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ENVIRONMENTAL INPUTS TO FISHERY POPULATION MODELS
FOR EASTERN BOUNDARY CURRENT REGIONS

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ABSTRACT

Methods for incorporating information on environmental variation in fishery management models are not presently well developed. Rational approaches are hindered by lack of detailed knowledge of the linkages between environmental fluctuations and their effects on fish stocks. Empirical approaches are limited by lack of sufficient data points.

Recent advances have been fostered by the development of several promising hypotheses based on laboratory and field experiments and on comparative studies of geography and seasonality of spawning strategies. In addition, time series indicators of the important environmental processes involved in these hypotheses are becoming available. A review of developments concerning environmental effects on recruitment in a number of California Current stocks is presented.

The state of the art in the production of fishery-environmental indicator time series for eastern boundary current regions is surveyed. Fishery modeling is discussed from the points of view of rational models of the early life history and juvenile stages and of empirical models based on data from the post-recruit stage. In these post-recruit models, early life history and juvenile processes are incorporated by means of empirical stock-recruitment functions which may contain environmental dependencies.

Further progress is anticipated through laboratory and field experiments, dynamic process models, and seasonal-geographical comparative studies. Newly-developed techniques for aging of larvae promise dramatic increases in data on larval survival processes. It is pointed out that the four major eastern boundary current regions of the world, i.e., the Canary, Benguela, Peru, and California Current regions, involve similar environmental dynamics and contain very similar assemblages of economically-important fish stocks; inter-regional comparative studies are advocated.

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INTRODUCTION

Recent precipitous declines in important fishery stocks around the world have pointed out an urgent need for advances in fishery management science. A particular need is for realistic models which can predict and simulate effects of various management options. In most existing management models, the surplus production of a stock is assumed to be a relatively constant function of stock size. Recent events have shown this assumption to be inadequate under conditions of environmental perturbation.

Properly incorporating environmental effects in fishery models can be a difficult problem. There are two basic approaches: (1) the rational (cause-effect) approach which is based on an understanding of the physical and biological processes involved, and (2) the empirical approach in which the functional relationships are defined by analysis (by means of statistical regression, etc.) of available data.

A strictly rational approach is usually not feasible. The complex linkages between environmental processes and biological consequences are incredibly difficult to observe or to investigate experimentally; the quantitative information needed to construct rational models of those linkages is most often unavailable. On the other hand, the empirical approach is hampered by a chronic lack of sufficient data points. Fishery data characteristically yield one estimate of stock size or recruitment per year; the available time series generally does not exceed several decades and most often is of the order of 10 to 20 years. To sort out a multitude of possible environmental effects by statistical means from a series of 10 to 20 data points is not possible. Moreover, the time series often contain significant autocorrelation, indicating a lack of independence of data points, which further depletes the severely limited degrees of freedom.

Generally, a combination of the two approaches allows the greatest amount of available information to be incorporated. The rational approach is used to generate hypotheses and to test and quantify those processes which can be measured or addressed experimentally. Then the empirical approach is used for testing, verification, and calibration. The demarkation between the two approaches is important. Often in fishery science an hypothesis is generated on the basis of experience, and since rational explanations can be constructed (because of the multitude of possible interacting processes occurring in marine biological communities it is nearly always possible to find a rationalization for any empirical result) the hypothesis comes to be regarded as rational when in fact it is basically empirical. Then when the hypothesis is "tested" against the time series of available data, which nearly always contains the period of experience which generated the hypothesis, a "verification," not surprisingly, is indicated. When basically the same data is used to test a hypothesis as was used to formulate it, obviously no real test can occur. For this reason many published fishery-environmental "relationships" are in reality untested hypotheses; it should not be surprising that they often fail almost immediately after publication.

Even when there is considerable rational input available, it is necessary to limit the choices of explanatory environmental variables to minimize the chances of spurious "fits" to the very limited time series. Thus as much rational input as possible must be utilized in formulating pertinent environmental indicators. In the past, measured environmental properties have often been used to produce correlations with fishery data in the belief that the same environmental processes which alter the measured properties would also alter the fish stock parameters. However, the linkages between the environmental processes and the observed properties may be just as (or more) tenuous and subject to independent alteration, as those between the processes and the biological consequences of interest. Certainly, a property is easier to measure than is a process, and a property has the reassuring attribute of having a single scalar value at a given point in space and time. In addressing a process one must come to grips with a space - time continuum in which a choice of scale is critical. However, due to the lack of any excess degrees of freedom to deal with additional linkages it is advisable to focus as directly as possible upon the actual involved processes in formulating environmental variables for fishery modeling efforts.

Recently several promising rational hypotheses concerning environmentally-caused recruitment variation in fish stocks of eastern boundary current regions have appeared. (1) A sensitivity of reproductive success of pelagic fish stocks to the dissipation of fine-scale food strata by wind mixing during early larval feeding (Lasker, 1975, 1978) has been indicated through a remarkable series of

laboratory and field experiments. (2) A detrimental effect on coastal fish stock of offshore transport during the larval drift period has been suggested by comparative studies (Parrish, Nelson and Bakun, MS) of the seasonal and spatial characteristics of reproductive strategies and drift conditions in the California Current region. (3) Since it is generally thought that the massive fish stocks inhabiting eastern boundary current regions depend on the primary production supported by the vigorous coastal upwelling characteristic of these regions, it is expected that long time scale fluctuations in upwelling intensity would be linked to fish stock variations.

The four "classical" eastern boundary currents (Wooster and Reid, 1963) are the Canary Current off the Iberian Peninsula and northwestern Africa, the Benguela Current off southwestern Africa, the Peru Current off western South America, and the California Current off western North America. These also comprise the four main upwelling regions of the world, as cited by Cushing (1969). They are characterized by rather broad, slow equatorward flow, high primary productivity, and massive pelagic fish stocks which have experienced extreme fluctuations. Very similar assemblages of fishes appear to constitute the major portion of the exploitable biomass in all four regions. In each, there is an anchovy, pilchard (sardine), horse mackerel (jack mackerel), hake, mackerel and bonito. The species are very closely related and several of the species are found in more than one region (Table 1). The similarity of the pelagic fish community in the eastern boundary currents suggests that the processes occurring in these systems may be direct analogs. It is possible that the environmental processes which regulate the recruitment and population fluctuations of a species group, for example the anchovy (*Engraulis*), are similar in all of the eastern boundary currents.

TABLE 1. Dominant anchovy, pilchard, horse mackerel, hake, mackerel and bonito in the four major eastern boundary currents.

CALIFORNIA CURRENT	PERU CURRENT	CANARY CURRENT	BENGUELA CURRENT
<i>Engraulis mordax</i>	<i>Engraulis ringens</i>	<i>Engraulis encrasiolus</i>	<i>Engraulis capensis</i>
<i>Sardinops sagax</i>	<i>Sardinops sagax</i>	<i>Sardina pilchardus</i>	<i>Sardinops ocellatus</i>
<i>Trachurus symmetricus</i>	<i>Trachurus symmetricus</i>	<i>Trachurus trachurus</i>	<i>Trachurus trachurus</i>
<i>Merluccius productus</i>	<i>Merluccius gayi</i>	<i>Merluccius merluccius</i>	<i>Merluccius capensis</i>
<i>Scomber japonicus</i>	<i>Scomber japonicus</i>	<i>Scomber japonicus</i>	<i>Scomber japonicus</i>
<i>Sarda chilensis</i>	<i>Sarda chilensis</i>	<i>Sarda sarda</i>	<i>Sarda sarda</i>

DEFINITION OF ENVIRONMENTAL VARIATION

If fishery environmental studies are to lead toward management systems which are capable of adapting to environmental variations, the data required to indicate these variations must be of a type that can be obtained on a continuing basis. Thus, it is advantageous to base these studies on the sort of data that are routinely gathered, or that can be obtained by a minimal survey effort.

Generally, the physical characteristics of the environment which are thought to have important effects on recruitment variations can be grouped into four major categories:

1. The field of horizontal advection,
2. The field of vertical stability,
3. The field of temperature,
4. The field of convergence and divergence of flow at the sea surface, which is linked to the field of vertical advection.

In addition there are available certain physical indicators which are sometimes considered as "integrators" of several (or many) environmental effects.

Horizontal advection

Biological processes in the sea tend to integrate very short-scale variations in the physical environment. For instance, in the case of transport of planktonic fish eggs and larvae, since spawning generally is distributed in time and space, and eggs and larvae may passively drift for an extended period, short-scale flow variations tend to be averaged out by the space-time continuum of drifting organisms (Parrish, et. al., MS).

On large time and space scales, flow in the ocean is well approximated as a simple combination of the geostrophic current field and the field of Ekman drift induced by the horizontal force exerted by the wind on the sea surface (Greenspan, 1968). The conceptual picture, therefore, is of a thin surface layer of Ekman wind drift which varies in phase with large-scale atmospheric weather patterns, superimposed on the deeper, more slowly varying geostrophic flow field. The Ekman layer is thought to extend no deeper than 50 to 100 meters below the sea surface, and most of the transport probably occurs in the upper 5 to 30 meters.

The geostrophic current at the sea surface is directly proportional to and at right angles to the slope of the sea surface. The constant of proportionality is a function of latitude, being a minimum value at the poles and increasing to an infinite value at the equator; thus the geostrophic approximation is useless directly on the equator but Montgomery and Stroup (1962) have indicated it to be a useful estimate of current velocity as near as several degrees of latitude to the equator.

The standard method for estimating the sea surface slope is by measuring the temperature and salinity of the ocean at various depths, thereby determining the field of density of the sea water. For water to be motionless at some deep level there must be no horizontal variation in the weight of the water column pressing down from above. Thus, the horizontal differences in thickness of the column, and thereby the sea surface slope, can be computed from the internal density field (Sverdrup, et. al., 1941). Although there is probably no level at which the ocean is completely motionless, the geostrophic velocities at great depths tend to be much smaller than those at the surface, and so this method provides an acceptable approximation.

Surveys using this method have been made in all the major eastern boundary current regions. In the California Current, the CalCOFI surveys have made regular observations since 1949. The flow patterns described are quite detailed. However, methods for applying this wealth of detail to biological problems are not well worked out; as yet, little use has been made of these data in explaining biological variations. Such surveys are expensive, and obtaining the required space-time continuity of coverage is a problem.

For some purposes a schematic picture of the normal seasonal variation of geostrophic flow is required. This is not necessarily easy to get. Simple averages of the few available samples of sea surface topography as done by Wyllie (1966) and Hickey (1979) can be dominated by atypical features. This procedure can also introduce spurious features that never occurred in any of the measured samples. For example, during a particularly warm year the sea surface would tend to stand higher than normal throughout a given region; this would not generate any current features since currents are related to the gradient of surface height. Since spatial coverage is seldom complete in any one year, if observations from the warm year are averaged with those from several more normal years, the locations containing data from the warm year would tend to be higher than other locations. The surface slopes thus generated would determine current patterns that never actually existed.

