée à une grande plasticité démographique. Cela lui permet une meilleure utilisation d'un enrichissement temporaire dû à la variabilité climatique, mais en retour la population subit le contrecoup de façon plus drastique lorsque les conditions deviennent défavorables.

Cette analyse comparée des stratégies démographiques permet de mieux comprendre certaines causes de l'instabilité des stocks de *S. aurita* comparée à la relative stabilité des stocks de *S. maderensis*. La nécessité de gérer les stocks en considérant la stratégie de vie des espèces qui les composent est ainsi soulignée.

mots-clés: Sardinelles, Afrique de l'Ouest, stratégies démographiques, dynamique des stocks.

Soumis à Ocean. Acta.

FLUCTUATIONS SAISONNIERES ET INTER-ANNUELLES DES VENTS AU SENEGAL : IMPACT SUR L'ECOSYSTEME

SEASONAL AND INTERANNUAL FLUCTUATIONS OF WINDS OFF SENEGAL : IMPACT ON THE ECOSYSTEM

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Mots clés : Sénégal, upwelling, vent, transport d'Ekman.

Key words : Sénégal, upwelling, wind, Ekman transport.

RESUME

A partir des mesures de vent effectuées de 1961 à 1986 à la station météorologique de Dakar-Yoff (Sénégal), le signal saisonnier du vent (vitesse et direction) et sa variabilité inter-annuelle sont décrits. Ces différents paramètres ont subi des modifications importantes au cours des vingt six années de mesure. La période 1961-1986 est caractérisée par l'alternance de période d'intensification et de relaxation du vent d'une durée moyenne de 7 ans. En saison d'alizés, on observe une forte variabilité inter-annuelle de la direction moyenne du vent. Les alizés de secteur N-NE sont dominants au cours des périodes de vents forts.

A l'aide du transport d'Ekman, l'impact de ces fluctuations saisonnières et inter-annuelles sur l'écosystème ont été évaluées. Une disparité importante entre les zones situées de part et d'autre du Cap Vert est apparue. Les résultats obtenus suggèrent que la zone située au sud de la péninsule est l'objet d'un enrichissement plus intense et de plus longue durée que la zone située au nord, notamment en période d'alizés faibles. En saison d'alizés, les teneurs en sels minéraux au sud de la péninsule sont supérieures à celles rencontées au nord. Les facteurs abiotiques (turbulence et topographie du plateau continental) semblent également favoriser la zone située au sud du Cap Vert.

Quelques exemples, tirés de la littérature, illustrant l'impact de l'hétérogénéite spatio-temporelle de l'upwelling sénégalais sur les maillons supérieurs de la chaine trophique sont donnés.

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SELECTIVE PRESSURES AND DEVELOPMENTAL SWITCHES : AN HYPOTHESIS TO EXPLAIN SOME ASPECTS OF LONG TERM FLUCTUATIONS IN COASTAL PELAGIC SPECIES

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Abstract

The extinction of some coastal pelagic marine stocks during much longer phases than species life cycle duration, followed by a quick and abundant reappearance, is sometimes observed. Japanese sardine (*Sardinops melanosticta*), Pacific sardine (*Sardinops sagax*) and Peruvian and Chilian anchovy (*Engraulis ringens*) are presented as examples. Interpretations of these stocks fluctuations are reminded. Climate or exploitation impact does not always appear to be sufficient to explain the recovery of these stocks.

A self-regenerating stochastic model is considered. It combines a basic self-regenerating model where recruitment is obtained from a spawning stock with a stochastic Ricker stock-recruitment model. When a stock is depleted (very weak biomass), its recovery can be simulated after various time periods when a good recruitment occurs. Thus this simulation can describe the instability and unpredictable fluctuations of these stocks. A multispecies approach taking into account interactions between one or more species can also describe the fact that low biomasses are attractive to dominated species.

