Andrew Bakun

6. Definition of Environmental Variability Affecting Biological Processes in Large Marine Ecosystems

ABSTRACT

Attempts to relate variations in reproductive success of fish populations to variability in the environment or in the biological community have been generally unsuccessful. A variety of processes, varying widely over a broad range of time and space scales, is potentially involved. Continuous observational coverage over such a range is impossible. Under the circumstances, defining the crucial variations involved presents a challenging set of problems. A serious need exists to develop generalizations that might provide the basis for unifying the available fragments of experience in a usefully coherent framework so as to make optimal use of the few empirical data available in a given situation. Interregional comparative studies, systematic observations of vertical distributions of organisms, studies of within-year variability in survival, and use of time/space statistical techniques, are advocated.

INTRODUCTION

In terrestrial ecosystems, the atmosphere has little capacity to store heat and other properties, and most sources of materials, etc., are fixed to a nonmoving substrate. In contrast, marine ecosystems exist in a continually moving, nonhomogeneous, dense fluid which has a large capacity to store heat, materials, and momentum. As a result, marine ecosystems are characterized by long period, large amplitude variability. During recent decades, catastrophic declines of some of the world's largest fishery stocks have had severe human consequences. During 1983 the ecosystems of the eastern Pacific were experiencing the most intense environmental anomalies of the past half century; it is likely that transient responses associated with this "El Niño" event will continue to perturb these ecosystems for years to come. The present lack of understanding of the mechanisms governing the interaction of environmental variation and fishery exploitation in causing large fluctuations in "recruitment" (i.e., the numbers of younger fish entering a fished population) is recognized as perhaps the most serious scientific problem hindering more effective management of living marine resources. Discussion in this chapter focuses on examples from eastern boundary current pelagic fishery stocks, as being illustrative of research problems common to a variety of large marine ecosystems and associated biological communities.

THE DILEMMA

Demonstrating that change occurs in these environmental/biological systems is not difficult. But to qualitatively and quantitatively specify the changes in a way that can form a basis for empirical understanding of the linkages involved presents a challenging suite of problems. Since the number of fish surviving to adulthood may be four orders of magnitude lower than the initial number of newly hatched larvae, such eventual survival is quite a rare event for individuals. Thus spot sampling of small numbers of realizations of individual life cycle events would be unlikely to yield useful information about total recruitment of a particular stock unit, even if the stock were homogeneously distributed and survival processes were linear. In fact, nonlinear interactions which are highly variable over a broad range of time and space scales typify the growth and mortality processes of pre-recruit fishes and most other marine organisms. Thus the ability to identify particularly crucial environmental conditions and to properly integrate their effects over the reproductive region and season associated with a stock unit, so as to reflect the net effect on reproductive success, appears to be a prerequisite for effective empirical approaches to understanding biological variability in large marine ecosystems.

Crucial Time Scales

Certain time scales appear to be of particular interest. For example, Lasker (1978) has indicated that anchovy larval survival may be seriously impaired by dispersion of fine-scale strata of microorganisms, required for food of "first-feeding" larvae, by wind-related turbulent mixing. Assuming that the time for accumulation of such concentrated strata is longer than one day, the relevant temporal considerations involve the interaction of the several days required for larval starvation, atmospheric storm activity with periods of variation of the order of a day to several weeks (examples shown in Figure 6.1), and the temporal variation of spawning activity over the spawning season.

At somewhat longer time scales (several weeks to several months) a variety of mechanisms may have significant effects. These include advection to favorable or unfavorable habitat, match/mismatch of spawning peak with food or predator organisms, interaction of temperature or food-regulated growth rates with size-dependent predation, adult feeding conditions which may affect formation of reproductive products.

The annual periodicity tends to be very dominant (Figure 6.1c); even in equatorial regions seasonal monsoon effects may be important. Biological processes tend to be well tuned to the annually repeating environmental variations, such that anomalies from normal climatic conditions are likely causes of disruptions in reproductive success of endemic populations. The dominance of the characteristic annual cycle of variation (compared to anomalies from it) causes problems in empirical analysis. For one thing, the degrees of freedom in within-year series available for empirical analysis tend to be substantially reduced because of the difficulties involved in properly filtering the large annual signal. Perhaps even more crucial is the fact that responses by natural selection to the large seasonal variation have probably, in many cases, resulted in seasonal tuning of basic biological--environmental linkages, such that underlying relationships among variables may be highly non-stationary over the annual cycle. These difficulties have motivated the conventional practice of studying recruitment processes on the basis of annual composites of the shorter scale events which may be actually involved.