Parrish, et. al. (MS) used the long-term mean temperature and salinity summaries produced by Robinson and Bauer (1973) to produce a smoothed long-term mean geostrophic pattern for the California Current region in which atypical features are suppressed; however, lack of indication of the typical seasonally varying features is a major deficiency. Because temperature observations are much more numerous than salinity observations, Husby² has produced some interesting seasonal patterns by combining

2. Personal communication, David M. Husby, Pacific Environmental Group, Southwest Fisheries Center, National Marine Fisheries Service, NOAA, Monterey, California, 93940.

seasonal temperature fields with long-term mean salinity fields. Other approaches include the association of non-observed salinity values with observed temperature values through the use of a characteristic temperature-salinity (T-S) relationship (Emery, 1975) and the filling of data gaps by curve fitting to existing data points by harmonic analysis³.

An ideal situation is where the sea surface slope variations can be directly measured; the long-period variation in the difference in measured sea height between two sea level gauges on either side of an ocean current is directly proportional to the variation in the space-averaged geostrophic surface flow across a line drawn between the two gauge locations. Saur (1972) produced a very large space scale index of monthly variations in geostrophic surface flow between sea level gauges located in San Francisco and in Honolulu. Christensen et. al. (1979) used sea level differences between Guadalupe Island and the coast of Baja California to indicate flow variations on a scale which is probably more pertinent to coastal fish stocks. Wyrтки (1974) showed that an array of sea level gauges on tropical islands could successfully monitor changes in the equatorial current system of the Pacific.

In most cases there exists no convenient island located the proper distance offshore to indicate flow variations on a scale upon which they would be affecting fish stocks. In these cases it may be reasonable to assume that the largest sea level variations will be at the solid coastal boundary and thus that a single coastal sea level station can be an index of major alongshore geostrophic flow variations. The most likely offshore length scale to be involved in such an index is the baroclinic Rossby radius of deformation (Mooers and Allen, 1973) which is of the order of 10 to 20 km in the subtropical eastern boundary current regions. For example, Smith (1974) and Reid and Mantyla (1976) found correspondence of coastal sea levels at certain California Current locations with measured variations in alongshore flow. Marthaler (1976) indicated that the monthly mean near-surface currents over the Oregon continental shelf could be estimated from a regression with coastal sea level to a precision of ± 6 cm/sec where the annual range is 60 cm/sec. Off the New England coast of the eastern North America, where the continental shelf is relatively wide, Beardsley and Butman (1974) found that, if they assumed a constant sea level at the shelf break, a coastal sea level measurement could indicate the alongshore geostrophic flow (averaged over the shelf width) to $\pm 15\%$.

Sea level measurements are available in long time series in all the major eastern boundary current regions. The Permanent Service for Mean Sea Level⁴ lists monthly mean values for the California Current since the turn of the century (e.g., San Francisco since 1897, San Diego since 1906), nearly as long for the Canary Current (Lagos since 1908, Santa Cruz de Tenerife since 1927), for the Peru Current since the early 1940's (eg. Matarani since 1941, Talara since 1942) and for useably long time series for the Beneguela Current region (eg. Walvis Bay, 1958-72). Sea level time series are subject to distortion by geological uplifting and downwarping of coastal regions but these are usually of much longer time scale than the fishery variations of interest, and so can be easily corrected by linear or first-order curvilinear detrending, or by low-pass filtering. Sudden discontinuities due to earthquakes, etc., are usually well documented.

The other major component of flow, the surface wind-induced Ekman drift, which combines with the geostrophic flow to determine the actual water movement in the ocean surface layer, presents a different sort of problem. It cannot be inferred from any signal that is measured within the ocean and varies rapidly, adjusting to wind variations on a time scale of less than a day (except very close to the equator). It can be estimated from the field of wind stress on the sea surface. This stress field must be constructed from scattered reports from ships at sea and from observations at coastal stations which may be distorted by effects of local land topography. Because of the rapid variation, frequent sampling is required, preferably at intervals of twelve hours or less. Standard reporting periods have been established by international convention to provide synoptic samplings which are disseminated globally. These are arranged into consistent analyzed fields by various national meteorological agencies, commonly at 6-hourly, or even 3-hourly intervals.

3. Method developed by Ronald J. Lynn, Southwest Fisheries Center, National Marine Fisheries Service, NOAA, La Jolla, California, 92037.

4. Institute of Oceanographic Sciences, Bidston Observatory, Birkenhead, Merseyside L43 7RA, England.

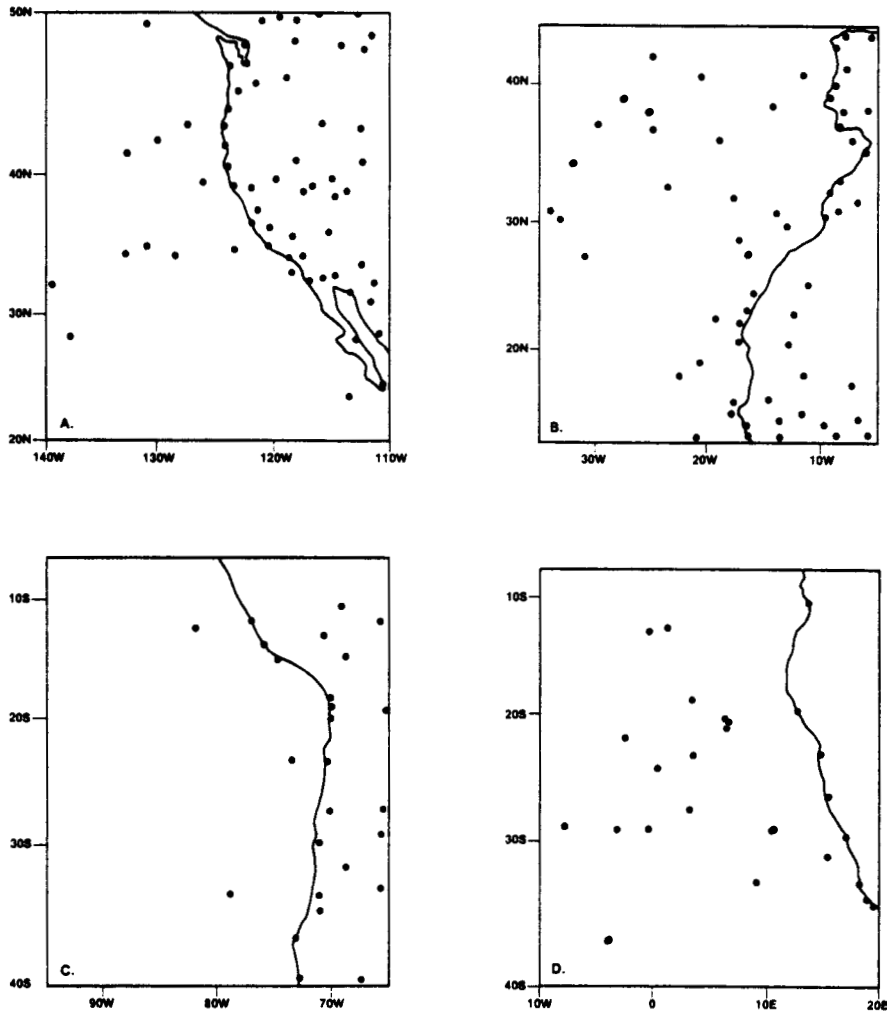


Figure 1. Typical synoptic report distributions in the four major eastern boundary current upwelling regions: A. the CALIFORNIA CURRENT (distribution shown is for 0600 GMT, Jan. 11, 1980), B. the CANARY CURRENT (0000 GMT, Feb. 12, 1980), C. the PERU CURRENT (1800 GMT, Feb. 7, 1980), and D. the BENGUELA CURRENT (1900 Gmt, Feb. 7, 1980).

The report density available in any synoptic sampling for any of the major subtropical eastern boundary current regions does not normally exceed several per 5-degree latitude - longitude "square" (Figure 1). In order to form consistent time series from such sporadic report distributions, it is necessary to spread the large-scale information represented in the observations to consistent geographical locations and to suppress measurement and transmission errors and small-scale information which is nonrepresentative of the large-scale. The analysis procedures used by meteorological agencies to prepare synoptic data fields for forecast purposes are designed to accomplish these same results, and thus provide a resource for the production of sea surface wind stress time series. Many of the standard analysis

procedures (e.g. Holl and Mendenhall, 1972) are designed for use in temperate latitudes and make use of the strong geostrophic coupling between wind and atmospheric pressure distributions to employ both types of observations and thereby increase the data base. In the tropics, where the geostrophic coupling becomes weak these methods do not work well. However, there are certain analysis procedures designed specifically for the tropics (e.g. Lewis, 1972) which are in routine use at the present time.

Once an estimate of the wind field over the sea surface is available it can be readily converted to an estimate of the surface Ekman transport field in the ocean. However it is important to note that the linkage of wind velocity to wind stress is non-linear. Thus, where time averages are to be made, the averaging should be performed after the stress computation. Bakun (1973) has shown that time series of monthly alongshore stress estimates computed from monthly mean winds at locations near the west coast of North America correlate highly with corresponding series of monthly means of synoptic stress computations. The high correlation is probably due, at least in part, to the effect of coastal topography in constraining the directional variation of the wind. Thus, although it seems likely that similar high correlation would occur in other eastern boundary current regions with coastal mountain ranges, it remains an untested assumption. In regions where the directional variance of the wind is high, in the mid-latitude central ocean, for example, such an assumption is probably unwarranted. Bakun (1973, 1975) has discussed certain other problems in using analyzed atmospheric fields near coastal boundaries.

A major unsolved problem is the assignment of "error bars" to the stress estimates computed from atmospheric analyses. The estimates appear to be quite adequate for defining variations on the energetic "synoptic atmospheric event" and "seasonal" scales, and to identify major interyear differences. However, their adequacy in defining subtle differences among groupings of years remains undemonstrated.

Ekman transport is calculated as the ratio of the wind stress magnitude to the local value of the Coriolis parameter and is directed 90° degrees to the right (left) of the stress in the northern (southern) hemisphere. The fine-scale vertical structure of the Ekman drift velocity field depends on vertical eddy viscosity characteristics which are not well known; however the total transport of water in the layer between the sea surface and the depth at which the drift velocity becomes negligible does not depend on these characteristics, and can be inferred from the wind stress alone. The depth of negligible Ekman drift velocities is likewise not well known. However, as mentioned above, most of the transport probably occurs in the upper 20 to 30 meters. It is unlikely that appreciable Ekman drift would penetrate below the surface mixed layer into the stratified portion of the water column. Aggregates of organisms which are continually being mixed over a depth range as deep as or deeper than the Ekman layer can be assumed to move with the Ekman transport; in this case a drift speed can be assigned by dividing the Ekman transport by the depth of mixing.

The upper portion of the Ekman layer would tend to move at a lesser angle to the direction of the wind stress. Classical Ekman theory, assuming a constant vertical eddy viscosity, predicts the free ocean surface to move at an angle of 45° to the wind. An analysis by Madsen (1977), in which he assumes an eddy viscosity varying linearly with depth, yields a surface deflection of about 10° . Empirical studies reported by Stommel (1954) found speeds of drift at the sea surface to be of the order of 1/20 to 1/30 of the wind speed, with deflection angles usually between 30° and 60° .

