

Dome or U-Shaped Physiological Responses of Populations, and Ecosystems

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There is nothing so difficult as to hypothesize plausible causal relations in biophysical systems as to be without understanding of, or concern for underlying principles.

ABSTRACT

Clearly human manipulation and exploitation have taken the projected tolls in aquatic ecosystems, and show little promise of relent. The contrast between the successes of the two contemporary approaches to better understanding aquatic systems ecology, one based on principles of empirical physiological ecology, and the other based on parameterized population dynamic responses, is invoked to explain the present impoverished status of marine fisheries management. Decades have passed with few or no good examples of how to secure either 'sustainable yield', or even how to define it in a rational context. Given the historical perspectives on global patterns of climate-driven resource variabilities, the basic 'stability' concept is certainly inappropriate as a prime objective. Basic tenets of economics and general ecological principles have also been ignored as one resource population after another has been 'defined', regulated, negotiated, and litigated, while being systematically decimated in the name of economic stability, and short-term profit taking. Within this same

period the numbers of environmental and resource scientists have multiplied, yet the results of their efforts have been devastation, not conservation. Peer-induced mediocrity through vetted agency fund chasing has replaced quest for applicable knowledge. In fact, we have come full circle, to the point where all the emergent observing technologies and information systems that were suggested to be enhanced during the late 1960s and 1970s for needed monitoring of resource habitats and ocean and atmosphere systems, so that ecological resource status could be understood, have been dismantled, their promoters retired or moved on, and replaced by a generation of inept resource modellers. Agency funds, once available for primary research, are increasingly squandered on bureaucratic councils, committees, and litigation. It is no wonder that we are having to start over again, to link knowledge that we have had, with system knowledge that we could not obtain, to manage resources that are already pressed beyond any reasonable limits, by social systems that are in perennial denial.

RÉSUMÉ

Les activités anthropiques ont fait beaucoup de dégâts dans les écosystèmes aquatiques et font preuve de peu de signes d'amélioration. Le contraste entre les deux approches contemporaines utilisées pour comprendre l'écologie des systèmes aquatiques, l'une fondée sur les principes empiriques de l'écologie et de la physiologie, l'autre fondée sur les modèles quantitatifs de la dynamique des populations, est évoqué pour expliquer les pauvres résultats de l'aménagement des pêcheries. Les décennies ont passé sans apporter aucun exemple permettant d'assurer un niveau soutenu des captures, ou proposant un contexte rationnel à l'aménagement. L'observation sur longue période montre que la variabilité des ressources est déterminée par des changements climatiques globaux et se donner la stabilité comme objectif premier est certainement inapproprié. Les principes de base en économie et en écologie ont été ignorés, les ressources ont été les unes après les autres « définies », administrées, objets de conflits et de négociations, alors qu'elles étaient systématiquement décimées au nom de la stabilité économique et du profit à court terme. Durant la même période, le nombre de scientifiques spécialisés dans l'environnement et les ressources s'est multiplié ; aujourd'hui, on constate que les résultats de leurs efforts ont été plus dévastateurs que conservateurs. La médiocrité auto-entretenu par les scientifiques à la chasse de fonds de recherche a remplacé la recherche d'un savoir applicable. Les techniques d'ob-

servation et les systèmes d'information mis au point à la fin des années 60 et des années 70 étaient nécessaires au suivi de l'habitat des ressources, des océans et des systèmes atmosphériques, de façon à comprendre le statut écologique des ressources. Ils ont été démantelés, leurs promoteurs sont partis et remplacés par une génération d'inaptes modélisateurs des ressources. Les agences, bailleurs de fonds jusqu'alors disponibles pour la recherche de base, ont alors commencé à gaspiller leur argent pour des conseils et autres comités bureaucratiques. Il n'y a pas de doute, il faut tout reprendre à la base, repenser le savoir que nous avons acquis, identifier dans la dynamique des systèmes les éléments que nous ne pourrions pas obtenir, pour aménager les ressources déjà exploitées au-delà des limites raisonnables.

INTRODUCTION

Fishery science is an applied science, fraught with conflicting perspectives, and short, fragmentary information sets. Fortunately, we have the legacies of von Bertalanffy, Fred Fry, and their myriad intellectual grandchildren to guide us in interpretations of physiological responses by fishes to physical environmental variables. Kinne (1970, 1971) provides a thorough summary of the variety of known responses. Nearly all of these responses, alone, or particularly when combined, form U- or domed relationships with fish distribution and behavior.

Otherwise, we have a morass of virtual populations, computer generated pseudo-biological 'virtual reality', generally with more basis in mathematical convenience than precise empirical observations. The problems facing groups such as CEOS include the responsibilities of explaining the patterns of cause and effect that have been hypothesized, and described. This is not a new challenge, it is simply a professional responsibility.

The vast information base from which anyone has to draw experience and help support innovations includes a huge, aging literature based on decades of careful laboratory studies, and long-term comparative studies of the sort advocated in recent decades by A. Bakun, R. Parrish and their colleagues. This tactic has been long practiced within the Fred Fry school of physiological ecology, originally with a focus on the fishes of the Great Lakes.

It was recently brought to my attention that William Ricker, putative father of North American stock assessment, spent his early efforts at the University of Toronto studying the consequences of environmental variability on trout populations. The global marine resource management focus on Ricker's equilibrium-based stock assessment methods is thus another example of a good start gone awry. Historically, most innovations tend to fail, although at their inception they often appear to be appropriate within the local context of the problems being faced.

In fact, this is a good example for problems in resource conservation science. Although it might have appeared that equilibrium-based population concepts might be applicable within the human life-span, it is the minuscule nature of a

single generation, whether of humans, fishes, or daisies, and the denial of the naturally induced population variabilities, and the importance of marginal subpopulations, that has cost the world so dearly within recent decades.

In support of the CEOS effort to identify the causal processes in coastal pelagic fish population variations, and eventual development of rigorous forecast models, I hope to reawaken the concepts of physiological ecology within the context of a not-always-random, even quasi-cyclic series of environmental changes. These are not new concepts. They just get denied.

Laboratory studies are the reproducible, critical information sets that provide 'corrective lenses' that can facilitate interpretations of what are now distinct, but poorly defined illusions of understanding. Neill *et al.* (1994), using of Fry's (1947) concepts of 'environmental factors and scope', provide a unique series of discussions and insights into ecophysiological responses of fishes.