On interyear time scales, marine biological time series very often exhibit substantial variance in the 3- to 12-yr period band (e.g., Figure 6.2). This is a band corresponding to appropriate periods of variation for various oceanic and atmospheric phenomena including baroclinic Rossby waves (Mysak et al., 1982) and variations of the global coupled ocean/atmosphere system known as El Niño-Southern Oscillation (ENSO) events. Other classes of variations also occupy this band (e.g., sunspots, etc.) and are sometimes incorporated into empirical "models" of biological variation; this is a band where the available time series is generally too short to contain more than a very few realizations of such multiyear variations and particularly in cases where direct linkage mechanisms are not well defined, the likelihood of spurious relationships is high.

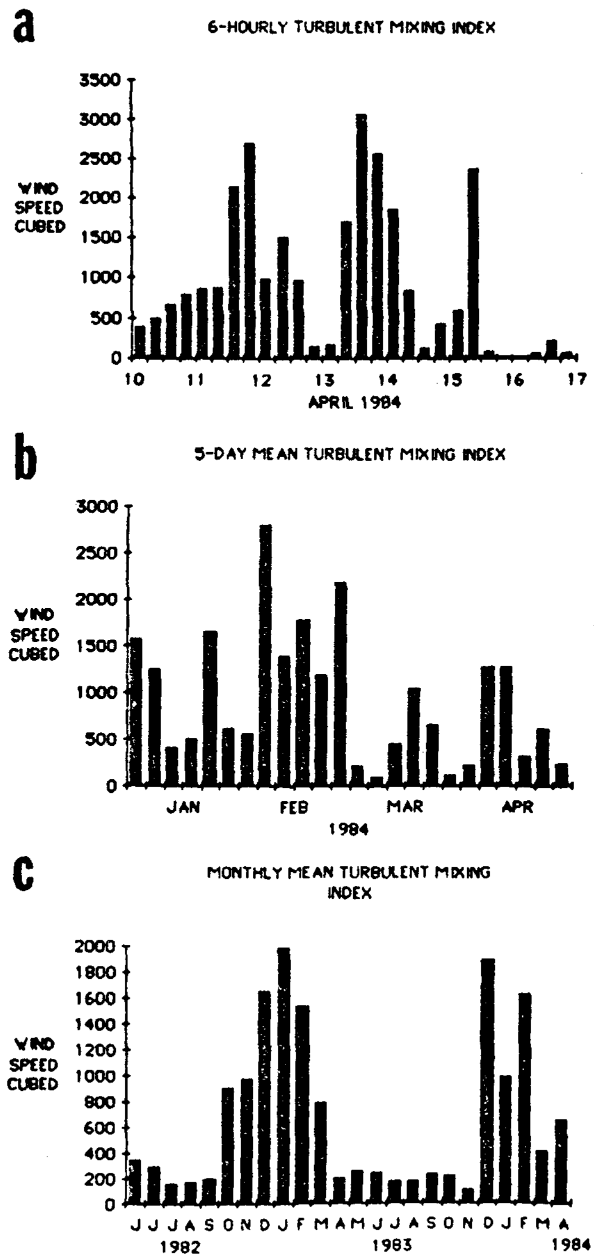

Figure 6.1. Index of rate of addition of turbulent mixing energy to the water column by the wind (e.g., Husby and Nelson, 1982). The index is computed as the third power (cube) of the speed of the large scale wind, as derived from synoptic surface pressure/wind analyses obtained from Fleet Numerical Oceanography Center. The location illustrated is off the coast of Washington State, at 48°N 125°W. Units are m^3sec^{-3}. (a) 6-hourly synoptic computations. (b) 5-day means of 6-hourly computations. (c) Monthly means.