Detailed specification of the vertical distribution of Ekman velocity is not available. The classical Ekman spiral is not generally observed. The interaction of Langmuir-type circulations (Scott, et. al., 1969), etc., is not well understood. However, we can be quite certain that the Ekman transport concept is realistic, at least in a time- and space- average sense, both from dynamical necessities (Greenspan, 1968) and from climatological correspondences of wind and oceanic distributions (e.g. Wooster and Reid, 1963; Wooster, Bakun, and McLain, 1976). For fisheries applications, it appears necessary to make do with the concept of Ekman transport, modified by a somewhat vague notion that the very surface moves at an angle more directly downwind than does the depth-integrated transport. At the equator the Coriolis parameter goes to zero and so the Ekman transport relationship "blows up"; the evidence of equatorial divergence of ocean surface waters indicates some degree of Ekman effect acting even very near the equator.

Direct measurements of ocean flow cannot generally provide the required time and space coverage required for operational fishery management purposes. One type of direct measurement which has been useful in climatological studies of eastern boundary currents (Wooster, et. al., 1976; Bakun, et. al., 1974; Bakun and Nelson, 1977; Bakun, 1978) is the so-called "ship drift" observation. These are differences, attributed to ocean currents, between dead-reckoning and verified positions as recorded in ships log books. These have been gathered since the last century and have provided the basis for much of our knowledge of large scale ocean currents. The data contain a very large error variance, being based on differences between rather uncertain navigational fixes, estimates of ship speed, etc., and require a very large sample to achieve a meaningful estimate of mean current speed. Although observations are rejected when wind speeds are very high, the data are undoubtedly contaminated by the effects of wind on the ships super-structures. The data appear adequate to define long-term mean seasonal variations, but are not numerous enough to be useful in indicating interyear variability.

Vertical Stability

Recent work (Lasker, 1978) has indicated extreme sensitivity of anchovy reproductive success to the breaking up of fine-scale food strata by wind mixing during early larval feeding. We can estimate variations of wind mixing energy added to the water column from available analyzed wind fields; the energy added varies in rough proportion to the cube of the wind speed (Elsberry and Garwood, 1978). The stability of the upper water column, which would oppose such mixing might be estimated from vertical temperature and salinity structure. Little is known concerning the time scales of aggregation of food strata or the ability of the food organisms to themselves resist dispersion by turbulence. It is difficult to formulate a proper index of the wind effect in this case. A first impulse is to look at interyear variations in the cube of the wind speed averaged over a spawning season as the relevant factor. However, it probably is not the average intensity that is critical, but the existence of sufficient time-space "windows" within which wind-induced turbulence does not exceed a certain critical value. We do not know what the critical value is and we do not know the length of time required for formation of the food concentrations needed for successful first feeding of larvae. This appears to be a very fruitful ground for research. Application of recent advances in oceanic mixed layer modelling should be helpful in determining at what point turbulence would be initiated. Repetitive samplings of biological microstructure under varying wind conditions would begin to define time scales of aggregation and ability to resist dispersion. Perhaps comparative studies of conditions in areas where fish normally spawn (i.e. favorable to larval survival by natural selection), as opposed to conditions in areas where spawning does not occur, would yield some information on normal requirements for reproductive success. Such information might then be used to define a formulation to correctly indicate the effect on year-class success of interyear variations in wind-induced turbulence.

Temperature

Sea temperature is probably the most commonly used environmental variable in studies of biological variations. There are several reasons for this. Probably most important is that temperature has a direct physiological effect. The rates of biological processes increase and decrease with temperature, and extremely unfavorable temperatures can be lethal. Thus, temperature can define limits of occurrence; anomalous temperature conditions, by changing growth and maturation rates, can cause disruptions and mismatches in the timing of critical life cycle events. Of perhaps nearly equal importance is the availability of temperature data, due in some extent to the simplicity and ease of the measurement. Finally, temperature provides a signal of important ocean processes; for example in eastern boundary current regions, cool sea surface temperatures are often related to coastal upwelling or to horizontal advection from higher latitudes.

Sea surface temperature is routinely measured and reported by ships at sea. The observations are distributed internationally through the World Meteorological Organization (WMO). Subsurface temperature observations are much less plentiful, but these are also gathered and distributed by WMO and the Intergovernmental Oceanographic Commission (IOC) through the IGOSS program. Sea temperature is also routinely measured at many coastal stations. These observations have the advantage of being a generally continuous time series at a consistent location. They are sometimes subject to very local

influences, often being located in or near harbors and estuaries. Temperature signals from coastal stations located within a region occupied by a single fish stock can exhibit a disconcerting degree of noncorrelation.

This brings up the problem of how to choose from a variety of available temperature signals in attempting to define a useful relationship to biological events. The procedure of searching a number of possible signals to find the "most pertinent" one, i.e., the one that yields the best correlation, and then applying a standard significance test to the regression results in a misleading overestimate of significance. After all, a 95% significance level signifies only that the chance of an equivalent degree of correlation from unrelated random series is one in twenty. Thus if one tests four unrelated series the probability of finding a correlation significant at the 95% level is increased to one chance in five, corresponding to an 80% significance level which may be inadequate to confidently reject a null hypothesis of no relationship.

Various methods are employed to summarize scattered temperature observations to produce time series indicative of conditions in the environment. None should be used blindly. The space scales of temperature variation in the ocean may be quite small and not well sampled by the available distribution of observations. Thus the variation in distribution of reports may introduce spurious variability capable of obscuring the true variation. Averaging by areal segments of the ocean surface (e.g. McLain, 1978) can be a particular problem in coastal upwelling regions where horizontal temperature gradients are large.

Use of meteorological-type "objective analysis" procedures (e.g. Laevastu and Hela, 1970), where available data is spread to areas where data is lacking, may involve similar time series distortions. Often climatology is used in these procedures to fill large space-time data gaps. The resulting time series can be difficult to interpret; methods for establishing error limits are not available.

Recently there has been widespread use of empirical orthogonal function (or principal component) analysis in studies of climatic fluctuations (Preisendorfer, 1977). In this way temperature series from several locations can be combined into a single series, based on the linear combination which explains the largest fraction of the total variance of the individual series (Weare, Novato, and Newell, 1976). These techniques have not yet been widely used in fishery studies. They can probably be useful if properly employed. However, there should always be a firm physical basis for believing that the linear combination which contains the most variance is a more pertinent indicator of the effect upon the biological process of interest than is some other possible combination. Otherwise, one is simply adding another time series to a situation in which the major need is to limit the choices of explanatory series so that the concept of statistical significance can be meaningful.

Convergence, divergence, upwelling

An important aspect of the surface Ekman drift is that it is subject to strong convergences and divergences, convergence being a net gain of surface water at a point due to spatial gradients in horizontal transport, and divergence being a net loss. Thus sinking waters are generally found immediately below surface convergences, and rising waters below divergences.

Floating organisms would tend to be concentrated in areas of convergence and dispersed in areas of divergence. The rising waters in areas of divergence can aid non-motile phytoplankton in remaining in favorable light intensities for photosynthesis. Rising deeper waters replenish exhausted nutrient concentrations at the surface and cool the surface layers. Spatial gradients in surface convergence or divergence can tilt the subsurface density structure and establish sea surface slopes which alter the underlying geostrophic current field. Thus convergence and divergences in the surface wind drift affect the biological environment in a variety of ways and on a variety of scales; variations in the wind stress at the sea surface are probably the major external driving forces leading to biological perturbations.

The strongest convergence and divergence can occur next to a coastal boundary where transport gradients essentially reflect a step increase from zero on the continent to a finite value in the ocean. Where the surface transport adjacent to the coast is directed offshore, the result is locally wind induced

coastal upwelling. Bakun (1973) produced time series estimates of monthly variations in the onshore-offshore component of Ekman transport. These were called "upwelling indices" (after Wooster and Ried, 1963) to call attention to the fact that, lacking direct measurements of coastal upwelling intensity, the variations in the local driving force, the alongshore wind stress, may be the best available indicator of upwelling variations.

Recent research has indicated the likelihood of poleward propagation of upwelling characteristics. This appears to be less important, at least on the seasonal scale, in the higher latitude eastern boundary current upwelling regions (Smith, 1974; Bakun, et. al. 1974; Wooster, et. al. 1976) than in the lower latitude regions, for example, the Peru (Smith, 1978) and Guinea (Bakun, 1978) coasts. However, even in Peru, Smith (1980) finds that the onshore-offshore component of flow is well represented by the locally wind-induced Ekman transport.

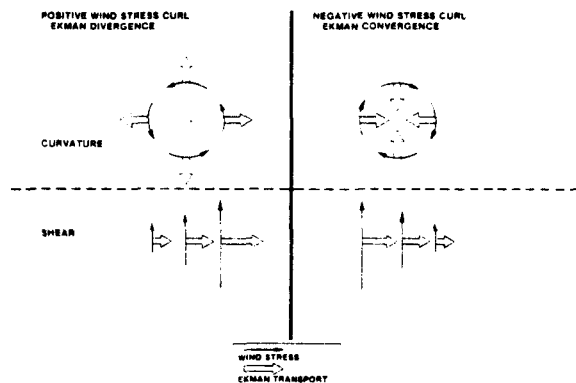


Figure 2. Wind stress curl and resulting Ekman transport. Positive curl expresses the anti-clockwise (cyclonic) rotation due to either curvature or shear in the wind field; since the Ekman transport is directed perpendicularly to the right of the stress the result is Ekman divergence in either case. Negative curl expresses the clockwise (anticyclonic) rotation in the field; the result is Ekman convergence.

variations computed in this manner and low frequency variations in the onshore-offshore contrast in flow of the California Current, i.e., the tendency for the flow to be less southward (more northward) near the coast than in the offshore region.

The coupling of the surface convergence or divergence associated with the coastal boundary with that occurring offshore of the boundary zone presents possibilities for various combinations (Fig. 3) of probable biological significance. For example, a situation of coastal upwelling with negative wind stress curl causing offshore convergence (Fig. 3(d)) would favor concentration of drifting organisms upon being transported out of the coastal upwelling zone. This particular situation appears to be typical of the central Baja California upwelling center (Bakun and Nelson, 1977).