Marine and terrestrial ecology but also evolutionary biology approaches may lead to improve the understanding of the biological reasons for the maintenance and recovery of depleted biomasses. The severity of interspecific competition for the low biomass level species is discussed. The possible consequences of strong selective pressures on population dynamics and adaptive potential of pelagic species are emphasized. Lastly developmental switches that appear when a species is becoming rare are considered. In regards to these considerations we assume that the long attractive periods are the results of strong selective pressures and minor impact of climatic fluctuations. The recovery of depleted biomasses would be the result of an adaptive process (micro-evolution). A model using catstrophe theory is proposed to illustrate the long term regulation of these ecological systems. Natural selection and regulation of population could evolve together within a common time scale.

IMPACT OF THE ENVIRONMENT ON THE LOCATION OF THE NURSERIES, THE TIMING OF THE REPRODUCTION AND THE RECRUITMENT OF THE WEST AFRICAN CLUPEOIDS

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ABSTRACT

The effect of the environment on recruitment of pelagic fish has been widely discussed and different theories have emerged. Availability of food or physical constraints involving stability in the euphotic layer or offshore transport are now considered as important factors that affect larvae survival.

Clupeoid stocks located along the West African coast are of interest for testing these hypotheses. These stocks live in a fluctuating environment where seasonal or permanent upwellings occur and strongly affect biological productivity. From Morocco to Senegal the upwellings are forced by the local winds; off Ivory-Coast and Ghana, remote forcing by the wind from broadscale areas generates the upwelling. In the first case strong upwelling is associated with high turbulences (wind mixing) and not in the second case.

The main nurseries are distributed discontinuously along the West Arican Coast and not always located in the most productive areas. High reproduction activity is found where the morphology of the coast and of the continental margin minimize offshore transports.

In remote forced upwellings, reproduction takes place during the upwelling season. In Ekman type upwellings reproduction is maximum before and after the upwelling season. In the first case the timing of the reproduction is set to offer maximum food availability, in the second case it is set to fit better abiotic conditions i.e. higher stability and less offshore transport. From these observations it appears that in Ekman type upwelling the timing of the reproductive process have to compromise and to find an optimum between stability and food availability; in remote forced upwelling, wind mixing is not a limitating factor and the reproduction process matches the maximum planktonic productivity.

Environmental conditions strongly affect interannual variability of recruitment. Using empirical optimal transformations in multiple regressions, relationships between recruitment variability and annual upwelling indices appear to have a dome shape in Ekman type upwelling and is linear for a remote forced upwelling. High productivity in Ekman type upwelling is also associated with high turbulence and therefore has a negative effect on larval survival. This limitation does not exist in the case of a remote forced upwelling.

QUESTIONS ABOUT CLIMATIC ANOMALIES AND TUNA FISHERY IN THE TROPICAL ATLANTIC

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ABSTRACT

The surface tuna fishery in the eastern tropical Atlantic is assumed to be strongly associated with environmental features such as thermal fronts and upwellings. Previous studies demonstrated that the annual migrating patterns of different species and the annual space and time dynamics of Catch Per Unit of Effort (CPUE) were coherent with the seasonal cycle of upwellings. On short time scale basis (fortnight) time series analysis demonstrated the link between past temporal evolution of Sea Surface Temperature (SST) and the following CPUE. The purpose of this paper is to analyse at a longer time scale the relationship between interannual environmental anomalies (upwelling intensity) and the observed fluctuations of local abundance or catchability estimated by CPUE.

Two areas with intensive and well defined seasonal fishing activities are selected, the first one off Senegal and the second one off Ivory Coast. In both areas the fishing season is associated with the occurence of a seasonnal upwelling. Local abundance from 1970 to 1984 were estimated from catch and CPUE data. Upwelling intensity during the same period were estimated from SST collected by merchand ships and tuna vessels.

Our investigations show no apparent or poor relationship between the interannual fluctuations of upwelling intensities and the apparent fluctuations of local abundance. Both areas were selected because they are known areas where tunas migrate and feed or concentrate along thermal fronts. As upwelling intensity affects the intensity of thermal fronts or the ecosystem productivity and therefore the available food, this result is very surprising.

This results question the traditionnal assumption that tunas catches in the tropical Atlantic is strongly associated with environmental conditions : if the mean annual space and time patterns of fishing activities and the migration of fishes are associated with the environment (fishes migrate from one productive area to another and fishing activity follow the migration of fishes), interannual anomalies of the environment (strong or week upwelling) do not seem to affect local abundance in the fishing areas. These results suggest that the basic assumtion we made at a local scale, which links upwelling intensity, production and local abundance or catchability is somehow wrong. Therefore, interannual variability of local abundance could be only related with migration fluxes. These results also suggest that the link between climate and fishery is not simple and linear : relationship between both parameters depend on the space and time scale used.