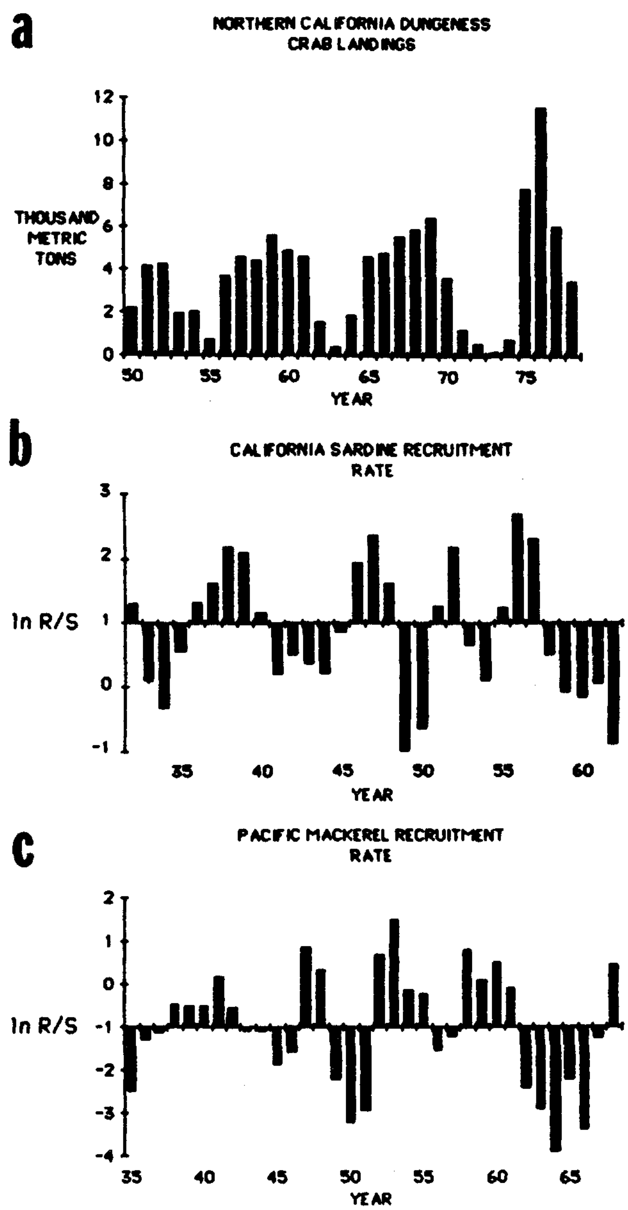

Figure 6.2. (a) Commercial fishery landings of dungeness crab in northern California (after Wild, 1983). Units are thousands of metric tons. Year indicated refers to the calendar year containing the end of a given annual fishing season. (b) Natural log of the ratio of California sardine recruits (10^6 fish) to parental biomass (10^3 metric tons). Values for 1947-1962 are based on the estimates of MacCall (1979). Values for 1932-1946 are based on the estimates of Murphy (1966). (c) Natural log of the ratio of Pacific mackerel recruit biomass to parental biomass (after Parrish and MacCall, 1978).

It is becoming apparent that there may be hierarchies of El Niño episodes, such that the events of 1957-1958 and 1982-1983 stand out as being global in character. These two episodes represent such extreme outliers in many California Current biological time series that they tend to control relationships based on "least square" fitting procedures. There is reason to believe that basic mechanisms underlying relationships among variables may be altered during these extreme episodes. Therefore, analysis of data from these particular years, together with data from the more normal years, may obscure any real relationships existing in either subset. The period between these two extreme episodes is 25 yr; this period is comparable to the total length of most pertinent data series from the California Current ecosystem. Deriving any substantial insight from an empirical analysis based on as little as two actual realizations is difficult, to say the least.

An even longer time scale may be highly pertinent to fishery management considerations. Smith (1978) has pointed out indications that the total biomass of pelagic fish stocks in the California Current system may have been as much as several times larger in the early part of this century than at the present time, or even than in the late 1930s when heavy exploitation commenced (Figure 6.3). This poses some important questions. Does the presence of large fish populations somehow increase the ability of the ecosystem to support the maintenance of these large populations? Do massive shifts in partitioning of basic organic production among exploitable and non-exploitable ecosystem components occur? Can management actions influence these shifts? Obviously, this is a time scale that we are not prepared to address experimentally and must rely on available "proxy" records, such as fish scale deposition rates (Soutar and Issacs, 1974) or guano deposits (e.g., Crawford et al., 1983), for empirical data analysis.

Crucial Space Scales

Lasker's hypothesis involves fine-scale vertical strata which may be centimeters or less in thickness. Crucial horizontal scales include spawning patch, food organism patch, juvenile school, small eddy, surface convergence zone, etc., diameters which may range from meters to kilometers (Smith, 1978; Owen, 1981). Offshore transport of reproductive products is thought to be an important regulator of reproductive success in eastern boundary systems (Parrish et al., 1983); pertinent offshore length scales are thought to include the internal Rossby radius of deformation (10-20 km off