The effect of such couplings on the geostrophic current pattern can apparently have biological consequences. For example, the negative curl area off central Baja California corresponds to an apparent "blocking" of northward counterflow along the coast during the fall relaxation of upwelling-induced southward circulation (Bakun and Nelson, 1977). Semi-independent gyral circulations occur in the positive curl regions to the north and south (Fig. 4). These correspond to the areas of occurrence of separate subpopulations of California Current pelagic fishes including sardine (Clark, 1947), Pacific mackerel

The onshore-offshore scale of the coastal divergence is related to the baroclinic Rossby radius of deformation (Moore and Allen, 1973) which is of the order of 10 to 20 km in subtropical regions, although features of the continental shelf topography may, under certain circumstances, cause seaward expansion of this scale (Huyer, 1976). Offshore of this coastal boundary region, the convergence and divergence of surface Ekman drift is controlled by the wind stress curl (Fofonoff, 1963), which is a measure of the "rotation" in the wind field represented by curvature or shear (Fig. 2). Monthly surface layer divergence indices based on wind stress curl estimates were proposed by Bakun and Nelson (1977). The problem of establishing expected error bars on these estimates is even more bothersome in this case than in the case of Ekman transport indices since the process of taking derivatives amplifies errors. This problem is presently unsolved and the significance of computed wind stress curl anomalies is uncertain at this point. However, Chelton (1980) has reported a significant relationship between wind stress curl

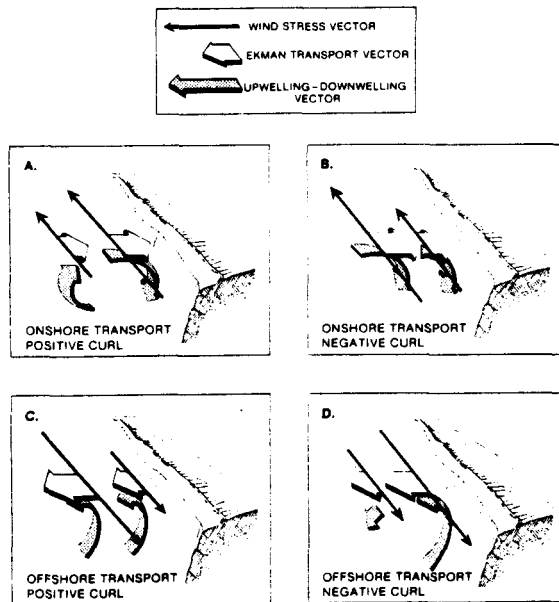


Figure 3. Types of couplings between surface convergence or divergence at the coast (due to the onshore-offshore component of Ekman transport) and that (due to wind stress curl) occurring offshore of the coastal boundary zone. A. Onshore Ekman transport and positive wind stress curl; convergence and downwelling at the coast, divergence and upwelling offshore. B. Onshore Ekman transport and negative wind stress curl; convergence and downwelling at the coast, continued convergence offshore. C. Offshore Ekman transport and positive wind stress curl; divergence and upwelling at the coast, continued divergence offshore. D. Offshore Ekman transport and negative wind stress curl; divergence and upwelling at the coast, convergence offshore.

The infra-red or microwave radiation sensors are not as yet accurate enough to define the subtle long-term variations which would be reflected in fish stock fluctuations. Satellite mounted altimeters may be capable of recognizing the existence of sea surface slopes characteristic of swift ocean currents such as the Gulf Stream; their precision does not yet approach that required to indicate fluctuations in broad-scale mean flow velocity in eastern boundary currents, although it may be adequate to recognize major eddy structures.

The wind sensing capabilities of satellites offer some very enticing prospects for uses in fishery management studies. The 50-km resolution which is designed for the microwave scatterometer which was placed on SEASAT-A would allow synoptic viewing of features the size of the negative wind stress curl lobe off central Baja California (Fig. 4(a)), i.e., on the scale that wind stress features may actually affect fish stocks.

(Roedel, 1952) and northern anchovy (Vrooman and Smith, 1971). This suggests the possibility that fluctuations of the wind stress curl pattern could influence exchanges between subpopulations. Indeed, Parrish and MacCall (1978) find variations in the wind stress curl in the region of separation to be significantly related to recruitment variations in the Pacific mackerel stock to the north.

The smaller scale features of the stress and stress curl (Fig. 4(a)) distribution produced by Nelson (1977) by compositing many years of data, cannot be resolved by the observations generally available in a synoptic sampling (Fig. 1). Thus time series indicators can only be produced on a considerably larger scale (Bakun and Nelson, 1977). Estimates of fluctuations of wind stress features of the size of the negative curl lobe must presently rely on an untested assumption that such features would fluctuate in phase with and in the same sense as the larger scale pattern in which they are embedded.

Satellite Measurements

Measurements from earth-orbiting satellites have been heralded as the answer to many of society's environmental monitoring data needs. Recently, the U.S. Government placed into orbit a satellite (SEASAT-A) specifically designed for ocean science purposes. Satellite measurements have been valuable in indicating sea temperature structures as a tactical aid to fishing operations; satellites have also improved the weather advisory services which are vital to the operation of a fishery. However, we are not aware of their use to date on the fishery management problem.

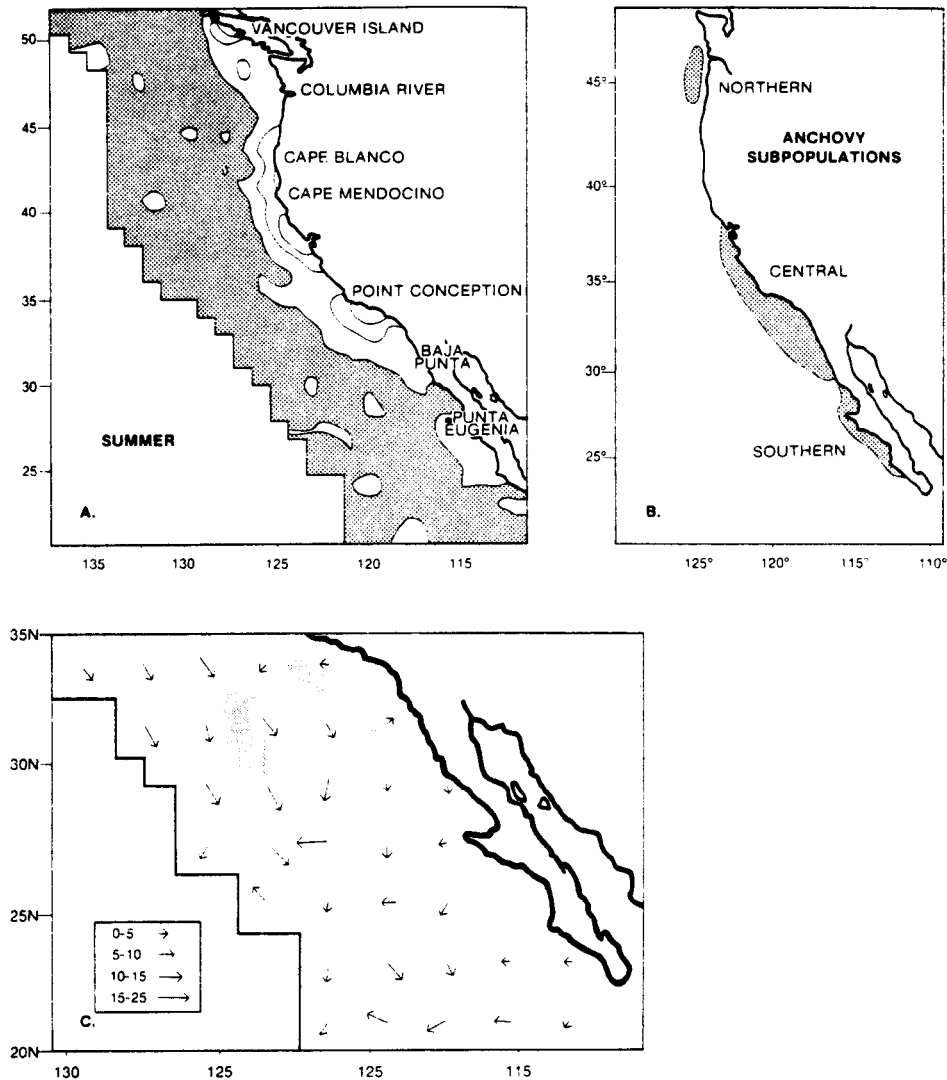


Figure 4. (a) Wind stress curl distribution during summer (June through August long term means). Contour interval is $0.25 \text{ dynes cm}^{-2}$ per 100 km. Negative curl values are shaded; positive curl values are unshaded (after Nelson, 1977). (b) Spawning distributions of the central and southern subpopulations of northern anchovy (Paul E. Smith, personal communication). (c) Ship drift during October, November, and December. The small arrows, indicating mean drifts, are scaled according to the key at the lower left. Large arrows suggest the inferred circulation pattern (after Nelson, 1977).

Another general requirement for wide application to fishery management is that a data source be available in long time series so that models based on it can be verified against observed fish stock variations. This necessitates some years lag between the introduction of new technology systems such as satellites and telemetering buoys, and their usefulness in this sense. This delay can be eliminated if the new available information can be used to "calibrate" existing time series. For example, if the ability to

view small scale wind stress curl patterns would allow us to define their relationship to the large scale synoptic weather patterns which can be defined by the density of synoptic ship reports available historically, models using the small-scale physical mechanisms could be based on the large scale time series.

Integrators of multiple processes

Where possible, it is preferable to use indicators of the particular processes which are actually affecting the organisms. Sometimes such indicators are either not available or else a precise notion of the relative importance of various processes may be lacking. In these cases, using time series which reflect more than one process or which are considered indicative of general environmental transitions may be the only resort.

An important example of this sort of time series is the Southern Oscillation Index (Bjerknes, 1969) which is indicative of major transitions in the coupled ocean-atmosphere system; Quinn (1978) has used this index to predict El Nino invasions off Peru. Indeed, El Nino itself has come to be regarded as an important index of Pacific-wide variations. Chelton (1980) has reported a correspondence between changes in the broad-scale background flow of the California Current and El Nino occurrence. Baumgartner, et. al. (1979) report that conditions in the Gulf of California are dominated by variations corresponding to El Nino occurrences.

Long time scale variations in atmospheric pressure are sometimes used as an explanatory variable in empirical studies of fish stock variation. (See section on Pacific mackerel, below.) It is unlikely that the actual pressure experienced by the organisms has any significant effect on survival; a change in depth of a couple of feet would involve pressure changes comparable to any atmospheric pressure fluctuations. However, just as barometric pressure is useful in indicating weather changes, it is related to variations in atmospheric effects on the ocean environment. Where low atmospheric pressure is related to occurrence of cyclonic storms, anomalous mean barometric pressure may be indicative of (1) anomalous Ekman transport conditions which disrupt upwelling normally produced at the eastern edge of a subtropical high pressure system, (2) negative wind stress curl, (3) increased wind-induced mixing of the upper ocean, (4) decreased solar radiation due to cloud cover, etc. However, each of these effects can be estimated separately; in our opinion it is preferable to indicate separately each process involved in as precise a manner as possible. If it is considered necessary, because of limited degrees of freedom, etc., to combine multiple processes into a single series this should be done in a rational manner, based on the available understanding of the interacting effects of the processes involved.

Other "integrators" which have been used in fishery studies include tree ring width (Cushing, 1979), sunspot activity (Favorite and Ingraham, 1978), and very long term average air temperature (Cushing, 1979).

Even carefully designed indices of individual processes can unavoidably become integrators of several interacting environmental effects. As described above, surface layer divergence indices indicate both the effects of the divergence or convergence of planktonic material and the linked effects of the wind stress curl on the geostrophic flow field. Upwelling indices are related to variations in upwelling or downwelling, offshore transport, and the near-coastal alongshore current. Sea temperature variations can be linked to biological variations through direct physiological effects, and through the dependence of temperature on upwelling, horizontal advection, and turbulent mixing. Obviously, the fishery-environmental problem is not simple, and in the situation of severely limited degrees of freedom, it is well to take great care to avoid generating statistical nonsense.