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UPWELLING ET PECHE DES ESPECES PELAGIQUES COTIERES DE COTE D'IVOIRE : UNE APPROCHE GLOBALE

UPWELLING AND COASTAL PELAGIC FISHERY OFF IVORY COAST : A GLOBAL APPROACH

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RESUME

Un modèle global intégrant l'effort de pêche et des indices d'upwelling est proposé afin d'expliquer les fluctuations des PUE (Prises par Unité d'Effort) des espèces pélagiques côtières de Côte d'Ivoire entre 1966 et 1981.

Le modèle prenant en compte les indices d'upwelling de l'année en cours et de l'année précédente ainsi que l'effort de pêche permet un bon ajustement aux données de PUE. Il permet d'expliquer 73% de la variance des indices d'abondance observés. Les conditions climatiques à elles-seules jouent un rôle important pour décrire la variabilité de ces mesures. Les contributions respectives des indices d'upwelling de l'année en cours et de l'année précédente dans l'explication de la variance des PUE sont analysées. A l'aide de ces résultats, des hypothèses sont avancées concernant l'action de l'hydroclimat sur ces stocks.

Pour de très faibles ou de très forts upwellings, il semble que le recrutement soit influencé par les conditions du milieu. L'environnement dans lequel évolue la pêche semble également influencer les rendements de la flottille. Ceci confirme, a posteriori, l'interêt d'introduire dans le modèle deux paramètres décrivant le milieu, l'un caractérisant l'intensité des upwellings l'année de la pêche et l'autre l'année précèdente.

Mots clés : petits pélagiques côtiers, Côte d'Ivoire, upwelling, modèle global.

A paraître dans Ocean. Acta., 1987.

MIGRATION SAISONNIERE DU THIOF (EPINEPHELUS AENEUS) AU SENEGAL : INFLUENCE DES UPWELLINGS SENEGALAIS ET MAURITANIENS

SEASONAL MIGRATION OF THIOF (EPINEPHELUS AENEUS) OFF SENEGAL : EFFECT OF THE SENEGALESE AND MAURITANEAN UPWELLINGS

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Titre abrégé : Migration du thiof au Sénégal et upwellings

Migration of thiof off Senegal and upwellings

Environmental Influences on the French, Ivory Coast, Senegalese and Moroccan Tuna Catches in the Gulf of Guinea

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Both local and broadscale dynamic relationships were studied between catch per unit of effort (CPUE) for yellowfin and skipjack tunas in the Gulf of Guinea, and sea-surface temperatures (SST), and wind speed. The results suggested why a particular temperature during one time period will lead to high CPUE, while at another it will lead to low CPUE. Our analysis was not restricted to where fishing actually occurred.

We used a recently developed algorithm to complete missing CPUE and environmental data. Models were developed for eleven separate sub-areas of the Gulf of Guinea. Details of the method are provided in an appendix. Results from these models suggested that the environmental variables under study reflected an oceanographic process involving upwelling and concentration of nutrients a month prior to good fishing, followed by arrival of relatively warmer waters two weeks prior to good fishing.

We calculated dominant modes of variability for each parameter in time and space by six week and one year periods. The dominant mode for SST showed a space-time movement that was consistent with a recently developed theory of remote forcing in the equatorial Atlantic.

The dominant modes for CPUE for both yellowfin and skipjack showed relatively little discernible pattern. However, when dominant modes were calculated between SST and CPUE for the same periods and species of fish, the CPUE exhibited the same movement in space and time as SST, at about the same speed. This suggested the predictability of CPUE was largely due to a broadscale oceanographic process, which may have been associated with remote forcing in that region.

On a étudié les relations de la dynamique locale et à grande échelle entre la prise par unité d'effort (CPUE) de l'albacore et du listao dans le golfe de Guinée, les températures de surface (SST) et la vitesse du vent. Les résultats montrent pourquoi une température déterminée durant une période donne une CPUE élevée, alors qu'à une autre période elle entraîne une CPUE faible. Notre étude ne s'est pas limitée aux lieux de pêche actuels.