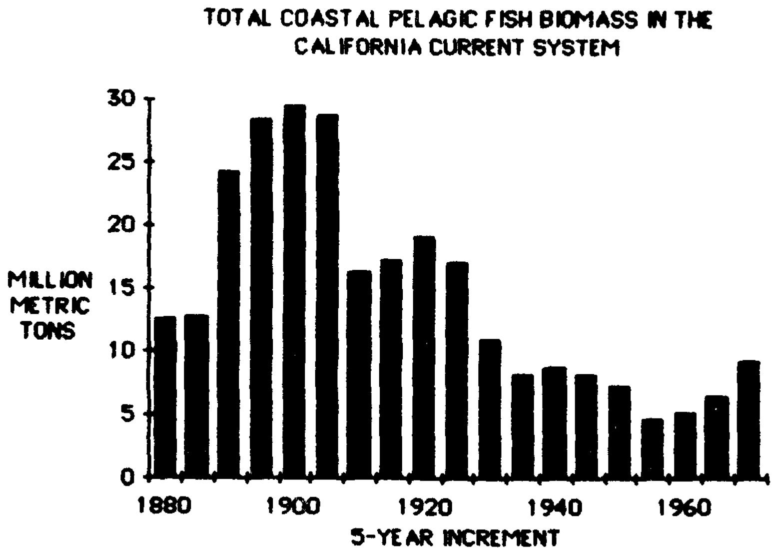

Figure 6.3. Biomass of the total coastal pelagic fish complex, consisting of sardine, anchovy, mackerel, saury and hake, in the California Current system at 5-yr increments, as inferred by Smith (1978) from analysis of present day stock sizes and from scale deposition rates determined by Soutar and Issacs (1974).

northern California, about four times greater in the anchoveta spawning region off northern Peru) and the width of the continental shelf (e.g., 20 km off n. California, 130 km off n. Peru). Major coastline features may delineate upwelling centers and coastal gyral circulations (length scales of tens to hundreds of kilometers). Spawning regions of coastal pelagic stocks may be of the order of a thousand kilometers in coast wise extent and several hundred kilometers in offshore extent. Larval drift and adult migrations may cover a thousand or more kilometers.

Environmental Data

Continuous observational coverage of such a range of time and space scales, using dedicated research ships, is not possible. One hope is to make use of routinely-gathered maritime weather reports which are available at 6-hourly synoptic intervals according to international convention. Historical files extend into the past century. Thus coverage is available over the range of desired time scales. However spatial resolution leaves much to be desired (Figure 6.4). Of some advantage is the fact that atmospheric length scales are large compared to oceanic length scales, and thus the major spatial scales of variation of wind, cloud cover (i.e., solar radiation input), etc., are at least minimally covered. Sea surface temperature varies relatively slowly compared to atmospheric properties and therefore observations from a number of synoptic samplings may be composited to improve coverage of finer-scale spatial features.

Fortunately, several currently-favored hypotheses concerning environmental regulation of reproductive success feature mechanisms involving wind, sea temperature, and solar radiation. In Lasker's (1978) hypothesis, wind-generated turbulent mixing energy is the causative factor. Wind-driven offshore surface transport, causing offshore loss of reproductive products (Parrish et al., 1983) is related to the product of the wind speed with its alongshore velocity component. On the other hand locally wind-induced coastal upwelling is driven by this same offshore surface transport which, therefore, may favor reproductive success at appropriate temporal and spatial lags by enhancing primary production and leading to adequate larval food particle concentrations, while being an unfavorable factor when coincident with spawning activity. Solar radiation also is involved in primary production, while sea temperature has direct effects on physiological rates; since larvae of many species inhabit the surface mixed layer, surface temperature often provides a useful indicator of