Due to the poverty of physical context observations since the adoption of ritual stock assessment tools, systematic translations of carefully constructed fisheries data sets have yet to provide sufficient evidence of direct causality, or even of firm categories of measurable and traceable processes with direct, predictable results. This goal will be difficult to obtain, but worth the effort. Once achieved it will mark the maturation of fisheries research into a predictive, rather than hind-cast science. Unless the interpretive process is completed, the CEOS efforts might well be labeled as only another 'novel' methodology, with little or no genuine basis. Such are the problems of getting a new concept onto the table for more than discussion as another oddity.

1. ENVIRONMENTAL FORCING AND SOCIO-ECOLOGICAL CONSEQUENCES: WHAT'S NEW?

Sears and Mérriman (1980) provide historical insights into oceanographic observations and the birth of oceanography as a science. An important consequence of the age of exploration by sea, via the sequence of events arising from ancient Persian astrology, through western civilization's fixation on astrology, were the developments of navigational tools. The chronometer eventually provided sailors means for locating themselves on the high seas, providing the capability to chart paths to and from new found opportunities. The history of exploration of our planet is about integration of known but poorly understood processes, technologies, and occult phenomena.

Some few examples will suffice to initialize my concerns. In 1786 Deputy Postmaster General of the American Colonies, Ben Franklin published the now famous map of his Nantucket sea captain cousin, Timothy Folger, to help navigators avoid the time consuming countercurrent motion of the Gulf Stream for vessels headed from England to the Colonies. A century later, in 1878, the U.S. Coastal and Geodetic Survey was formed, to provide mariners with information about the U.S. coastal environment, and harbors.

Alexander Agassiz (1835-1910) inherited a naturalists eye for biological correlates in his long career as an ocean scientist. He became an icon for the 'Father of Oceanography', in its broadest sense. Realistically, the first ancient mariner that logged his observations, and shared them, holds rightful claim to that title. Another historically important scientist, among a cohort of 19th Century 'naturalists', was Charles Darwin. His notebooks while a naturalist observer aboard the H.M.S. Beagle gave birth to an array of oceanographic, geologic, and 'marine science' questions, many of which remain largely

unanswered to this date. In fact, we have a long list of true scientific heroes that can share the responsibility for progress in oceanography and related resource sciences.

It is difficult to conceive of where we might be without the influence of Matthew Fontaine Maury. He was first to organize ocean and atmosphere observations, initially for use in constructing his Wind and Current Charts in the 1850s. These became the first quality controlled records comprising the recent Comprehensive Ocean and Atmosphere Data Set (COADS), which CEOS utilizes in its formulations (see Roy and Mendelsohn, this vol.). These various stages of organized observations comprise a legacy of millennia of mariner's notes and maps of hazards and places since the advent of sea trade (Sears and Merriman, 1980).

The legendary disagreements between Norwegian Johan Hjort and his countryman colleague O. Dannevig initiated research into early life histories of fish resources around the turn of the 20th century. Alfred C. Redfield and his North American contemporaries, Henry B. Bigelow, Gordon Riley and their cohort, initiated a formal organization of thought, study and interpretation of constantly varying primary production processes in the ocean domain. There were undoubtedly many more local contributors leading to the increasing numbers of ocean resource scientists. The Challenger Expedition and the discourse over 'calcareous ooze' set the stage for the future scientific approaches to measuring and documenting ocean features and processes.

Most of the principle forcing functions in the upper ocean are well described, most within the recent fifty years. They have been studied individually, as well as in combination, and reported throughout the rapidly growing physical oceanographic literature. Since the beginning of organized ocean science, more biology and ecological interactions have been documented. Responses of fisheries to environmental variability has been studied and documented for nearly as long, but both sciences have only recently been converging onto the common objective of explaining the role of physical forcing on ocean production (Hjort, 1914, 1926; Cushing, 1969; Southward, 1974a, 1974b; Fasham, 1983; Csirke and Sharp, 1983; Sharp and Csirke, 1983; Platt, 1981; Longhurst *et al.*, 1995).

The recent Intergovernmental Panel on Climate Change reports (IPPC, 1990) on the potential climate change scenarios accept the basic tenets of 'Green House' warming arguments. Even though the analogy is imperfect, at best, it serves as a simple, if inappropriate, coded statement of a 'dread factor' and may thus stimulate research funding.

The importance of long-term climate records, and careful integration of ecological responses is well recognized by geologists (Soutar and Isaacs, 1969, 1974; Soutar and Crill, 1977; Anderson, 1989; Baumgartner *et al.*, 1989) and many enlightened geophysicists. These long term data sets are keys to understanding climate change, and credible forecasting.

For example, Figure 1 provides proxy indications of decadal and longer scale production of two pelagic fish species within the Southern California Bight over the recent 2 000 years. Note particularly the long term decline in apparent fish production. This accompanies the long term decline in global temperatures since 9 000 years before present. Note also, the changes in apparent system production after about 1100 AD.

The Medieval Warming epoch (~850-1200 AD) and the Little Ice Age (~1450-1780 AD) provide examples of extremes in climate within the recent millennium. The fact that the Little Ice Age ended only about 1780 or so provides the backdrop for the warming trend over the recent two centuries. Note also in Figure 1, that there appears to be a correlation between the dates of the little Ice Age, and fish debris abundance in the Southern California Bight. The general cooling of the period was interrupted by warm periods, probably inducing changes in global thermal balances that induced changes in coastal winds, and short periods of localized production evidenced within the data set. Likewise, there were short periods in the preceding 'warm' period, during which cool epochs would have reversed these patterns, contributing to the lower production periods within that sequence.