Independence of data points

Environmental time series are often found to contain a certain amount of serial correlation, i.e., a level of persistence affecting multiple data points. This can be caused both by real variations of period longer than the sampling interval and by inhomogeneties in the time series introduced by changes in sampling method, instrument location, etc. These causes are often difficult to separate.

For example, methods of producing atmospheric analyses such as are used as input data in Bakun's (1973) upwelling index computations have evolved from subjective hand analysis of reports in the 1940's and 1950's to fully automated objective procedures in recent years. In addition, the distribution of reports also changes over time; it is possible that the establishment of a reporting station in an area which was previously undersampled could cause a major disruption of the consistency of the indicator series. Even a direct measurement such as sea level is subject to vertical movements of the earth's crust upon which the gauge is mounted. Temperature series can be disrupted by such things as harbor construction near a measurement site, or by changes in the measurement technique such as the progressive conversion from bucket thermometers to sea water intake thermometers on reporting vessels.

Even when longer term features in a time series represent real environmental changes, they may be undesirable in an analysis. If a correlation is controlled by longer period features, the number of degrees of freedom assumed in order to estimate statistical confidence must be reduced to some fraction of the available number of data points. This represents a further limitation of the severely limited degrees of freedom typically available in fishery data series.

High-pass filtering of data series before testing for a relationship is one way to minimize the likelihood of arriving at unwarranted conclusions. If an apparent correlation disappears after high-pass filtering, then inhomogeneities must be considered as a source of error. The assumed degrees of freedom should be reduced to the number of observations which can be assumed to be independent of one another. (See section on Pacific mackerel, for example.)

POPULATION BIOLOGY CONSIDERATIONS

Population fluctuations of fishes are caused by an interplay between the biology of the organisms, (i.e. the genetic and age structure of the population) and the environmental conditions encountered by the population. In exploited stocks there is the further complication of alterations in the genetic and age structure of the population caused by selective fishing mortality. Before the understanding of a fisheries resource can go beyond rudimentary levels the stock structure of the resource must be adequately described. Knowledge of the number of reproductively isolated stocks, a description of their spawning grounds, distribution, and relative population size is a prerequisite to understanding their population dynamics. The lack of speciation in the pelagic fishes within the various eastern boundary current regions suggests that there is some degree of interchange within each region. In the pelagic fishes of the California Current region the number of reproductively-isolated stocks appears to be relatively small and these stocks appear to be separated into subregions which can be described by surface transport patterns (Parrish et al, Ms). Existence of smaller, reproductively-isolated units (stocklets) within the subregions has not been documented; however little research has been done to test this possibility. Once the stock structure is defined the principal research and management concern centers around the determination of fishing strategy that will maximize and stabilize long-term yield from the stocks or stocks. In small pelagic fishes the principal factor that prevents maximization and stabilization of yield is the high degree of variability in stock size.

Spawner-Recruit relationships

One of the most pervasive questions of fisheries biology is the relationship between parent stock size and reproductive success (usually referred to as recruitment). Near extremes of views on this question were presented in Clark and Marr's (1955) classic paper on the California sardine fishery. Clark suggested that at low and moderate stock sizes recruitment was directly proportional to parental stock size and that at high stock sizes recruitment declined with increasing stock size. Marr suggested that over the expected range of stock size recruitment was unrelated to stock size. These two views are shown graphically in Figure 5a. The relationship between parental stock size and reproductive success can be expressed in different ways. For example, is recruitment dependent upon parental stock size or is the rate of recruitment dependent upon stock size? In the first case the dependent variable is recruitment (i.e. numbers of recruits or recruit biomass) in the second case the dependent variable is the recruitment rate; (i.e. recruits per spawner or recruit biomass per spawning biomass). When viewed from the rate

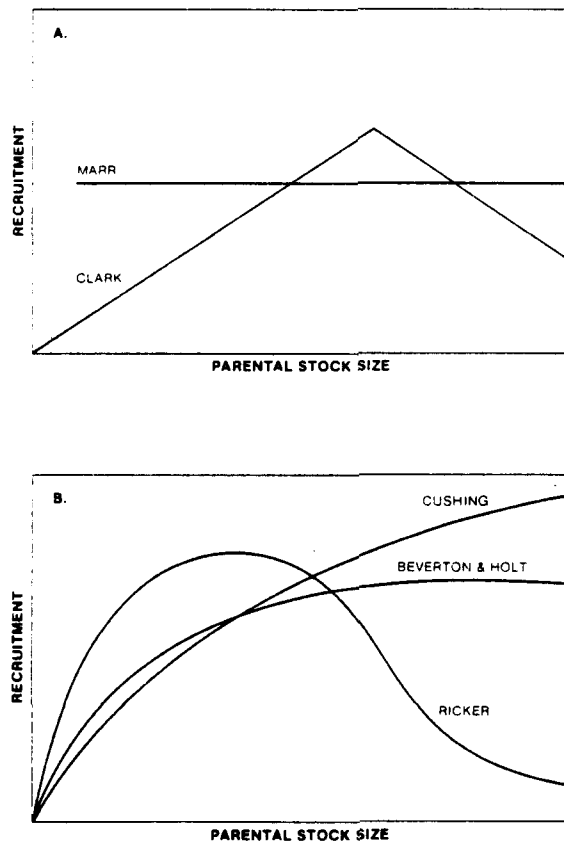


Figure 5. Stock-recruitment functions.

TABLE 2. Stock-recruit models

Ricker: $R = a P e^{-bP}$

Beverton & Holt: $R = P/(a + bP)$

Cushing: $R = aP^{-b}$

R = Recruitment

P = Parent stock size

a = density-independent coefficient

b = density-dependent coefficient

viewpoint Clark's model implies that recruits per spawner are independent of stock size at low and moderate parental stock sizes and are inversely dependent on parental stock size at high parental stock sizes. Marr's model implies that the number of recruits per spawner continuously declines as parental stock size increases; it is therefore density-dependent.

The recruitment rate can be viewed as the summation of a stock's reproductive, growth, and mortality rates up to the age at recruitment. If decreased stock size results in increased growth or reproductive rate or in decreased mortality, the recruitment is termed compensatory density-dependent. That is, the relative recruitment success increases at lower stock sizes. The mechanisms for this type of change include features such as intraspecific competition for food, lower growth rates, lower fecundity, and cannibalism at higher stock sizes. If the rate of recruitment decreases at low stock sizes the stock is said to have depensatory density-dependence. The principal mechanism suggested for depensatory density-dependence is increased natural mortality associated with smaller school sizes that might occur at small stock sizes (Clark, 1974).

The mathematics that have been used to describe the relationships between parental stock size and recruitment principally consist of alternative extinction curves. These extinction curves are used to describe the relationship between recruits per spawner and spawning stock size. The most commonly used models are those proposed by Ricker (1975: 282), Cushing (1971), and Beverton and Holt (1957: 49). These models are listed in Table 2 and shown graphically in Figure 5b. All three models have a density-independent term which can be envisioned as describing the intrinsic rate of increase, and a density-dependent term which is a compensatory term that has the effect of reducing the rate of increase as the stock size increases.

The Ricker (logistic) model has the largest compensatory term and implies that at high stock sizes recruitment is low; the potential shape of the Ricker curve is quite variable. The Beverton and Holt (asymptotic) model implies that at high stock sizes recruitment reaches an asymptotic maximum. The Cushing (allometric) model implies that recruitment increases with stock size but at a continuously decreasing rate.

The choice of which model to use for a particular stock should be related to the hypothesis that is envisioned to limit the stock. If there is good reason to believe that there are very strong density-dependent effects in recruitment, i.e. if the spawning grounds are much more limited in size than the feeding grounds or if cannibalism by adults is significant, the Ricker model may be appropriate. The anadromous stocks of salmonids for which the model was originally developed are a good example for the use of the Ricker model. If the "gate mechanism" is expected, i.e. if nursing grounds have a relatively constant carrying capacity, the Beverton and Holt model is appropriate. The plaice (Pleuronectes platessa), for which the model was originally developed are a good example for its use. If the critical stage (or match-mismatch) hypotheses is considered to be the principal factor controlling recruitment the Cushing model may be most appropriate. The California stock of sardine is a good example for the use of this model (MacCall, 1979).

The Ricker model, due to its flexibility of shape, can approximate the shape of all three of the above examples as long as it is only applied to the stock sizes for which there is sufficient data to justify its usage. Of course none of the regression fits should be extended beyond the range of the data to which it was fitted. The methods used for fitting the various models include linear regression, linear regression with transformed variables, and iterative nonlinear regression. Models fitted with logarithmically transformed variables are fitted to the geometric mean rather than the arithmetic mean and are biased towards low expected values. Corrections for this type of bias are described by Beauchamp and Ohlson (1973).

Life History Stages

Stock-recruitment models work best if the observed variation from the model is small and random. The models give biased predictions if the variation from the model is large, if it contains time series trends, or if there is autocorrelation in the residuals (Sissenwine, 1977). The predictive capability of stock-recruitment models has not proven to be of great value in stocks of small pelagic fishes which have high natural mortality rates. This type of stock, in which recruits comprise a large proportion of the exploitable biomass, appear to be susceptible to recruitment overfishing during unfavorable environmental periods (Paulik, 1971; Cushing, 1975; Murphy, 1972).

Research into stock-recruitment relationships requires extensive age composition sampling of the catch and many years of data at different stock sizes. Recruitment, while not easy to measure, can be reasonably estimated in stocks which have large fisheries and extensive sampling of the catch. The fact that only one data point is accrued per year puts a severe limitation upon the determination of factors influencing recruitment processes. Stocks which have extended spawning seasons with potential multiple peaks, such as the Engraulis stocks of the Peru and California Current regions, have special problems in estimation of recruitment. In the California Current only two pelagic stocks have enough data at different stock sizes to produce statistically meaningful stock-recruitment relationships (The California stock of Sardinops (Murphy, 1966; MacCall, 1979) and the California stock of Seomber (Parrish and MacCall, 1978)). In both of these stocks the stock-recruitment relationships are characterized by very flat curves with a large amount of scatter in the data points. In both, compensatory density-dependent processes appear to be minor and the Cushing model, which implies that highest recruitment occurs at large stock size, provided the best statistical fit. However, over the range of stock size that is likely to occur with heavy exploitation the Cushing, Ricker, and Beverton and Holt stock-recruitment functions would all produce similar curves.

If a significant portion of the variation in recruitment is associated with environmental fluctuations, spawner-recruit models can potentially be improved by inclusion of the associated environmental terms. Recruitment is therefore probably best described with models developed with multiple regression. The Cushing and particularly the Ricker models have several features that make them the best candidates for the development of density and environmental-dependent multiple regression models. As Ricker (1975) has pointed out the effect of environmental variation is expected to be multiplicative. The dependent variable in these two models are logarithmically transformed variables which allows the environmental terms to be exponential terms which have geometric effects. The Ricker model is particularly well suited

for the development of regression models as the dependent variable is the natural logarithm of recruits per spawner, or recruit biomass per spawning biomass ($\ln R/P$). Therefore the terms which best describe the survival rate are those included in the model. If the model that best describes " $\ln R/P$ " is developed with stepwise multiple regression with parental stock size and environmental variables as independent variables the model will be less biased than the case where the environmental variables are regressed against the residuals of the Ricker model (i.e., if the residuals are the dependent variable).