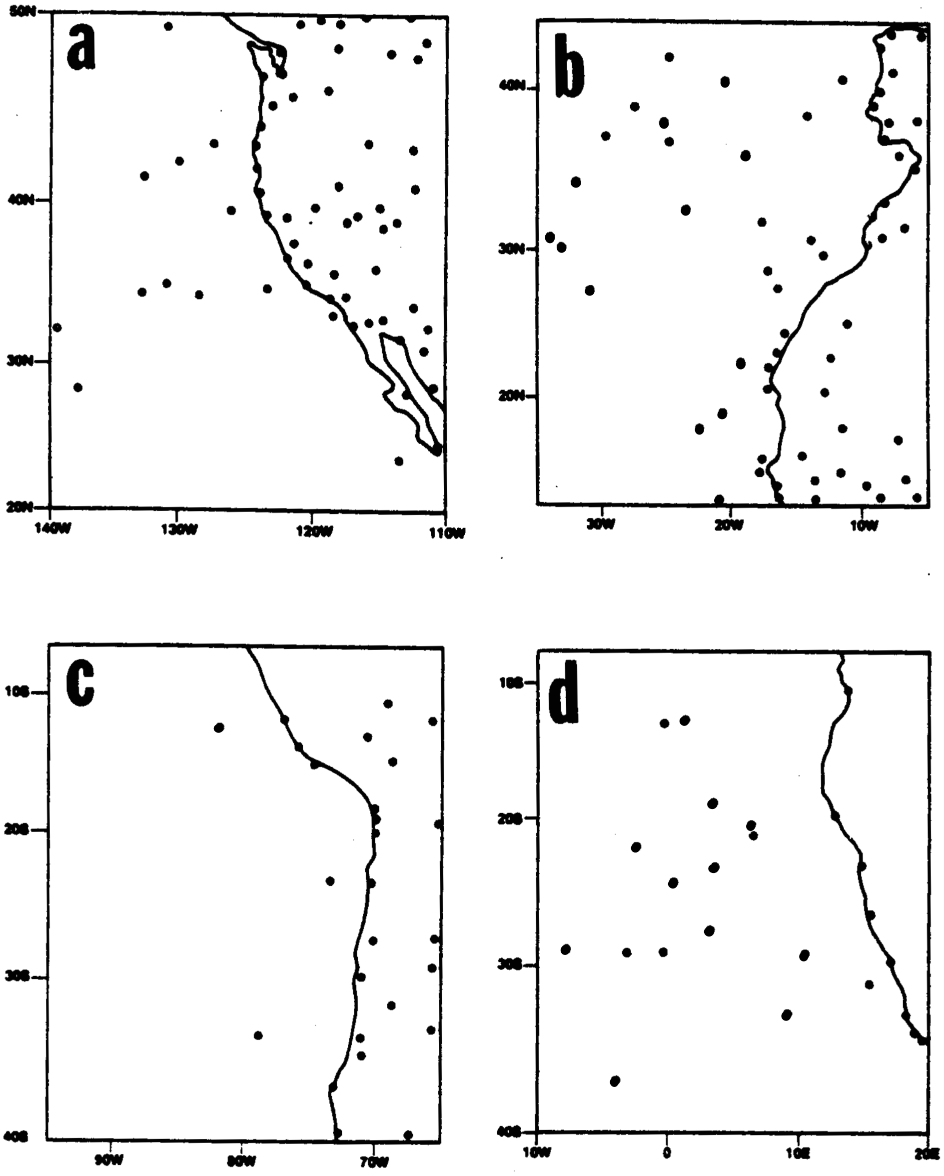

Figure 6.4. Typical synoptic report distributions in the four major eastern ocean boundary upwelling regions (after Bakun and Parrish, 1980). (a) The California Current region (distribution shown is for 0600 GMT, 11 Jan 1980). (b) The Canary Current region (0000 GMT, 12 Feb 1980). (c) The Peru Current region (1800 GMT, 7 Feb 1980). (d) The Benguela Current region (1800 GMT, 7 Feb 1980).

temperature effects. Wind stress curl drives upwelling and downwelling seaward of the coastal boundary zone, controls convergence and divergence in the surface Ekman layer, and through Ekman pumping is a primary driving agent for variations in the baroclinic structure of the upper ocean (which may subsequently propagate westward as Rossby waves of interannual time scale).

Precision of estimates based on summaries of scattered maritime reports is a matter of concern. Since our focus is generally on interyear variability, difficulty in perfectly filtering the strong annual cycle exacerbates the low signal-to-noise ratio problem. Comparisons of random subsamples from a ten-degree latitude/longitude quandrangle adjacent to a typical temperate eastern boundary coast (Bakun, in preparation) indicate that only the more extreme interyear variations may be definable by simple areal summaries of reports at typical densities available. For example, it appears that at 200 observations per monthly sample we can expect that only about 20% of interyear differences (i.e., the difference between a monthly value and the value for the same month one calendar year earlier) of wind-mixing index (3rd power of wind speed) will be significant at the 0.1 level. For summaries of alongshore wind stress and cloud cover the situation appears to be somewhat better; about 60% of interyear differences in these properties appear to be significant at this level at a similar data density.

Additional information can be incorporated by means of <u>objective analysis</u> techniques (e.g., Holl and Mendenhall, 1972). These techniques spread information in time and space in a physically realistic manner, using dynamic or statistical models. Thus, observations from previous and subsequent synoptic samplings or from neighboring locations may contribute to a better estimate of the expected value at a gap in data coverage than possible from simple interpolation. Objective data analyses produced routinely by national meteorological agencies generally also incorporate elaborate error checking and quality control procedures based on degree of conformity of observations to physical reality as defined by the models. In addition large scale analysis of wind observations may be improved by the incorporation of barometric pressure data through the geostrophic coupling which is quite strong on large scales in extratropical regions. Thus, the physical mechanisms underlying the models, and the temporally and spatially adjacent data, constitute additional information which may improve the estimates. Thus, we may expect that significance of indicated interyear differences in monthly values computed from objectively analyzed fields (e.g., wind mixing index as shown in Figure 6.1c) may be improved relative to simple areal averages of reports. However, the complexity of the analysis procedures make it difficult to quantify the expected degree of improvement.

Monthly "coastal upwelling indices" based on analyses of wind and atmospheric pressure, are intended to indicate interyear variations in wind-induced offshore transport of surface waters and resulting coastal upwelling. They have been found to yield significant correlations with a wide range of types of biological variations in the California Current region (Bakun and Parrish, 1980), involving such fishery species as Pacific sardine, northern anchovy, Pacific mackerel, dungeness crab, English sole, coho salmon, bonito, hake, and shrimp. However, precision estimates for the indicated variations are not available and associated difficulties in assigning confidence estimates on the apparent relationships limit their utility.