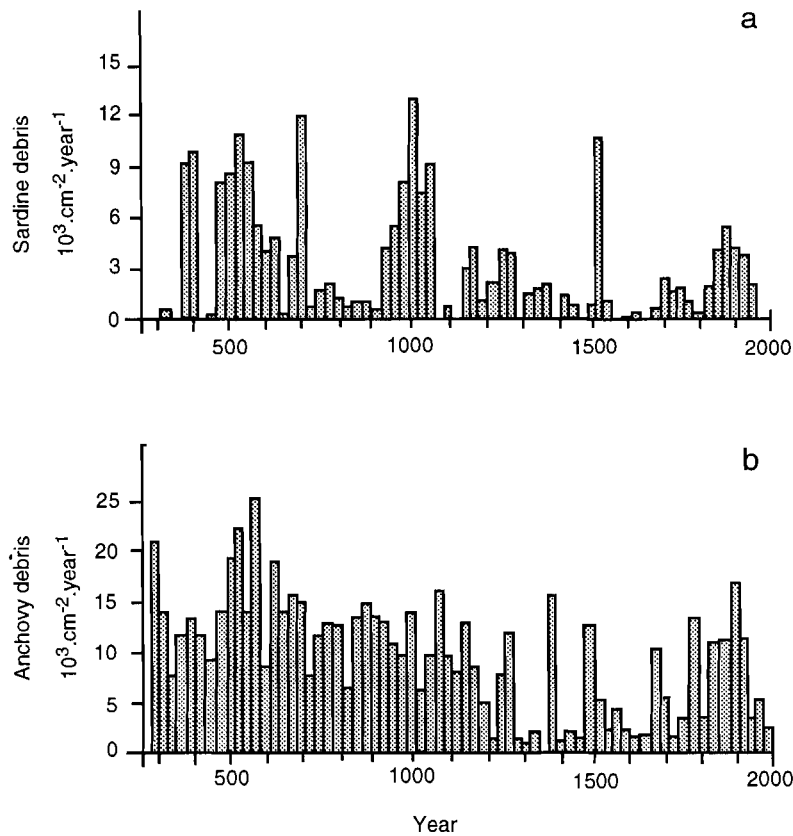


Fig. 1: The annual varve sediment records of the Santa Barbara Basin have been sorted and fish debris (e.g., scales, otoliths, hard parts) identified, and enumerated for contiguous segments for the recent two thousand year period (provided by Dr. Andrew Soutar, SIO, La Jolla, CA.). a) Pacific sardine ; b) Northern anchovy. These records have been the inspiration for much speculation about the periodic ebb and flow of pelagic species, and the climatic regimes that dominated each period. Similar records from dysaerobic sediments from Walvis Bay and from Peru record similar patterns of population responses to climate-driven ocean changes.

In fact, the greatest rate of warming during the recent two centuries occurred in the period from the 1920s through about 1940, accounting for 0.3°C of the 0.5°C temperature rise for the period around the globe. This is often touted as evidence for ‘anthropogenic Global Warming’. If anything, the northern hemisphere temperature was in decline from about 1945 until about 1972, at which time many changes were experienced around the globe (Sharp, 1992). Figure 2 shows example historical ocean records from the COADS. There has been relatively little global climate variation during the recent fifty year period, particularly considering the concerns about increasing positive biases over the period as the anemometer has been phased into use.

Climate change is the most dependable paradigm that we have. The issue is in response to what, and on what time and space scales? My colleagues in the paleoclimate research fields have little doubt that normal, natural climate variations occur well within a few decades, and over major geographic regions. The major forcing appears to be exogenous, with frequent and obvious punctuations by volcanic events. The popular concerns about anthropogenic forcing causing ‘Global Warming’ may even be misplaced given that we are nine thousand years into the next Ice Age. Surveys of paleological, and anthropological evidence would suggest that the worst things that have happened to humanity occur during cool, dry periods, and within the few warm and wet decades following the termination of these cool periods. Human populations have been devastated by over-growths of pests in response to natural lower trophic level ecosystem blooms. This is a result of declines (natural or human-induced) of limiting predator species during lowered trophic flow-through periods. Considering the present distributions and abundances of humans, and of natural predators, perhaps it is time to rethink the issues. Fish and fisheries will respond to climate change, as always, but the more important issues are related to reduced biodiversity.

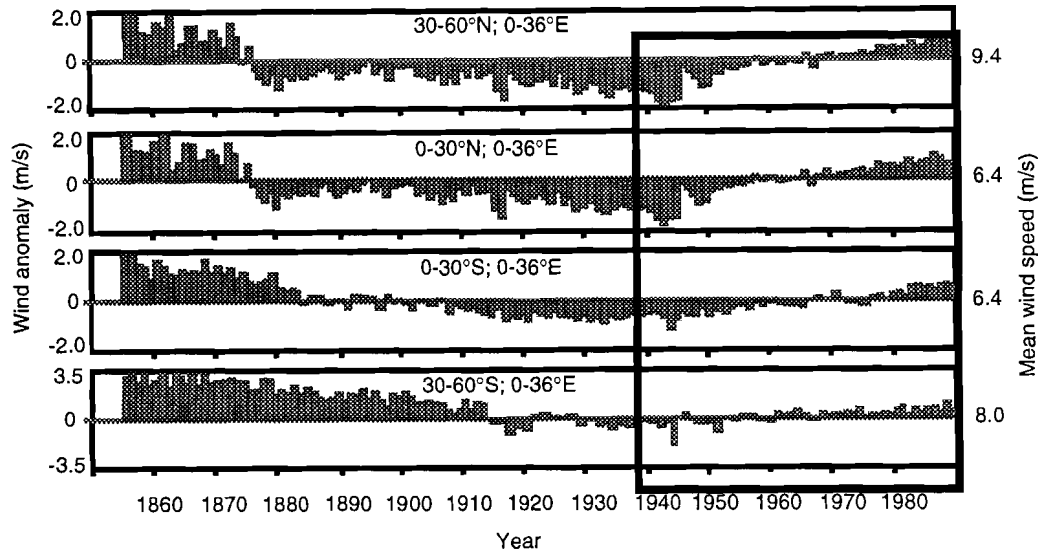


Fig. 2: The winter season scalar surface wind speed departures from the long term mean, from the COADS are portrayed for four 30 degree latitude swaths around the globe. The instrumental period is outlined by the box. The trends within the four examples are similar to the one that Bakun (1990) found in his upwelling index data, as expected. There are, however, some very notable patterns that this series of graphics show us. First is that the northern latitudes tend to lead the changes in the more southerly latitudes, which likely indicates the relative sea surface to land surface ratios. Second, the long term patterns of change are far more extreme than anything that has been observed during the recent five decades of the instrumental period.

2. PHYSIOLOGICAL RESPONSE PATTERNS AND NATURAL VARIATION OF CONTEXT

The following examples of known response patterns are presented only to rekindle the flame of several generations of careful experimentalists, so that CEOS might benefit from the insights of these, and thereby prove to be not only more credible, but more explicit about what causes the empirical relationships reported e.g. in this CEOS volume. These are principally behaviorally based, physiological and ecological responses, not mere mathematical 'truths'.

Ambient temperature is a primary variable in physiological ecology, particularly for poikilotherms. **Respiration rate**, as a measure of energy throughput, is the common currency of physiological studies. **Growth** is the record of success, and **reproduction** is the adult's reward for having at least survived the first course. The array of complexities and options that are exhibited by participants in this ecological game of life are myriad, yet there are generalities and principles by which the

game is played. Most of these are simple confirmations of the well known Laws of Thermodynamics. Others include unique genetic adaptations for coping with local habitat variabilities. These local variations are the important variables, each of which has certain limitations, hence constraints of context within which individuals within species must operate, or die.