The final multiple regression model, incorporating both density and environmental terms, can then be transformed (by exponentiation) to an expression of absolute recruitment. If desirable the bias in expected value resulting from the fact that the model is fitted to the geometric mean of the observed data can then be avoided by nonlinear regression. The coefficients developed with the stepwise multiple regression can be used as starting values in an iterative nonlinear regression. Environmentally-related variation is likely to be the result of many biotic and abiotic processes. Due to the limited number of observations and attendant problems with degrees of freedom only a small number of terms can be statistically justified. Therefore unless the environmentally-related variations in the rate of recruitment are dominated by one or a small number of environmental processes or features the inclusion of environmental effects is unlikely to be of much benefit.

The processes regulating the populations of exploitable marine fishes break naturally into three stages, based both upon life history phases and data sources. These stages are the early life history, juvenile and post-recruit stages. The early life history stage is limited to the period when the organisms are largely planktonic. This stage is characterized by very high mortality. The bulk of information concerning this stage comes from egg and larval surveys, field studies and laboratory experiments. The early life history, as used here, ends at about the time that the larvae become mobile enough to avoid egg and larvae survey nets. The juvenile stage is essentially the stage that is unsusceptible to capture by either egg and larvae survey nets or commercial fishing gear. From a modelling viewpoint the feature that characterizes this stage is the lack of information. The post-recruit stage is the stage that is susceptible to capture by commercial gear. A large proportion of the knowledge of this stage consists of information gathered from the fishery.

Modelling of any one of these three life history stages is a difficult task and there presently are no stocks for which fully developed models of all three life history stages are developed. Modelling of the individual life history stages is dominated by models of the post-recruit stage with a lesser total effort on the early life history stage and practically no effort on the juvenile stage. Modelling of any one of the life history stages must necessarily ignore many of the relationships and processes that occur in the other life history stages. The following sections describe some of the weaknesses of models which concentrate on only one of the life history stages.

Post-recruit modelling

The bulk of the current population models of fish stocks is composed of models which are focused on the post-recruit stage. Adequacy of the models is primarily limited by first order approximations of the parameters which describe the growth, mortality, and recruitment rates. Population fluctuations occur through the alteration of one or more of these rates and the mechanisms that cause these alterations are largely related to differences in stock size, environmental conditions and age composition of the stock. Determination of relationships of the environmental state, stock age composition and stock size to growth, mortality and recruitment rates requires data from extensive long-term sampling programs. Such data are very sparse and most of our current information is from a few well-studied stocks.

Growth is the easiest of the three required rates to measure. In addition, large numbers of samples can be taken each year. Growth, therefore, is the best described rate. For purposes of describing age-dependent growth, samples are largely independent if taken through catch sampling programs or exploratory fishing. This independence does not extend to the testing of the relationship between stock size and growth rate or that between environmental state and growth rate. For the testing of these relationships only one observation accrues per year and these observations may be autocorrelated.

Documentation of changes in growth associated with changes in stock size of post-recruit fishes is not common in the literature (Murphy, 1977). This may be partially due to the fact that data is not often collected in a manner to show such changes. For example, weight at age is a more meaningful measure of growth than the more commonly used length at age. Of course a stock must also fluctuate over a wide range of stock size before a relationship between stock size and growth rate can be determined. Another reason that density-dependent changes in the growth rate are uncommon or relatively small is that when surplus energy is available it may be utilized for gonadal growth rather than somatic growth. Compensatory gonadal growth can occur through earlier age at maturity, increased batch fecundity or increased numbers of spawnings per year. Earlier age at maturity at lower stock size is a common feature in the stocks of small pelagic fishes of eastern boundary currents and has been described in the California stocks of sardine (Murphy, 1966) and mackerel (Parrish and MacCall, 1978) and the Peru stock of anchoveta (Valdivia, 1978). Verification of variation in batch fecundity or number of spawnings per year is presently unavailable and will be difficult to obtain. Fecundity is usually considered to be proportional to body weight and is often expressed as the number of eggs per unit body weight. If this is the case, even if there are no compensatory changes in the number of eggs per unit weight, fecundity will increase with compensatory changes in the condition factor such as described for the California stock of sardine (MacGregor, 1959). Availability of surplus energy can be the result of compensatory density-dependence or favorable environmental state; with a limited set of observations it is difficult to sort out the two factors. Mortality rates are very difficult to measure accurately and natural mortality in exploited stocks is confounded with fishing mortality. Essentially nothing is known of the dependence of mortality, in the post-recruit stage, upon stock size or environmental state. Heavily exploited stocks of small pelagic fishes often exhibit increased total mortality with increased age within the post-recruit stage (Paulik 1970). It is not known if this is due to increasing natural or fishing mortality.

Modelling juvenile fishes

The present information on the juvenile stages of the pelagic fishes of eastern boundary current regions is too incomplete to be of much use in population modelling. Information on mortality rates and on the processes affecting mortality is lacking. The available field data base is largely limited to general descriptions of geographical distribution plus some information on sizes of fish. Data is needed on the vertical distribution of juvenile fish. Laboratory data is largely limited to growth data which is not verified against field data; although with the new daily aging techniques (Methot and Kramer, 1979) this is an area of active research.

The stock-recruitment relationships discussed previously group the processes affecting the early life history and juvenile stages into a single process (i.e., recruitment). The relative effect of the early life history and juvenile stages in determining recruitment fluctuations is not known. And it obviously must be determined separately for each stock. Although the early life history stage is critical on the short time scale, in that it has very high mortality, there is little evidence that year class size can be predicted by the numbers or concentrations of large larvae. For example, Smith (1978) has shown that the ratio of large larvae was nearly constant over the period of 1952 - 1956 and has suggested that the largest source of variation in sardine year-class size occurred during the juvenile stage. One of the most perplexing problems concerning recruitment processes in upwelling areas is the contribution of the large concentration of larvae which are found well offshore of the slope.

Modelling the early life history stage

Modelling of the early life history stage involves problems comparable to those of the post-recruit stage in addition to those particular to the early life history stage. The value of post-recruit models is largely determined by how well they predict the potential yields to the fishery and their adequacy is very sensitive to the accuracy of their stock-recruitment functions. Early life history models will eventually be evaluated on how accurately they predict the number of larvae entering the juvenile stage. The adequacy of early life history models will in a similar way be sensitive to the accuracy of stock-egg functions.

Both juveniles and post-recruits have the potential to reduce the survival of eggs and/or larvae through cannibalism or competition for forage. They also have the potential to increase the survival of eggs and larvae through predation on potential egg and larval predators. However, the most obvious effects that the post-recruit stage has on the early life history stage are those associated with the production and spawning of eggs. The numbers of eggs, their quality, and their distribution in time and space are determined by processes affecting the post-recruit segment of the stock. Fecundity and egg quality can be altered by density-dependent or environmentally related variations in the growth rate, condition factor, age at maturity, number of spawnings per year, and age structure of the post-recruit segment of the stock.

The distribution of eggs in time and space is influenced by oceanographic conditions (i.e. temperature, currents, food availability, wind events) which affect the geographical distribution of the adults. Features which trigger spawning, although not well understood, could also include oceanographic conditions. Stock size also alters the geographical distribution of spawning as a stock may increase the size range, of its spawning grounds as stock size increases. The stock may also saturate the available spawning grounds in both time and space when the stock is large. If this occurs the variance in the stock recruitment relationship should increase as stock size decreases. The age structure of the stock influences the time of spawning as older fish often start spawning earlier in the season than first time spawners. With species that have multiple spawning, older fish may have a longer spawning season than first-time spawners.

The rates at which all of the above relationships between adults and their eggs and larvae occur are potentially density-dependent. Density-dependent rate increases are more likely when lowered population size is caused by exploitation rather than when it is caused by environmental changes which may independently affect the rates at which the processes occur.

Several extremely sophisticated larval fish models have recently been published. (Vlymen, 1977; Bever, In press) These models are well designed to model individual spawning spots. Thus they are in many ways analogous to yield-per-recruit models in that they describe the survival and growth of a given amount of eggs or larvae. For the purposes of predicting reproductive success or recruitment of individual stocks for management purposes these types of models have severe limitations. The models were, of course, not intended for management purposes. The results of these models are dependent upon given environmental states. The limitations of the models are not primarily due to the structure of the models but rather to the lack of knowledge of the environmental variables in the models. Determination of the average environmental conditions encountered by eggs and larvae in a given year is beyond our present capabilities and resources. Even if we were able to establish the mean environmental conditions encountered by eggs and larvae it is likely that the use of mean data would not result in good predictive capability due to patchiness problems. The survival of individual eggs and larvae is dependent upon interactions that occur on very small space and time scales. These interactions are associated with processes which operate on a wide range of scales. Thus the survival from individual spawning spots is affected by a range of space scales from that of less than the size of a spawning spot to that of at least the size of the spawning grounds and a range of time scale from less than hours to at least the length of the spawning season plus the length of the early life history stage.

A possible solution to the integrating problem is the use of spatial compartment models to account for environmental state patchiness in the larger space scales. Smaller-scale patchiness could be accounted for by stochastic terms. Unfortunately while the environmental state may be considered to be an additive process the response of individual spawning spots to environmental conditions is not additive. For example the survival of larvae after two days of starvation is dependent both on the age of the larvae and the feeding conditions, (i.e., environmental state) on the days preceding the two days of starvation. The spatial compartment model must therefore include age groups. The fact that processes affecting egg and larval survival operate on short time scales implies that the models must be run with short time steps. Thus, the combination of requirements for adequate spatial detail, age composition, and short time steps will result in the requirement of a huge computer and considerable running time.

An alternative to the use of a large compartment model, which also requires less conceptual alteration of existing larval models, is to model individual spawning spots. The models could be moved around in fields of the environmental state as Lagrangian drifters.

Eastern boundary current pelagic fishes have such extensive spawning grounds and extended spawning seasons that integration of scales becomes a major, perhaps dominant feature of any predictive model of the early life history stage.

RECENT ADVANCES - CALIFORNIA CURRENT REGION

Anchovy

The data base on the northern anchovy *Engraulis mordax* is different from those for the other better known species in the California Current Region in that the majority of information comes from field and laboratory studies rather than being taken from the fishery. There is more information available on eggs and larvae than on post-recruits. Most recent larvae work is well discussed in companion papers in this volume; we will therefore limit our discussion of recent anchovy research generally to processes having a larger scale than that affecting individual larvae.

The anchovy is widely distributed throughout the California Current System. Blood serum studies (Vrooman and Smith, 1971) show that there are three reproductively-isolated stocks (Fig. 4(c)) which exhibit considerable differences in their seasonality of spawning. The spawning grounds of the stocks appear to be separated by oceanographic features. The northern and central stocks are separated at the Northern California upwelling maximum (Parrish et al., MS) and the central and southern stocks are separated in the region where negative wind stress curl approaches the central Baja California coast (Fig. 4(b)). The bulk of the information available on the anchovy concerns the central stock which extends from about 29°N to 38°N.