Specifying shorter-scale variations, in the energetic "storm event" frequency band (e.g., Figures 6.1b and 6.1c), is less of a problem due to the large amplitude of the signal relative to the noise (almost any sort of analysis of reports is adequate to indicate presence or absence of storm conditions). However, specification of the affected biological characteristics is seldom available on corresponding scales, and so the tendency has been to search for "bulk" relationships which integrate larger (but unfortunately lower in amplitude) scales of variation.

Measurements at coastal installations offer useful sources of data, covering desirable ranges of time scales at consistent geographic locations. Spatial aspects are less satisfactory. Coastal sea temperature measurements may sample very local scales of variation. Wind measurements are often distorted by coastal topography. Sea level measurements do reflect rather large scales but these scales are difficult to specify, which is a large problem because the main effect of sea level on the processes of interest is through its gradient.

Statistical Significance

In summary, we face a problem of substantial complexity with very little empirical information covering the range of time and space scales determining the final level of recruitment to a total stock. As long as we must attempt to relate "bulk" effects on larger scales (with lower signal amplitudes) than those on which the crucial processes are acting, we must expect weak relationships which do not have a high degree of statistical significance given the limited degrees of freedom available on interyear scales in fishery and other biological time series. In most types of situations it would be almost inconceivable that any one environmental mechanism could so consistently dominate survival processes as to yield a strong univariate relationship that was not, to some degree, spurious. This is not to say that a well-formulated exploratory data analysis is not a useful activity, or that its results should not be reported. But mere searches for relationships meeting significance criteria (i.e., publishable), among various combinations of data sets and formulations, are not very enlightening. The question of how to make use of the weak relationships, which may represent realistic levels of control by particular mechanistic linkages, poses a major challenge.

SOLUTIONS

An obvious need is to develop generalizations that might apply to wider classes of fisheries or ecosystems, and thereby provide a basis for unifying the available fragments of experience in a usefully coherent framework. Certainly, if each separate situation is fundamentally different from all others, there does not seem to be much hope of developing substantial understanding of any. For that matter, there would probably be few situations worth intense research effort if expected results were to have no broader sphere of application. The following paragraphs present some suggestions as to approaches which might lead to progress in resolving some of the problems outlined above.

Interregional Comparative Studies

The large marine ecosystems of the four major subtropical eastern ocean boundary regions appear to be controlled by similar environmental dynamics and contain very similar assemblages of exploitable pelagic fishes (Table 6.1). They also exhibit similar histories of fishery growth and abrupt decline (Figure 6.5). The similarities suggest that the fish communities in these different systems may function somewhat similarly with respect to their environments and may have reproductive strategies adapted to solving similar environmental problems. Since natural selection implies that reproductive strategies reflect responses to the most crucial factors regulating reproductive success, compelling patterns of correspondence among reproductive habits and environmental characteristics are likely to reflect important causal mechanisms.

For example, Parrish et al., (1983) examined characteristic seasonal distributions of temperature,

TABLE 6.1.

Dominant anchovy, pilchard, horse mackerel, hake, mackerel, and bonito in the four major eastern boundary currents (after Bakun and Parrish, 1980).

California Current	Peru Current	Canary Current	Benguela Current
Engraulis mordax	Engraulis ringens	Engraulis encrasicholus	Engraulis capensis
Sardinops sagax	Sardinops sagax	Sardinia pilchardus	Sardinops ocellatus
Trachurus symmetricus	Trachurus symmetricus	Trachurus trachurus	Trachurus trachurus
Merluccius productus	Merluccius gayi	Merluccius merluccius	Merluccius capensis
Scomber japonicus	Scomber japonicus	Scomber japonicus	Scomber japonicus
Sarda chiliensis	Sarda chiliensis	Sarda sarda	Sarda sarda