Although a great amount of attention is given to mortality in aquatic resources research, there are insufficient documented records of when, where, which, and how individuals die. What we have, instead, are most often limited life tables, in which frequency distributions of size classes from samples collected after a fish takes a hook or is caught by net, and are then sorted into presumed age bins that are the bases for Life Table-based interpretations. Edward Deevey (1947) provided remarkably clear insights into the requirements for interpreting Life Tables, as he defined and introduced them. The missing key for the Life Table approach is a fast, automated technology that can age, credibly, any fish that is sampled. A representative sampling scheme then needs to be devised for each category of fish, and applied. Too much of present aging technique is poorly validated, and fraught with errors.

Another common-problem-solution in historical stock size estimation procedures has been the application of 'constant' mortality parameter (M). Vetter (1988) examined consequences of fishery-related mortality estimation procedures, and refutes the common assumption of constant mortalities, no matter where or how applied. This is particularly problematic in early life history stages of aquatic species, as their daily progress through size classes within any trophic pyramid can vary remarkably, with the issue being a simple binary situation in which they are either encountered by a predator, and eaten, or not. Which predator is encountered may not be consequential. Moreover, in coastal upwelling environments, where a single species can be overwhelmingly dominant, cannibalism may turn out to be a significant density dependent action (MacCall, 1990).

Another significant issue in the predator-prey relationships is the ecological efficiency of each predator, and how the consumed prey's energy resources are eventually distributed within the trophic web. One obvious, but often ignored direct consequence of temperature structure, whether horizontal, vertical, or in time, is the overall decline in ecological efficiencies as temperature increases, hence the decrease in resulting standing biomass at each higher trophic step with temperatures rise. The general response of aquatic ecosystems to warming perturbations is to speed throughput of energy, the expenditure of larger portions of that throughput on respiration, rather than growth and reproduction. Cooling causes the converse response.

There are also major consequences regarding both egg production in quantity, and quality. This issue is complex because the actual onset of gonadal maturation involves the mobilization of lipid stores from the somatic tissues, and their redeposition in the ovaries. The subsequent dissipation of this energy at each spawning event is important, too. Seasonal changes in somatic fat content and reproductive cycles are therefore inversely related. While less energy is stored at higher temperatures, and adult sizes are smaller due to hormetic effects, there is also a diminution of the size and numbers of eggs, although since onset of reproduction occurs earlier, at smaller size, there are often many more eggs produced. These issues are rarely fully resolved in present day stock models. Delivery of even these lesser quality, yet more abundant eggs into a recently warmed (e.g., ENSO-event) recently productive environment (with fewer predators) would seem to be one short-term Darwinian Game Winner. This may be the least complex reason for some of the great abundance variations in upwelling environments.

I like to think of each fish as a two-system entity. The somatic fish, and the gonadal fish, each of which has its own imperatives. The prime imperative of the somatic fish is to grow, and deliver a well stocked gonad to a location where the gametes stand a high chance of encounter with an opposite sex gamete, and where the fertilized eggs have some probability of hatching out into an environment where appropriate larval food will be available. The means by which each

gonad goes about arriving 'there', to reproduce, is the key to understanding both species diversity, ecosystems, and environmental dynamics.

The prime imperative of the gonadal fish is to deliver healthy gametes, well stocked to support early development in an uncertain, but often carefully selected environment. This can be anywhere within a fairly vast gradient system. Both the somatic fish and the gonadal 'symbiont' are preprogrammed to carry out their respective roles, but the gonadal imperative dominates the somatic needs after a developmental stage set by whole organism respiration processes (Pauly, 1984).

In many text books, it is presumed in the balance of energetic equations leading to energy for maturation of gonads that only energy in excess of a preprogrammed growth pattern is available. For fish, it is more realistic to describe the gonadal energetics as a complex forcing function that defines somatic growth potentials, where somatic growth is supported only up to some critical relative ratios of food intake, respiration rate, and a related apportionment between growth and somatic fat storage. Once a set of hierarchic physiological response criteria are met, and the soma begins to lose ground with respect to energy stores and respiratory demand, the gonadal imperative kicks in, and a series of hormonal signals are sent, mobilizing the somatic energy, and enhancing the gamete development and maturation system. That point in time is irreversible, and sets the parameters for remainder of the somatic fish growth. These are species specific, and plastic, as a function of individual experience. We call that plasticity adaptability, within the species' scope.

Life history strategies and somatic properties of individual species are harshly selected by their environment, in its broadest context. As long as the parent can sustain a positive energy balance that restores energy (primarily in the form of lipid), then a fish can spawn repeatedly, as per Hunter and Goldberg (1980). Sardines, anchovies and many scombrid fishes have been proven to spawn iteratively. Spawning potential is spread over a much larger area, and time, to enhance the likelihoods of survival of a next generation of gonads. Individuals can start the cycle at any time during the year. This also suggests a distinctly different approach to interpretations of year classes as compared to seasonal or 'event' spawners such as salmonids, herrings or osmerids.

Sar tander *et al.* (1983) provide estimates of reproduction of *Engraulis species* for the Peruvian and South African systems, respectively. Parrish *et al.* (1986) describe the changes in interannual growth, spawning and related reproductive parameters for northern anchovy off California. Pauly and Palomares (1989) estimate mortality from several predators species and the fishery mortality separately for the Peruvian fishery from 1953 to 1982, and also show seasonal and interannual growth vary considerably. The interpretations in these studies put to rest any myth of constant M, or the simplistic concept of fecundity for iteroparous species.

Spawning activity of pelagic fishes is usually a function of food availability and temperatures across the habitat. Spawning is induced in response to the physiological stresses associated with temperature induced increases in respiration rates. Overall, warming temperatures decrease ecological efficiencies across the biomass spectrum, resulting in higher turnover rates, and smaller individuals overall, although numbers of individuals may be larger (cf. Ulanowicz 1986, regarding his definition of system ascendancy). Even though primary production may actually be relatively high, the biomass can become sequestered in many more, but smaller individuals, and more energy dissipated due to their inherently higher respiration rates. Given a strong primary production basis, and that growth rates may be significantly enhanced, onset of reproduction is induced at smaller sizes, and younger ages, again resulting in lower ultimate sizes, as per Pauly (1984). Ambient cooling has opposite effects.

The concepts of hormesis, the enhancement of physiological performance due to environmental stress (Stebbing, 1981, 1982; Stebbing and Heath, 1984), provides insights into both the apparent increased growth rates, changing efficiencies, and the subsequent early onset of reproduction, as a stress induced consequence.

Once any individual from any species has been 'switched' over from somatic growth to gonadal development, there are dramatic irreversible changes in the handling of lipids storage, and the gonad is favored at any time physiological stress is encountered. This is a readily interpreted, and general evolutionary imperative that ensures that species will invest available energy optimally into reproduction, rather than continued growth in threatening environmental conditions.