Pour obtenir les données de CPUE et de milieu manquantes, nous avons utilisé un algorithme récemment développé. Des modèles ont été établis dans le golfe de Guinée et ceci dans onze sous-zones séparées. Les détails de cette méthode indiquent que les variables de milieu sous étude reflétaient un procédé océanographique comportant un affleurement et une concentration d'aliments un mois avant une pêche fructueuse, suivi de l'arrivé d'eaux relativement plus chaudes, deux semaines avant une bonne pêche.

Nous avons calculé les principaux modes de variabilité de chaque paramètre dans le temps et dans l'espace sur des périodes de six semaines et un an. Les modes dominants de SST montraient un déplacement spatio-temporel compatible avec la théorie récemment élaborée de la pression de facteurs éloignés ("remote forcing") dans l'Atlantique équatorial.

Les modes dominants de la CPUE d'albacore et de listao montrent un schéma assez peu défini. Néanmoins, lorsque les modes dominants étaient calculés entre les SST et la CPUE pour les mêmes périodes et les mêmes espèces de poissons, la CPUE signalait le même déplacement spatio-temporel que les SST, à peu près à la même vitesse. Ceci indique que la prévisibilité de la CPUE est surtout due à un procédé océanographique à grande échelle, qui pourrait être associé à la pression de facteurs éloignés ("remote forcing") dans cette région.

Se estudiaron las relaciones dinámicas locales y a gran escala entre captura por unidad de esfuerzo (CPUE), para rabil y listado en el Golfo de Guinea, temperaturas de la superficie del mar (SST) y velocidad del viento. Los resultados indican porqué una determinada temperatura durante un período conduciría a una CPUE alta, mientras que en otro período conduciría a una CPUE baja. Nuestro análisis no se limitó al lugar de pesca actual.

Para obtener los datos de CPUE y de medio ambiente que faltaban, hemos utilizado un algoritmo recientemente desarrollado. Se establecieron modelos en el Golfo de Guinea para once sub-áreas separadas. Los detalles de este método se facilitan en un apéndice. Los resultados obtenidos a partir de estos modelos indican que las variables del medio ambiente estudiadas reflejan un proceso oceanográfico que comprende afloramientos y concentración de materia nutritiva, con un mes de anterioridad a una buena captura, seguida por la llegada de aguas relativamente cálidas dos semanas antes de una pesca abundante.

Se calcularon modos dominantes de variabilidad para cada parámetro en tiempo y espacio durante períodos de seis semanas y de un año. El modo dominante para SST mostró un movimiento tiempo-área que guardaba coherencia con una teoría recientemente desarrollada de "forzamiento" por factores remotos en el Atlántico ecuatorial.

Los modos dominantes para la CPUE del rabil y listado mostraron modelos relativamente poco definidos. Sin embargo, cuando los modos dominantes se calculaban entre SST y CPUE para los mismos períodos y especies de peces, la CPUE indicaba el mismo movimiento en el espacio y en el tiempo que el SST, aproximadamente a la misma velocidad. Esto sugería que la capacidad de pronóstico de la CPUE se debía principalmente a un proceso oceanográfico a gran escala, que podría haber estado asociado al "forzamiento" por factores remotos en esa zona

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Fluctuations of a fortnightly abundance index of the Ivoirian coastal pelagic species and associated environmental conditions

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Fluctuations of a Fortnightly Abundance Index of the Ivoirian Coastal Pelagic Species and Associated Environmental Conditions

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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.

In this paper we analyze time series of catch per unit of effort (CPUE) from 1966 to 1982 of small pelagic species off the Ivory Coast using sea surface temperature (SST) collected by merchant ships. A fill-in model is used to estimate missing values of CPUE and SST in the areas in which the fishery operates. A multivariate time series model of the fortnightly data is able to explain 43% of the observed variance in CPUE from 1966 to 1982. A model estimated by using only the data from 1966 to 1980 produced reasonable forecasts of the fortnightly CPUE for 1981–82. A new approach for estimating optimal transformations of variables in the model is used to examine the form of the relationships between CPUE and its predictors. The biological interpretation of the estimated transformations is consistent with previous results on the dynamics of zooplankton in the same area.