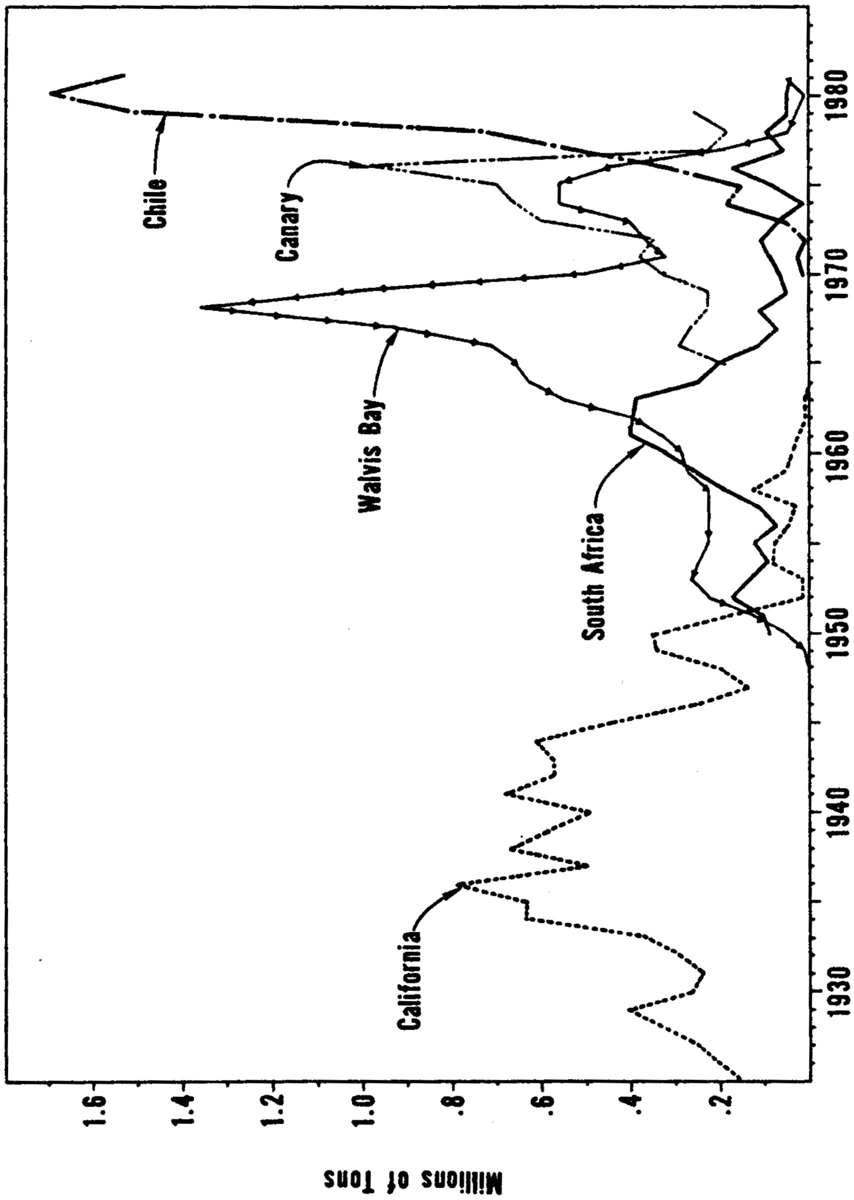

Figure 6.5. Annual sardine landings from several eastern boundary current stocks (after Parrish et al., 1983). Walvis Bay and South Africa refer to the two major Benguela Current stocks.

surface drift, wind mixing energy input, and upper water column stability in the California, Peru, Canary, and Benguela Current systems. They found several interesting patterns with respect to available information on spawning of anchovies and sardines. Avoidance both of substantial wind mixing of the upper ocean layer and of strong offshore transport seemed to be dominant characteristics of spawning habitat selection. Selection for any particular optimum temperature, within physiological limits, seemed less important. These findings, which are independent of time-series results, provide a guide for selection of variables for time-series modelling in a way that makes improved use of the scarce degrees of freedom available.

Certain initially-puzzling discrepancies from general patterns have proven enlightening. For example, it was noted that the spawning peak of the Peruvian anchoveta occurred in austral winter, the season of strongest offshore surface transport, rather than at the season of weakest transport, as is the general case. However, when viewed in conjunction with mixed layer depth climatology the discrepancy appears to be resolved; seasonal variation of mixed layer depth off Peru proceeds in phase with that of transport but has greater amplitude, with the result that the thinner mixed layer of austral summer is apparently carried offshore nearly four times as fast as is the deeper winter mixed layer, even though the winter volume of transport is nearly twice as large. Thus spawning indeed appears tuned to minimize the rapidity of offshore loss of eggs and larvae. This resolution of an initial discrepancy points out that, in treating the mechanism of offshore loss of reproductive products which are distributed through the mixed layer, wind-driven surface (Ekman) transport should ideally be divided by mixed layer depth to yield an Ekman velocity of the mixed layer. In this way, two environmental variables are combined to yield a single more meaningful variable, thereby preserving degrees of freedom for fitting additional pertinent variables in empirical modelling efforts.