The massive spawnings and decreased physiological condition of anchovies (or other species) during warm ENSO events is the confirming 'symptom' of this common set of processes. The continued growth, and later maturity of individuals during cool ENSO events, or at the cooler ends of habitat gradients is also well known, indicating the opposite consequences of lower ambient temperatures. There are other implications of this behavior. Table 1 provides the generic responses by most biological systems to shifting environmental temperatures.

Observed/Expected developmental patterns for most aquatic species (and many others) tend toward the following scenarios in response to temperature patterns and contexts:

- A. Ambient mid-thermal range; typical seasonal climate; low competition for resources. This is the 'usual' local pattern, where the seasonal cycle dominates the development, reproduction, and emergence of sequential generations of each species. Although often mistakenly labeled 'average' conditions, these are neither optimal for the individual species, nor all that common in nature due to the continuum of climate variability. In pelagic contexts, 'average conditions' are usually least likely to occur.
- B. Ambient cool end of thermal range of species; typical seasonal climate; low competition for resources. This is one extreme of the 'optimal' situation for most populations, in that this pattern promotes slow but continuous growth, to very large size, and late reproduction. Gametes from these populations tend to be optimized, in quality and numbers per individual, for survival through periods of relative deprivation, hence more young tend to survive to older stages and ages, for larger subsequent generations. This condition characterizes growth phases for many pelagic populations.
- C. Ambient upper thermal range of species; typical seasonal patterns, usual rates of competition for resources. This is the upper extreme of the 'optimal' situation for most populations. Although rapid growth is characteristic, early onset of reproduction due to physiological stress limits the adults to small size. Most of the energy consumed goes toward respiration. Reproduction rates tend to be highest, although gamete quality and survival rates tend to be low. Depending mostly upon predator abundances and food availability, this can be either a bloom, or bust period for a population.
- D. 'Hot House' ambient, in which all life history stages are enhanced by increased energy throughput. Reproduction is early, and life span often shortened, or compacted such that several 'cycles' can be induced within the usual seasonal cycle. This is the ENSO warm event analogy, in which many individuals are in physiological stress, growth rates are inhibited or even reversed, and 'reproductive imperative' is induced, in which all somatic energy is shunted to the gonads for a last effort toward the production of another generation.

Table 1: Generic individual, population and ecosystem responses to changes in ambient thermal patterns.

3. NEW APPROACHES TO OLD FISHERIES QUESTIONS

Elbert H. Ahlstrom (1943, 1959, 1966) and David K. Arthur (1956, 1976) were pioneers in the field of early life stage identification and feeding requirements and paved the road for all that followed. The California Cooperative Fisheries Research Program (CalCOFI, Anon., 1950) was initiated to study the declining California sardine fishery issues through the combined efforts of many, but O. Sette (1960) was the true believer, and genuine hero of this long, ongoing study of ecosystem dynamics in response to physical forcing.

I would like to pay my respects to several other strong individual contributors in the recent decades whose efforts brought to the marine resource sciences a modicum of field-testable hypotheses. More importantly, they all emphasized the concept that there is no single dominant factor that will explain day-to-day, or year-to-year population variability. This fact is too often ignored by recruitment researchers whose studies encompass small variable sets.

First will be J.H.S. Blaxter, for rekindling the interests in laboratory studies of early life history survival requirements (Blaxter, 1965). Underlying much of the progress in La Jolla at the Southwest Fisheries Center during the late 1960s and 1970s was the series of fish energetic studies by Lasker *et al.*, (1970), and John Hunter (1972, 1976). Hunter, along with a steady stream of students whose tenures in the all-important fish rearing facility of the Southwest Fisheries Center, produced many insights (Hunter and Thomas, 1974), made this 'Golden Age' of fishery research possible.

There is at least one unsung hero in this entire venture, Roger Leong, whose incredible dedication to the smooth functioning of the fish rearing facilities can only be termed 'legendary'. Leong's knowledge of fish, nutrition, and sea water systems grew with his experience (Leong and O'Connell, 1969). Over the years, his seven day, twenty four hour vigilance was renown. The numbers of manuscripts and thesis research projects that only could have occurred with his support is certainly notable.

Beyond fish rearing, the introduction of reading daily otolith marks for very small fishes opened the door for great progress in the interpretation of growth for at-sea sampling studies. The rediscovery of iteroparity, and daily aging were the keystones for the eventual emergence of the egg production method for estimation of spawning stock abundance (Hunter and Goldberg, 1980). Aging and staging of early life history stages of anchovy, along with Charles O'Connell's histological studies of the consequences of nutritional state (O'Connell and Raymond, 1970; O'Connell, 1976), in turn, stimulated more rigor in the interpretation of at-sea samples of first feeding anchovy larvae in regard to starvation induced mortality rather than simple predation.

In the background of these programs has been a continuous need for clever means for sampling the dynamic ocean and planktonic patterns. Again, Paul Smith, whose passion for obtaining answers to challenging questions about the ocean and its inhabitants, has provided research tools, means and logic for rigorous at-sea sampling (Smith and Lasker, 1978). Earlier, under the combined influences of Lasker and Smith, William Vlymen (1974, 1977) introduced a series of approaches and estimation procedures based on hydrodynamic principles that account for combined feeding energetics and swimming costs, which remain benchmarks in the integration of empirical fish behavioral studies and physical sciences.

By the mid 1970s Reuben Lasker and Gail Theilacker had emerged as the champions of at-sea bioassays of feeding stimuli, and along with enhanced methods for assaying nutritional status of anchovy, providing the bases for the Lasker Starvation Hypothesis. Lasker's Starvation Hypothesis at once stimulated great debate across the larger fish recruitment research community (Lasker, 1975, 1978, 1988). Lasker and Zweifel (1978) summarized an enormous effort to standardize treatments, and tried valiantly to cope with descriptions of results of many of these diverse experiments.

During this same period, Jan Beyer, a systems engineer, began his synthetic studies of the progression of early life history stages of fish, from first feeding on to their ultimate recruitment into fisheries, identifying the critical processes from the perspective of individual fish larvae (Beyer, 1976a, 1976b, 1981). Beyer was invited to give a lecture series at the University of Washington in 1977, and lectures at La Jolla, which emerged as Aquatic Ecosystems - An operational research approach (Beyer, 1981). This was another benchmark idea: a population is comprised of individuals.