The central stock of the northern anchovy, like the anchoveta of the Peru Current, spawns to some degree all year round, with peaks in February-March and August-September. In both the peak in the winter-spring transition is greater than the peak in the summer-fall transition.

Lasker and coworkers (Lasker 1975, 1978; Lasker and Smith, 1977; Lasker and Zweifel 1978; Smith and Lasker, 1978) have shown that first feeding is a critical period for anchovy. Success of first feeding is associated with the occurrence of small scale concentrations of dinoflagellates which can be dispersed by wind events. However, the fact that the anchovy has such a long spawning season makes it very difficult to predict recruitment on the basis of indices of wind stress or other environmental data. Good environmental conditions during any part of the year could conceivably dominate annual recruitment. A recent breakthrough on daily aging (Methot and Kramer, 1979) greatly enlarges the possibilities for analysis of the relationships between environmental conditions and larval survival. Adequate sampling of pre-recruits coupled with daily aging will allow assessment of the time of year and associated environmental conditions which result in significant recruitment.

MacCall (1979) has noted a correspondence between low second quarter (April-June) values of the upwelling index (Bakun, 1973) at 33°N in the period 1947 to 1952, and extremely low anchovy biomasses in the early 1950's. This corresponded to apparent recruitment failures in sardine in 1949-50 and Pacific mackerel in 1949-50-51 and to disappearance of bonito (*Sarda chiliensis*) in the late 1940's and their reappearance in 1954.

We might add that upwelling index values at 39N, which characterize the Cape Mendocino - Point Arena area where the most vigorous upwelling in the California Current system occurs, were chronically low through the second half of the 1940's. This may have adversely affected the general level of productivity throughout the entire system (See sardine model, below.) Thus the low spring upwelling of 1947-52 local to the Southern California Bight may have been superimposed upon poor conditions which were advected from the upstream upwelling maximum.

Two recent studies indicate direct interactions between adult and larval processes. Hunter and Goldberg's (1980) work on batch fecundity shows that the northern anchovy spawns approximately once a week over an extended spawning season, indicating that energy reserves and the availability of food to the anchovy may influence the number of spawnings per year. Hence total fecundity may be a function both of adult anchovy biomass and food availability. Hunter and Kimbrel (in press) found that approximately 17 percent of eggs spawned were cannibalised by filter-feeding anchovies, and they estimate that this may represent about 32% of the natural mortality of anchovy eggs.

Pacific mackerel

Substantial catches of Pacific mackerel commenced off California in the late 1920's. Economic conditions at the beginning of the 1930's caused a large drop in fishing effort, but a recovery of prices and demand resulted in rapid expansion of the fishery from 1932 to 1935. Landings reached a peak of 66,500 MT in the 1935-36 season. Thereafter, the fishery went through a long, fluctuating decline. In the 1953-54 season the fishery was nearly exhausted, but good recruitment in the 1950's (Fig. 6) rejuvenated the fishery for a while until a series of poor recruitments in the 1960's brought it to a temporary close. Recently the population has rebounded strongly.

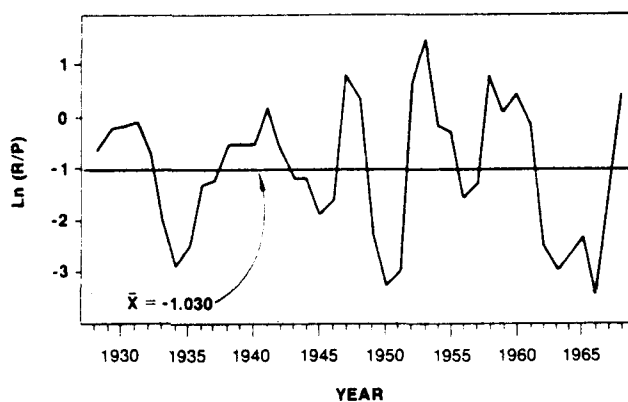


Figure 6, Time series of the natural log of the observed recruit biomass per spawning biomass in the California Current stock of Pacific mackerel, Scomber Japonicus.

A detailed analysis of the fishery, including population biology, cohort analysis, spawner-recruit models, and yield simulations, was presented by Parrish and MacCall (1978). Here we briefly abstract certain of their main findings concerning environmental dependence. These are in the area of empirical environmentally-dependent spawner-recruit models. Their post-recruit models do not address any environmental dependence, incorporating the usual assumptions of constant natural mortality rate, etc.

The authors consider a number of environmental variables, which are assumed to act mainly during the May-July spawning period. Thus, they are hypothesizing that environmental effects on Pacific mackerel recruitment occur at the spawner-egg and the early life history phases. Several linear combinations of months were considered, including (1) a simple average over the 3-month May-July period of peak spawning, (2) a simple 3-month April-June average to test for lagged effects (e.g. upwelling would provide suitable food particles only after some lag, assumed to be of the order of one month), and (3) "prorated" averages of both 3-month periods, where each monthly contribution is weighted by an estimate of the percentage of spawning which occurred during that month in each particular year of the time series.

The environmental variables for which these linear combinations produced the best correlations with recruitment are given in Table 3 (Parrish and MacCall's Table 18). Other variables tested which did not

yield significant correlations included Saur's (1972) index of very large-scale subtropical gyral circulation based on Hawaii to San Francisco sea level difference. Separate tests against all the individual monthly values produced lower correlations than those against the linear combinations (Table 3) considered characteristic of the entire spawning season.

TABLE 3. Correlation Coefficients of Linear Combinations of Monthly Values of Environmental Variables with logarith of Pacific mackerel recruitment.

Variable	N	May-July mean	Prorated May-July	April-June mean	Prorated April-June
SPIER	41	.270	.416**	.276	.255
BARP	41	.030	-.165	-.007	-.059
SSTC	38	.434**	.432**	.432*	.392*
WINDC	38	-.354*	-.380*	-.289	-.306
SLLJ	41	-.542**	-.391**	-.514**	-.392**
SLEV	41	-.509**	-.348*	-.509**	-.366*
UP	23	.458**	.319	.575**	.713**
CURL	23	.528**	.610**	.486*	.584**

SPIER -Sea surface temperature at La Jolla
 BARP -Barometric pressure at San Diego
 SSTC -Sea surface temperature, Marsden Square quadrant 120(2)
 WINDC - Wind speed, Marsden Square quadrant 120(2)
 SLLJ -Uncorrected sea level height at La Jolla
 SLEV -Sea level height at La Jolla corrected for atmospheric pressure
 UP -Upwelling index at 30°N
 CURL -Wind stress curl (surface layer divergence) index at 30°N
 * -Significant at 5% level
 ** -Significant at the 1% level

The highest correlation of all was found with the April-June composite upwelling index, which is conceptually satisfying since upwelling would be expected to have a lagged effect. Highest correlations with sea temperature and with surface layer divergence (wind stress curl) were with the May-July prorated variables, again conceptually satisfying since these effects would seem to act directly on the larvae without lag. The correlation coefficients with temperature are positive, suggesting that warm temperature contributes to reproductive success; in this case the temperature appears to indicate a physiological effect, since a temperature-upwelling-productivity linkage would result in negative correlation coefficients with temperature. The correlations with surface divergence were positive; this is somewhat puzzling since one would expect convergence (negative divergence), by concentrating food organisms, to favor survival. Perhaps convergence could be detrimental by concentrating mackerel larvae in frontal structures where they would be highly vulnerable to predation. An alternative explanation could be that the relaxation of the blocking of northward coastal counterflow by the negative wind stress curl lobe off central Baja California could have allowed augmentation of the exploited northern subpopulation by the southern subpopulation (See subsection on convergence-divergence in the section on environmental variability, above). Negative correlations are found with coastal sea level; this could be related to the upwelling effect since strong upwelling would tend to depress coastal sea level.

Parrish and MacCall present a number of empirical models containing various formulations of density-dependence (including those presented in Table 1 and in Figure 5(b)) and the environmental variables (Table 3). Since the upwelling index and surface divergence index series are available only since 1946, models containing these variables treat only the latter part of the historical record of the fishery. In order to retain reasonable degrees of freedom for each explanatory factor these models were restricted to a density factor and two environmental factors. Models treating the total time series were allowed to contain three environmental factors in addition to a density dependent factor. None of the density dependent formulations were as significantly correlated with recruitment as were various environmental

terms; density dependence alone could account for no more than 24% of the observed variation. However, the authors felt that some form of density dependence was a conceptual necessity and so a density dependent formulation was forced to appear in each multiple regression model. However, the fitting of the density dependence was accomplished in concert with the environmental terms. This is a fundamentally different procedure than that used by Nelson, Ingham and Schaff (1977) who first fitted an assumed density dependence and then fitted environmental variables to the residuals. In our opinion the procedure of Parrish and MacCall is more valid, since fitting a density dependence before accounting for environmental variation assumes that environmental variability does not affect the fit; if this were the case there would be little need to include environmental terms.

A model containing a Ricker density dependence, and an upwelling index and a wind stress curl (surface layer divergence) index as environmental terms, was significant at much greater than the 99% level and explained 76% of the observed recruitment variation since 1946. A model containing sea temperature, coastal sea level and barometric pressure, as well as a Ricker function was again significant at the 99% level and explained 59% of the variation in the longer series covering the total fishery.

The two intense declines in the Pacific mackerel stock correspond to periods of poor recruitment in the late 1940's and early 1950's and in the mid, 1960's (Fig. 6). During the first period, there was an extended series of poor upwelling years in the upwelling maximum region off Northern California (Bakun, 1973). During the decline in the 1960's, anomalously low upwelling in the local Baja California spawning area was indicated. It is interesting to note that in the recent period, not treated by Parrish and MacCall, extremely vigorous upwelling is indicated for the mid 1970's, while excellent relative reproductive success in 1974 and 1976 has enabled the Pacific mackerel stock to rebound from its previous collapsed state.

The environmentally-dependent functions produced by Parrish and MacCall have allowed them to run simulations of management options containing a realistic spectrum of environmental variance, i.e. an aperiodic cyclic pattern as opposed to the random environmental noise usually assumed (e.g. Allen 1973, Walters, 1975). These simulations have been used by the State of California in establishing a management strategy for Pacific mackerel, which is now in operation.

Before concluding our survey of this work, a comment on independence of data points is relevant to the purpose of our present paper. The ratio of recruitment to parental biomass (Fig. 6) obviously contains substantial autocorrelation; the series in no way resembles random "white" noise. Rather, runs of multiple years of good and poor recruitment dominate. In this case the assumption of an independent data point each year probably results in a substantial overestimate of available degrees of freedom (Table 2). However, one can visually convince himself that there are at absolute minimum some ten or eleven independent data points determining the function in Fig. 6 and at least eight in the series since 1949 (by counting extrema or crossings of the zero line, etc.). A recomputation indicates that the significance of Parrish and MacCall's major relationships is still at an acceptable level even when the assumed degrees of freedom are so reduced. However, in cases where the relationships may be less pronounced, this issue of independence of data points may be critical. A formula for choosing the reduction in degrees of freedom in an autocorrelated time series is presented by Sutcliffe, Loucks, and Drinkwater, (1976).