Beyond comparisons of spawning habitat climatology, it would seem to be fruitful to compare actual time-series relationships among similar regional ecosystems. Under an assumption of analogy, weak empirical relationships having a similar general form in several systems could be assigned greater confidence than would otherwise be warranted. Conversely, a high correlation found in one system might be questioned if no suggestion of a similar type of linkage was found in other systems appearing in other respects to be analogous. Arraying identically formulated empirical models from different regional systems might yield patterns among model parameters that could provide new insights as to proper transfer of experience among systems in order to predict outcomes of actions taken in one system from the record of similar actions taken previously in other systems. Such efforts would ideally involve interregional and international cooperative activities to assemble analogous variable sets, and provide informed interpretation.

Observational Activities Aiding Scale Integration

Comparative studies are an example of a deductive (i.e., indirect) approach. Because of the great range of crucial scales, more direct experimental approaches tend to involve an impractical observational investment. However, it may be possible to save some effort by designing sampling schemes that would enhance our interpretation of larger scale, more easily specified variations in terms of their effects on processes occurring at smaller scales. As an example, it is conceivable that weakly swimming organisms might exert considerable control over their advection by simply adjusting their depth in the water column. In subtropical eastern ocean boundary regions, clear weather often accompanies an offshore atmospheric high pressure system which produces equatorward winds and corresponding offshore-directed surface Ekman transport. Stormy weather would involve the opposite conditions leading to onshore surface transport. Thus, organisms that position themselves deeper in the water column during clear weather than under cloudy conditions would be aided in avoiding detrimental offshore advection. In addition, the very surface "skin" of the ocean travels in a different direction with respect to the wind than does the Ekman layer; other surface skin effects may act somewhat independently of the wind, e.g., onshore movement of surface slicks generated by passage of internal waves (Shanks, 1983). Knowledge that has been developed concerning the physical transport mechanisms would allow interpretation of vertical biological structure in terms of the function and importance of these mechanisms in natural selection. It appears that well-determined characteristic vertical distributions of planktonic organisms are not widely available, although the sampling techniques are not extraordinarily difficult (e.g., compared to quantitative population estimation). Some detailed sampling of the vertical distributions under different conditions, which might constitute a practical degree of effort, could reveal much about the manner of biological response to these conditions. With increased understanding of these responses, monitoring of the larger scale conditions might in some way substitute for continuous time/space observation of the actual fluxes of organisms.

Sampling of "Integrated" Effects at "High Signal" Scales

The logical way to seek the greatest empirical return for an observational investment is to sample the integrated results of processes occurring on smaller scales, at scales which are more readily sampled but where the signal-to-noise ratio remains relatively high. Conventional recruitment estimates derived from fishery statistics integrate within-year variations to yield a single annual composite. This process suppresses and obscures signals from shorter scale, possibly higher amplitude, components of the variability in survival. In addition, the process of forming composites necessitates an integration of energetic environmental "event" frequencies with accompanying decline in signal-to-noise ratio in specifying the environmental context. Working with annual composites also yields minimal degrees of freedom for empirical investigation of linkages.

In connection with the International Recruitment Project (IREP) of the Intergovernmental Oceanographic Commission's Program of Ocean Science in relation to Living Resources (OSLR), an experimental program has been conceived (Anon., 1983) which appears to be uniquely promising because it addresses the energetic within-year scales. It involves determining fish egg or larval abundance within a spawning region of a given stock unit, at increments through an extended spawning season. Subsequent survival is estimated by sampling late larvae or early juveniles, determining their birthdate distributions using recently-developed daily ageing techniques (Methot and Kramer, 1979), and comparing birthdate distributions to the corresponding estimates of egg abundance. Interference from annually-tuned mechanisms is minimized by the process of incrementally-determining both the inputs (eggs or early larvae) and the outputs (survival). Integrations of environmental conditions over the intervening time increments can then be examined to determine the degree of "fit" represented by alternate causal mechanisms and formulations. The program does imply a considerable sampling effort to adequately encompass the pertinent scales of variation over a total stock unit.

Time/Space Statistical Analysis

With the rapid increase in economical computing power, application of a very powerful class of methods of exploratory data analysis is finding increased application in fishery/environment studies. Basically, they allow the computer to do much of the work in sorting out time/space structures among data sets (work that may previously have been done less systematically by laboriously plotting and comparing time series of mapped distributions). For example, Mendelssohn and Roy (in press) have used spectral empirical orthogonal functions to demonstrate wavelike propagation in tuna distributions and in sea temperature which conforms to a Kelvin wave interpretation. Such examinations of space/time structures in the behavior of ecosystem components, in the light of known structures in the characteristics of particular environmental mechanisms, appear to offer substantial promise. However, it may be well to note that rather than being a mechanical process, both the formulation of the variables and the application of the methods involve important interpretive aspects requiring skill and judgment; without these, the increasing ease of access to electronic data banks, substantial computing power, and software for complex analysis procedures, would appear to have potential for generation of a much greater volume of published output, without any correspondingly greater degree of enlightenment, than the correlation searches of the past.

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