Sharp (1981) brought together theorists and field scientists to discuss the dynamics of climate-forced upper ocean mixing, on a local to regional scales to debate not only the relative importance of Lasker's Starvation Hypothesis, but to also help identify unifying concepts in an effort help organize global fish recruitment research into focal topics about natural limiting factors. We could not but wonder at the problems of comparing larval fish rearing studies (Theilacker and Dorsey, 1981), given the usual near absence of contextual information provided, or measured by each investigator. Owen (1981) pointed out that the ocean is dynamically structured on several time and space scales, suggesting that understanding each scale is limited to matching appropriate structures with appropriate population questions.

In one sense, this seminal 1980 meeting gave root to the ongoing CEOS approach, as Bakun *et al.* (1981) described the similarities of the pelagic fish faunas of the major upwelling systems, within the contexts of the recruitment questions. These and several follow-up discussions led to further exploration and the eventual synthesis of conclusions from then recent recruitment research and environmental processes, as understood by Bakun *et al.* (1981), from which others took direction. The IOC Sardine, and Anchovy Recruitment Program (SARP) was born.

Just as quickly, SARP died a bureaucratic death, as a result of funding crises induced by new U.S. legislation mandates to fund a more complex fisheries management structure, including a series of regional Fisheries Management Councils. The Councils simply used up all available discretionary and most research funds of NOAA's National Marine Fisheries Service. This was the beginning of the end of the CalCOFI program as well. In fact, it was the beginning of the collapse of rational fisheries management in the USA, as politics overwhelmed facts, and general fishery data collection declined, leaving more room for legal debate than for research.

The issues of larval fish starvation and other empirical information relevant to Lasker's Starvation Hypothesis are described in two seminal studies that prove that early stage larval fish starvation related to low phytoplankton densities does occur in nature, with some samples comprising up to 65% starving larvae (Theilacker, 1986) To address the parallel issues of predation on fish larvae, Theilacker *et al.* (1993) have developed an immune-assay technique for identifying stomach contents at micro-scale on organisms ranging from euphausiids to fish.

Tools and relevant questions abound, yet funding for applied fisheries research has simply evaporated in recent years, as the substitution of empirical information via mathematical modeling and assumptions about how various factors are related has been adopted in fisheries management strategies. Clearly, this has been quite unsuccessful; for reasons I and others have discussed elsewhere (Walters and Collie, 1988; Cury and Roy, 1989; Cury *et al.*, 1995; FAO, 1992; Hilborn, 1992; Sharp, 1988, 1992; Vetter, 1988.)

Another critical component of present day understanding was the early development and sitting of the Pacific (Fisheries) Environmental Group by James Johnson and other supporters, providing a means for accessing global environmental data for fishery applications. Also in the late 1960s, Joseph Fletcher, and his colleagues at the University of Colorado began collating the Comprehensive Ocean and Atmosphere Data Set (COADS), which forms the nucleus for the present stage in CEOS research. Records of physical and ecological variabilities of the habitats over time, and the consequential patterns of variation of species distributions and abundances provide the bases for defining the causalities, and provides the most hope for development of predictive capabilities. Were it not for many of these people, we would likely not have ever gotten to CEOS.

The issue is loss of contextual information, and direct knowledge of fishing activities in response to short and long-term environmental processes.

4. CONTEXT, CONTEXT, CONTEXT!

There have been seminal works on the short- and long-term consequences of climatic processes, weather events, and their fisheries manifestations, (Uda, 1927, 1957; Hela and Laevastu, 1971; Southward, 1974a, 1974b; Southward *et al.*, 1975; Parrish and MacCall, 1978; Sharp, 1978, 1979; Pauly and Navaluna, 1983; Cushing, 1969; Parrish *et al.*, 1983; Rose and Leggett, 1988). However, the problem of identification of connecting mechanisms at all time and space scales remains a major task. There has since been general acceptance of the importance of environmental forcing in fisheries analyses. Although hypotheses abound, data sets are rare.

Cury and Roy (1989), and Cury *et al.* (1995) provided a new set of analytical tools, to work with available environmental and recruitment time series. Their 'discovery' that 'moderate is good' is in complete agreement with what physiological ecologists such as Priede (1977), and many others have been saying for years, from studies of individual fish in the laboratory, or in nature. The trick is to sort the causal properties from the correlates.

Surely, wind speed and direction are important driving variables in local contexts, although the fish are safely sequestered from their immediate, direct influence. On the other hand, the upper ocean is quite responsive, and a suite of processes ensues as wind speeds change, persist, or shift in direction over time. All of the known secondary responses have direct influence on the physiology, and the behaviors of affected fishes.

These local wind-driven consequences include:

- 1) upwelling of cool, often poorly oxygenated water;
- 2) advection; convergence and associated downwelling;
- 3) long-shore or other structured current changes that affect individuals on a short-term, diel basis.

Regional consequences include:

- 1) production shifts;
- 2) predator displacements, and changes in locale due to shifting production patterns;
- 3) blooms and declines of entire fauna assemblages on event scales, e.g. warm events El Niño, or cool events; and
- 4) ecosystem responses on seasonal population reproduction time scales.

At regional to ocean basin scales, we have many examples of climate related fisheries variation collated from fisheries literature, and these are discussed within various forums. In spite of the general agreement of the importance of climate, the subject remains poorly incorporated into resource management strategies. The necessary steps have been documented by Csirke and Sharp (1983), and more recently the U.S. National Academy of Science (Ocean Studies Board, 1994) has encouraged their incorporation. Until there are retirements within the management systems, little progress is likely. The issue at hand is that of converting a series of empirical relations into a set of causal relations, a task no less daunting than explaining any other statistical relations. The advantage that CEOS provides is its basis for comparative studies of several distinctly different physical systems, that provide contexts for the requirements of a common species composition, namely *Sardinops*, *Engraulis*, *Scomber*, *Trachurus*, *Sarda*, and *Merluccius species* (Bakun *et al.*, 1981).

5. CLIMATE CHANGE, SEA SURFACE TEMPERATURE, WIND SPEED AND DIRECTION: SO WHAT?

Moser *et al.* (1987), and Smith and Moser (1988) from CalCOFI data and showed that during the 1951-1960 period of known climatic transition there were distinct fauna shifts, amongst all species, not just the commercially important ones. There are several lessons from the recent decade that need to be integrated into the general picture of comparative studies. Among these are the basic hints from the long coastline including Ecuador, Peru, and northern Chile, from Chiloe in the south, to perhaps the Gulf of Guayaquil in the north. The observations for each region have been kept separately, and only on occasion treated as a whole. IFOP (1985) documents the fauna responses to the 1982-83 ENSO warm event along the Chilean coastline. Also, on greater spatial and temporal scales, Avaria (1985), showed that the fish production center moved from southern Peru into northern Chile as the anchoveta collapsed onshore into coastal refuge, and sardines moved onshore and southward in response to the larger system changes. Similarly, to the south in central Chile, a small sprat, *Strongomera bentickei*, locally called sardina comun, collapsed from its northerly extension from about Valparaiso, southward along the coast into Bahia Concepción, the Rio Bio Bio outlet.