Les auteurs analysent une série chronologique de prises par unité d'effort (PUE) de petites espèces pélagiques capturées de 1966 à 1982 au large de la Côte d'Ivoire en fonction des températures de l'eau en surface (TES) relevées par des navires marchands. Ils ont utilisé un modèle à blancs pour déterminer les valeurs manquantes des PUE et des TES pour les pêcheries exploitées. Un modèle des séries chronologiques à plusieurs variables aléatoires pour des données bimensuelles permet d'expliquer 43 % de la variance observée des PUE obtenues de 1966 à 1982. À l'aide d'un modèle généré par les données recueillies de 1966 à 1980, ils ont obtenu des prévisions acceptables des PUE bimensuelles pour 1981–82. Une nouvelle approche pour l'estimation des transformations optimales des variables du modèle est utilisée pour étudier la relation entre les PUE et leurs éléments extrapolés. L'interprétation biologique des transformations estimées est en accord avec les résultats antérieurs sur la dynamique du zooplancton dans la même région.

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The purse-seine fishery for coastal pelagic species off the Ivory Coast annually lands around 20 000 metric tons; this makes the fishery of local socioeconomic importance. The fishery also is of scientific interest because coastal pelagic species are important worldwide and are believed to be significantly influenced by environmental factors (see for example Parrish et al. 1983). The fishery off the Ivory Coast occurs in a region with two upwelling seasons, a smaller one around January and a larger one later in the year, which are followed by periods of strong rainfall, which affects salinity levels in the environment of the fish. Understanding the fishery dynamics in this area and how the dynamics are influenced by the environment can increase our understanding of other pelagic fisheries of greater economic importance.

In this paper our primary goal is to model the relative impact of the environment on the availability of pelagic species off the Ivory Coast in Africa and the manner in which the environment affects the dynamics of catch per unit of effort (CPUE) for these species on time scales as short as 2 wk. Previous studies suggest that the availability and abundance of these stocks are strongly influenced by the environment. Marchal (1967) and FAO (1974) presented evidence that sea surface temperature (SST) and salinity are important influences on the intrayear fluctuations in abundance of these stocks. Annual fluctuations in the abundance indices for the main Ivoirian or Ivoiro–Ghanaian stocks also have been related to changes in upwelling and rainfall (ORSTOM 1976; Binet 1982; Cury and Roy 1985). However, short-term fluctuations of these stocks never have been considered before.

Our approach to this problem is to use multivariate autoregressive moving-average (ARMA) models as described in Tiao and Box (1981) to model and forecast an index of relative abundance for the pelagic species off the Ivory Coast. We also use a new technique developed by Breiman and Friedman (1985) to analyze more closely the form of the relationship between CPUE and the relevant environmental variables. This technique allows us to examine the nonlinearities and discontinuities in the data that a priori are believed to exist but whose

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TEMPORAL AND SPATIAL DYNAMICS OF A COASTAL PELAGIC SPECIES, *SARDINELLA MADERENSIS*, OFF THE IVORY COAST.

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PRESSIONS SELECTIVES ET NOUVEAUTES EVOLUTIVES : UNE HYPOTHESE POUR COMPRENDRE CERTAINS ASPECTS DES FLUCTUATIONS A LONG TERME DES POISSONS PELAGIQUES COTIERS

SELECTIVE PRESSURES AND DEVELOPMENTAL SWITCHES : AN HYPOTHESIS TO EXPLAIN SOME ASPECTS OF LONG TERM FLUCTUATIONS IN COASTAL PELAGIC SPECIES

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RESUME

L'extinction de certains stocks pélagiques côtiers marins durant des périodes dépassant très largement la durée du cycle de vie des espèces, suivie parfois d'une réapparition brutale et en grande abondance de l'espèce est observée. Les exemples de la sardine du Japon (*Sardinops melanosticta*) de la sardine du Pacifique (*Sardinops sagax*) et de l'anchois du Pérou et du Chili (*Engraulis ringens*) sont présentés et l'interprétation des fluctuations d'abondance qui en a été faite est rappelée. L'action du climat ou de la pêche n'apparaissent pas toujours satisfaisants pour expliquer les processus de récupération de ces stocks.