Loeb and Rojas (1988), in a compelling study, examined the ichthyoplankton samples collected along Chile and found that during the late 1960s, it was not merely a north to south collapse of habitat, but a general decline occurred in coastal upwelling-associated fishes, distributions changed, and an increase occurred in abundance for an oceanic fauna assemblage, including sardines.

The key point in both these studies was the fact that the anchoveta did not change its distribution during the entire period of fauna changes. Anchoveta merely collapsed into coastal refuge, which are indicated along the west coast of South America by coastal promontories with northward facing bays, or substantive embayments such as the Gulf of Arauco, Coquimbo, or Iquique. The common denominator was an upstream gyre that forms whenever there is substantive northward, along shore water motion, inducing upwelling and primary production. Because this coastline is over 2 400 nm in length, and there are so many distinctive forcing patterns as a function of the El Niño-Southern Oscillation and shorter seasonal patterns, this coastline provides several dozen independent production centers, some of which happen to provide opportunities for fishing ports and fish processing facilities.

The entire coastal upwelling region of South America has actually never been exposed to simultaneous fishing pressure, and, in fact, what one can discern from the anchoveta and sardine catch patterns is that travel beyond a sailing day from any processing port was very rare, simply because these vessels were not refrigerated. The impact of offshore movements of the sardines during the recent decade has not been fully appreciated, although the similar, but even grander scale distribution of the jack mackerel, *Trachurus murphyi*, (Serra, this vol.) has recently caused a stir amongst entrepreneurs who wished that there were some economical means to capitalize on the recent bloom of that population into the offshore waters, and along the west wind drift into the Tasman Sea (Keith Sainsbury, pers. comm.).

As one means of stratifying fishing records to compare with environmental records, the South American coast provides a near-linear north-south latitudinal gradient, without the added burden of a series of major surface temperature gradients. On the other hand, the absence of fishing over the entire onshore-offshore gradient, or at distances far beyond about a 150 nm radius from each processing port can cause some distortions of the historical catch signals, as the seasonal and epochal changes perturb the centers of production, and the areas where fish graze. As the Chilean sardine fishery

collapsed in recent years, distances traveled offshore and away from ports increased, but not dramatically until recently, as refrigerated holds have been adopted.

Similar concern can be voiced for the California coast, particularly north of Ensenada, where there is significant SST gradiental variation, and a complicating series of topographic forcing features. The contrast between the Gulf of California, and the Pacific coast of the California is, again, a complex issue, in that there is strong seasonal forcing from the tropical ocean within the Gulf of Mexico, that manifests quite differently north of Cabo Colnett, Baja California. The complex hydrography of the Gulf of California can confound simplistic evaluations, as the variances of combined tidal forcing and wind events on a daily basis can be as great as anywhere in the world, and needs to be dealt with in a careful fashion (Hunter and Sharp, 1983).

The 'sea breezes' that characterize the Mediterranean coastlines of eastern boundary current systems — with their deserts and dunes — induce upwelling, and summer stratus clouds over much of the coastal pelagic habitat. Oceanographic studies suggest the general nature of upper-ocean forcing in response to low cloud cover. Among the relevant probable consequences of clear-sky induced upper ocean mixing for species that require plankton concentrations for survival is the question of the role of stratus clouds and fogs on nocturnal upper ocean mixing that is normal under clear sky conditions. Alternatives discussed by Sharp (1981), along with the Lasker Hypothesis, suggest that larval anchovies in eastern boundary currents would more likely encounter phytoplankton concentrations in seasons when stratus clouds prevail because the clouds would suppress cooling associated with night time long-wave back radiation, and its consequent upper ocean mixing. It will also be interesting to study the seasonal spawning successes of these fishes as a function of cloud cover, cloud type, and fog, where records have been routinely collected. One suspects that this would presently only be possible in regions where major airports exist near the coastal regions. However, airports are only rarely sited in such regions because of the consequences of low clouds and fog.

The issues of which specific variables are important at various spatial scales, and when, cannot be ignored. The affects of cloud cover, and type, on night-time back radiation, and nocturnal upper ocean turbulence processes are at least as relevant as wind-driven turbulence. It is not a moot point that cloud cover patterns are related to wind speed and direction.

6. TURBULENCE, FOOD ENCOUNTER RATES AND OPTIMAL ENVIRONMENTAL WINDOWS

MacKenzie and Leggett (1991, 1993) and MacKenzie *et al.* (1990) provide discussions and reviews of the microturbulence related to feeding of relatively immobile larval fishes, pointing out that feeding rates are enhanced as wind speeds increase from low speeds (i.e., 2 ms^{-1}) to higher speeds (i.e., 6 ms^{-1}), until 'storm' level winds of 10 ms^{-1} , or more cause the entire upper water column to homogenize. This is consistent with the Optimal Environmental Window concept of Cury and Roy (1989). It was not clear, except perhaps for mathematical convenience, why the examples MacKenzie and Leggett (1991) started from a homogeneous, but low density of food organisms, unless their point was to show that fish larvae would somehow benefit from enhanced turbulence at lower food densities. However, the important dynamics of feeding patterns, strike rates and other behaviors (Vlymen, 1977) got put aside, simply because of the problem of not having empirical data.

The scenario that I and others have envisioned over the last decades is that during low wind mixing, the plankters serving as larval fish feed tended to aggregate, and if larval fishes were naturally programmed to move up and down vertically, then they would have a far greater chance of encountering high enough densities to stimulate feeding responses (Hunter, 1972; Lasker, 1975). Coming out of a well-mixed situation, such as following a storm event, there is a natural resetting of the system to one of aggregations, or new colonies of prey species as a general response to the mixing of new nutrients into the upper ocean, hence new production, and new feeding opportunities. At issue is not that these mixing events occur, but whether their effects last long enough to cause significant starvation mortality. That starving larvae have been observed in nature is not irrelevant. Nor is the fact that many other larval fish species have not yet been observed in this state.

Although I also follow the argument that microturbulence can give increased encounter rates, my own mental image is one of having not only more targets appear per unit time, but that the targets would be moving at considerably faster relative speeds, hence there would be an increasing requirement for the larvae to sight these moving prey, respond, and react appropriately.

The difference between these several scenarios is perhaps best explained by analogy. In one case, a hungry individual finds a density of food stuff, lets say a vegetable market, where it is possible to identify large, esculent clusters, and stay in one place to feed in a leisurely fashion. In a second set of scenarios, the market is gone, and the individual is now on a continuously moving escalator, and some lesser proportion of all the individual food items are being slowly or maybe not so slowly tossed near enough to be identified, and snatched one at a time, if one is vigilant. Now increase the speed of the escalator, and the frequency of encounters to a point where the effort required to feed exceeds the value of the encountered food stuff, and we have another extreme of the myriad possibilities. Too little and too much can also define these limits (Priede, 1977; Cury *et al.*, 1995).

The problem, as I see it, is where in the spectrum that the energy balance becomes negative, or worse, where does either perception or response time fail to serve the larvae? First feeding fish larvae in particular are relatively naive. Hunter (1972) and Hunter and Thomas (1974) described fairly complex sequences of behaviors for *Engaulis mordax* that would not be well suited to a very rapid increase of relative contrary motions between predator and prey, given the timing that was necessary for each particle to be within the field of view, for repositioning and coiling of the fish larva in response, and then to strike successfully. One must wonder at the consequences of not only changes in encounter rate but also the speeds at which these two-body interactions must occur. Once mobility and full sensory capabilities are developed, and sufficient learning by trial and error has occurred, a healthy larva should be able to successfully handle a broadening spectrum of turbulence, and related feeding encounters as they progress to larger sizes, and more complex behaviors.

7. COMPARISON AND CONTRAST OF ENVIRONMENTAL CONTEXTS: INFORMATION FOR WHOM?

Comparing and contrasting coastal dynamics has mostly been anecdotal, to date, and will remain anecdotal until there is a systematic development of an ocean-observing system. What to measure and monitor is certainly a primary question needing answers. Careful reasoning of where to place monitoring systems will also be required. At issue is which questions about what problems should be emphasized. The Sardine and Anchovy Recruitment Program (SARP) was an attempt to

organize the local scale sampling strategies that might provide answers about local, individual responses to environmental forcing, and subsequent survival. In their attempts to obtain insights, Leggett *et al.*, (1984) and colleagues have directed their efforts at local population responses, and bridged the scales to regional systems (Carscadden, 1983; Rose and Leggett, 1988; Carscadden *et al.*, 1989). These are important inquiries.

The CEOS comparative approach was initially designed to examine population responses to regional and subregional scales of local and regional mosaic populations. This is an integrated view, from available time series that were by necessity limited in scale, and representation due to data limitations. Because the example data sets tend to represent mostly only one bloom and recession cycle, there is the distinct possibility that the empirical relations that emerge from the CEOS analyses might be analogous to those described in Sharp and McLain (1993a) in which the data from a single cycle will not be coherent with similar previous, or subsequent cycles. The Stock-Recruitment 'loop' is a good example. Theory is not met as one observes that the declines in recruitment do not retrace the ascendant pathway(s). Kondo (1980), Kawasaki (1983), and Sharp (1981, 1987 and 1992), and Sharp and McLain (1993a, 1993b) have taken the larger view, in which systems and their decadal scale patterns of variation are examined to better understand the shorter time scale processes and events, nested within this larger context.

Clearly, combination of these approaches would be best, although not yet within grasp, primarily due to the differences in national resource management policies. Also, data limitations impose restrictions on both scientifically credible forecasting and hindcasts based on catch and effort statistics. Although the former is required for rational resource management, the latter is preferred because it is cheap, although mostly ineffective as more than providing post-mortem perspectives. The more integrated approaches are data-hungry, and presume constant monitoring of both the environment, and the fisheries. The environmental monitoring systems required are not in place. This is also a question of agency responsibilities, and national priorities.

Whether a global ocean observing system should focus on weather forecasting efforts, or climate issues, or natural resource and agricultural issues are not simple, readily resolved issues. A major insight into how to resolve these issues might be provided by the ocean resources managers and agricultural industries, by pointing out that beyond extreme events, there are more subtle variations that can have more economic impact, over longer term, than only a classic 'storm warning' system offers. More to the point, it is not only storms or El Niño events that need to be tracked, but the full spectrum of climate-driven ocean processes, until a full understanding is in hand, and a more appropriate monitoring scheme might be devised that will service natural resource management, as well as agricultural and urban societal needs.

By convention, fisheries have been treated as renewable resources. Due to the near economic collapse of many fisheries over the recent decades (FAO, 1992), these resources are only now being recognized as having the potential to shift to non-renewable status. One would think that the experience with whales, dodo birds, and forests would have sufficed to quell this governance 'Pollyanna' before now. Clearly, a renewed effort to reorganize resource management, and requisite monitoring is due.

A major issue to be overcome, and put within a 'food security' framework, is the dominance of recent climate observing system design for El Niño forecasting and climate change research. If these systems were set up to answer pragmatic management problems such as coastal ocean system dynamics within the global and ocean basin contexts, then we could be well on our way toward a rational fisheries and agriculture forecasting system.

As these climate and ocean monitoring programs are presently constituted, they provide little useful information to anyone except a few ocean modelers, who are principally involved in generating a credible 'event' forecast. They have as yet failed to clearly identify the 'event' in terms that anyone else might use.

Ocean model products of greatest direct utility such as changes in thermal structure and local turbulence dynamics could

be produced along with the SST and wind speed and direction data. The point here being that major changes in the focus of these environmental monitoring activities will be required before such pragmatic, global human food security issues will ever be made truly manageable.

8. AFTER A GOOD BEGINNING, WHERE TO NEXT?

CEOS has already begun a revolution by compiling in useful formats the COADS, for general access by researchers at their desk tops. The combined efforts of the CEOS network has focused on one of the largest single classes of foodstuff dynamics known, that of the world's coastal pelagic fisheries, and their epochal variations. It is moot that these several systems produce over twenty percent of the world's protein from the sea during their peak combined production periods. What is problematic is the periods when these production systems bottom out, and the important catches are no longer made.

Having done everything wrong, first, or too late when it was a right thing to do, California's sardine management story has provided grand examples of what not to do (Radovich, 1981; Ueber and MacCall, 1992). My own suggestion is that we take the responsibility to correct the distorted vision imposed by studying highly smoothed catch statistics and mean values from various measuring devices, by applying the half century of experimental observations on responses of aquatic species to known habitat changes during the next revision of the CEOS approach. Forecasting by analogy is the first order of business, now that at least one, and sometimes several cycles has occurred. The next obvious step is to apply what we already know about physiological ecology of organisms, and begin to integrate real-time environmental information into the forecast process. I am not so sure that ecosystem management is as difficult as some would like to suggest. Certainly it cannot be less protective than what has passed for fisheries management over recent decades.

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