Le comportement d'un modèle stochastique autorégénérant simple est étudié. Il combine un modèle classique décrivant la phase recrutée et une relation stock-recrutement de type Ricker affectée d'une source de variabilité. Lorsque le stock est éteint (très faible niveau de biomasse) son recouvrement peut être simulé après un laps de temps très variable, suite à un bon recrutement. Ce type de simulation utilisant les théories classiques de la dynamique des populations peut permettre de rendre compte de l'instabilité et de l'évolution naturelle non prédictible de ces stocks. Une approche multispécifique prenant en compte la compétition entre deux ou plusieurs espèces peut aussi décrire le fait que les très faibles biomasses constituent des états attractifs pour l'espèce dominée.

Les travaux menés en écologies marine et terrestre ainsi qu'en biologie évolutive permettent de mieux comprendre les raisons biologiques du maintien et de la récupération des biomasses amoindries. La sévérité de la compétition interspécifique pour l'espèce qui connaît un faible niveau d'abondance est rappelée. Les conséquences possibles de fortes pressions sélectives sur la dynamique de population ainsi que le fort potentiel adaptatif des espèces pélagiques sont soulignées. L'aptitude d'une espèce à exprimer une nouveauté évolutive lorsqu'elle est devenue rare dans le milieu est envisagée. Ainsi les longues périodes d'extinction au caractère attractif sont interprétées comme le fruit de pressions sélectives fortes et du moindre impact des fluctuations climatiques. La reconstitution de biomasses qui se sont éteintes mettrait en jeu un processus adaptatif (microévolution) qui permettrait de sortir de l'état attractif que constitue les faibles biomasses. La sélection naturelle pourrait ainsi se mêler aux mécanismes de régulation des populations pélagiques.

mots-clés : petits pélagiques côtiers, fluctuations à long terme, recouvrement des stocks effondrés, biologie évolutive.

Discussion and Conclusions

While there must be caution in making interpretations of our space-time analysis for reasons mentioned previously, the general pattern that emerges is that of a west-to-east migration followed by an east-to-west migration. The fish appear to migrate mainly between areas 7 and 4, perhaps avoiding the fishery in the central area by going too deep for the gear. Environmental processes, measured here by the dynamics in SST, appear to influence these migrations. It is interesting to compare this proposed migratory pattern with the dynamics of zooplankton in the same region. During the main cold season there is a general enrichment of zooplankton with an eastern movement associated with the Guinea Current. The zooplankton then make a return migration to the west (area 7) around August, associated with an undercurrent (Binet 1976). During the warm season, the western part of the Ivoirian gulf (area 7) is the area most favorable for zooplankton enrichment and fishing also usually is favorable during this period. Area 5 generally is the area poorest in zooplankton (Binet 1976) and also generally has the lowest levels of CPUE.

Fishermen in the area have observed a lack of fish in the central areas and that the fish appear to migrate very quickly from one area to another It is difficult to compare two different biological processes, especially when the evidence is circumstantial, but there appears to be enough evidence to develop some rough ideas and to point to the underlying environmental processes and fish behavior that would have to be studied further to clarify some of these issues. The short (fortnight) time scales in which we find movement in the CPUE as well as the changes in the environment that lead to high levels of CPUE all seem to support the idea that the fish are migrating between areas where they can take advantage of sudden increases in zooplankton biomass caused by favorable environmental conditions (see Binet 1976). Further simultaneous studies of both zooplankton and *S maderensis* in the same area would help to clarify some of these issues

Our analysis has presented evidence that the dynamics of *S. maderensis*, both in space and time, appear to be influenced to a considerable degree by the environment. The space-time analysis suggests that the environment may be an indirect influence: favorable environmental conditions may be causing an increase in and aggregation of zooplankton biomass, as in Binet (1976, 1983), and the fish move and take advantage of the increased biomass.

We have also shown that the relationships between CPUE and the environment most likely are highly nonlinear. If we are to better understand the dynamics, we must be careful to work on the appropriate functional scales. Simple linear methods will often obscure relationships that exist both in the data and in the real world