Sardine

The Pacific sardine (*Sardinops caerulea*) fishery expanded rapidly in the years prior to World War II to become the largest fishery in the United States with 774,000 MT landed in the 1936-37 season. The exploited stock spawned in the region of stability and favorable transport south of Point Conception (Parrish, et. al., MS) but during the period of abundance migrated as adults to feed in the region of vigorous upwelling to the north, an important fishery arising as far north as Vancouver Island. A period of relative stability in the catch ended in 1945, whereupon the catches begin to decline disastrously to the point where the fishery essentially vanished in the early 1960's.

There are two sets of recruitment estimates published for this stock. Murphy's (1966) cohort analysis presented numerical values through 1960. In this analysis, Murphy assumed a change in natural mortality rate from 0.4 in the years previous to 1949, to 0.8 in subsequent years in order to match independent stock estimates based on egg and larvae surveys. MacCall (1979) showed that this change was unnecessary and presented recruitment estimates through 1965.

Since no studies of sardine which incorporate time series indices of environmental processes have yet been published, we here present results of a preliminary hypothetical model formulated to include density dependence and environmental effects represented by upwelling index and wind stress curl index time series. Four such time series were hypothesized as indicative of environmental effects on larval survival.

These included an upwelling index and a wind stress curl index computed at 30°N latitude (symbols: UP30 and CURL30), found by Parrish and MacCall (1978) to be the most significant variables in their Pacific mackerel model, and a wind stress curl index at 33°N latitude (CURL33), considered characteristic of surface layer divergence within the Southern California Bight and possibly related to the strength of the gyral circulation in that area. Each of these three index series was averaged over the 5-month period, February through June, of maximum sardine spawning (Murphy 1966).

A fourth environmental variable (UP39) is the average over the calendar year preceding spawning of the upwelling index computed at 39°N latitude. The inclusion of this variable, which does not characterize the specific season or the location of spawning, was motivated by correlations noted between longer-term upwelling index variations (Fig. 7) in the area of the Northern California upwelling maximum and indices of spring zooplankton abundance⁵ in the downstream areas extending from Central California to southern Baja California. A multivariate response such that strong upwelling off northern California during the previous summer and fall quarters was associated with highest zooplankton concentrations in the downstream offshore regions relative to the concentrations directly inshore of those regions was the most robust relationship found. The spring zooplankton concentrations in the various offshore regions along the coast have a tendency to vary directly with the northern California upwelling index but the various univariate relationships are less pronounced than are those which are associated with the multivariate nearshore/offshore contrast (significance: .90 v.s. .98).

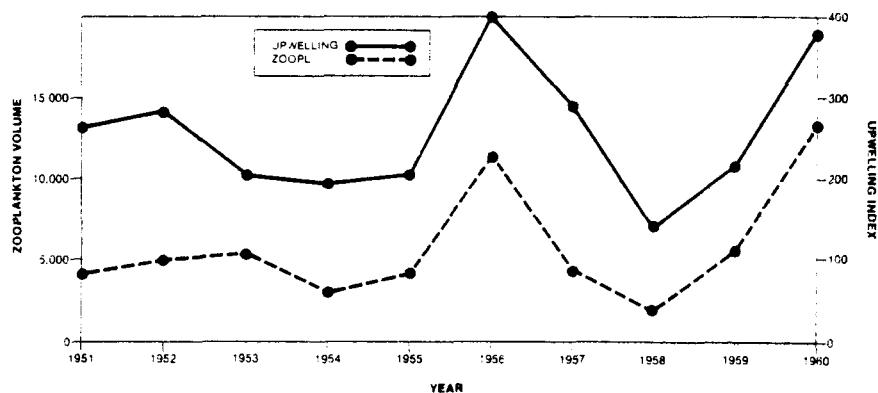


Figure 7. Central California offshore zooplankton abundance during spring (Paul E. Smith, personal communication v.s. upwelling index at 39°N latitude (Bakun, 1973) averaged over previous 12 months.

Density dependent effects were incorporated by including parent stock size as a variable (STOCK). A final variable which was a simple linear trend (TREND) was added to reflect long-term changes, such as possible competition due to the rise of the northern anchovy population during the time period modeled. The modeled period covered only the decline of the stock since the upwelling and wind stress curl indices are not presently available for the period prior to 1946.

We expect the effects considered to alter the proportion surviving of whatever number of eggs were spawned rather than "killing" or "not killing" any fixed number. Since we wish as much weight given, for

5. Personal communication, Paul E. Smith, Southwest Fisheries Center, National Marine Fisheries Service, NOAA, La Jolla, California, 92037.

example, to a halving of expected recruitment as to a doubling, a regression against the logarithm of the ratio of recruits to spawners is appropriate. The formulation of our model is therefore:

$$\ln(\text{RECRUITS}/\text{STOCK}) = a_0 + a_1 \text{UP30} + a_2 \text{UP39} + a_3 \text{CURL30} + a_4 \text{CURL33} + a_5 \text{STOCK} + a_6 \text{TREND}$$

Note that upon transformation to a prediction equation by taking the exponential of this model equation, the term containing the variable STOCK corresponds to a Ricker function (see Table 2).

The model was run on both the Murphy and MacCall population estimates; we look for results which are consistent in the analysis of both of the two separate sets as being perhaps less subject to distortion by deficiencies in our knowledge of the real population variations.

Against MacCall's estimates the full model was significant at 0.95. When the two least significant variables, UP30 and CURL30, were dropped from the model the significance improved to better than 0.99 ($r^2 = .7$). Regression coefficients were positive for variables UP39 and UP30, and negative for CURL30, CURL33, STOCK and TREND. Thus strong upwelling appears to favor survival, strong curl (surface layer divergence which would oppose formation of concentrated patches or organisms) corresponds to decreased survival. There appears to be compensatory mortality (negative coefficient for STOCK) and an apparent declining trend in survival over the period (possible competition from the increasing northern anchovy population). Of course the regression coefficients for UP30 and CURL33 should not be taken very seriously since significance increased dramatically when these variables were dropped.

The most significant variable by itself is UP39; the regression against this variable alone is significant at above .90. However, with STOCK and TREND in the model with UP39, UP39 is the least important of the three in reducing unexplained variance. The model with STOCK and TREND only is significant at .995; however, against either STOCK or TREND alone the regression is completely non-significant. The model with the three variables STOCK, TREND and UP39 is significant at better than .995 ($r^2 = .67$).

Murphy's (1966) estimates yield a series five years shorter than MacCall's (Fig. 8). This further depletes the seriously limited degrees of freedom. In this case the full model has an R-square of 0.92 and is significant at the 95 percent level. UP39 and UP30 have positive regression coefficients, STOCK and TREND have negative coefficients, as before. CURL33 has a negative coefficient as before but now CURL30 has a positive coefficient. This positive effect of a lessening of the ordinarily negative values of CURL30 is the same pattern noted by Parrish and MacCall in (1978) for the Pacific mackerel. The most significant single variable is STOCK, yielding significance at better than 90 percent and an R-square of .30. If TREND is then added, significance increases to the 99 percent level. If UP39 is introduced at this point its added contribution is significant at the 95 percent level. Subsequent addition of CURL30 to the model already containing STOCK, TREND, and UP39 is significant at somewhat better than 90 percent. The model containing the four variables, STOCK, TREND, UP39, and CURL30 is significant at better than the 99.5 percent level. R-squared is .92.

The variable UP39, which is designed to measure the effect of annual-scale variations in the northern California upwelling maximum, has appeared as an important factor against both population data sets. A period of generally weak upwelling commencing after the Second World War lasted through 1963, (Bakun, 1973) broken only during 1951 and 1955-56, which as a matter of fact were followed the next year by relative sardine year-class success (Fig. 8) and 1959, when the population was already at quite low levels. Murphy (1966) has reported a tendency for the spawning of sardines, before the population collapse, to be situated offshore relative to the spawning of anchovies. We have here noted the tendency for UP39 to reflect increases in offshore zooplankton concentrations relative to those near the coast during the spring spawning season. It seems a possibility that the long term variations in upwelling in the upwelling core of the California Current region could have been a factor in the rise of the anchovy at the expense of the sardine.

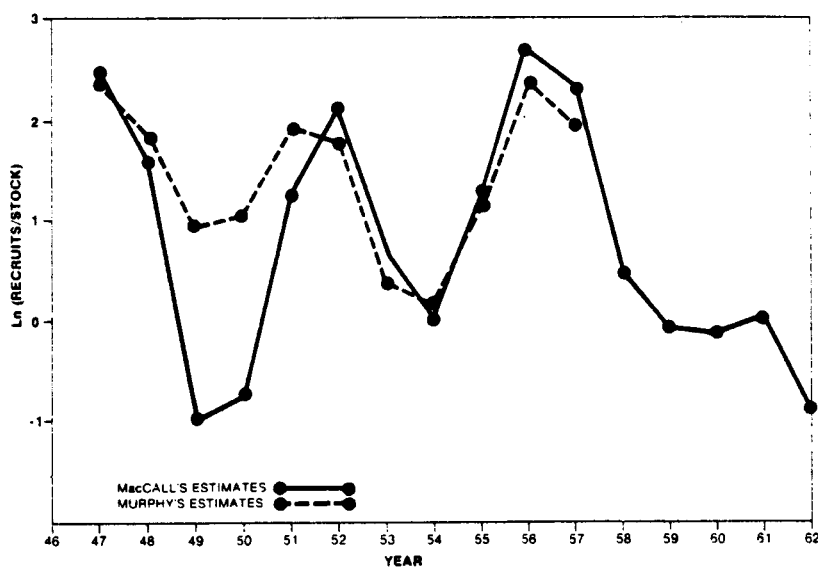


Figure 8. Natural log of the ratio of recruits (10^6 fish) to parental biomass (10^3 metric tons) based on the estimates of Murphy (1966) and MacCall (1979) over the modeled period of decline of the Pacific sardine fishery.

Regression analyses of both data sets indicate a compensatory effect of stock size and a negative trend in the rate of recruitment of sardine after 1946. The compensatory effect was obviously not strong enough to keep the population from collapsing under the combined effect of heavy exploitation and a declining trend in the rate of recruitment. The declining trend in the rate of recruitment could have been related to increasing competition with the rising anchovy population or it could be the result of overestimation of the potential spawning biomass due to an increasing proportion of sardines of southern origin as the stock declined as was suggested by MacCall (1979).

Again this is a situation where the data offer some tantalizing indications, but the available degrees of freedom in the historical time series are far too limited to yield final conclusions.

Hake

Substantial catches of Pacific hake (*Merluccius productus*) commenced abruptly in the mid-1960's. Smith (1975) has reported a geographical shift in larval hake abundance, coincident with the heavy fishing pressure, such that larvae became more abundant off Central California and less abundant off Baja California. He hypothesized a linkage whereby the fishery resulted in a relative depletion of larger sized fish, which may either have traveled farther south to spawn or have participated in multiple spawning, the latter of which would have occurred farther south along the annual migration route.

Bailey (In press) presented a model supporting this hypothesis and further showed that the offshore extent of larvae off Central California was correlated ($r = 0.70$, significance 0.99) with offshore transport as indicated by interyear variation of the January monthly upwelling index (Bakun, 1973) at 36°N latitude. Off Baja California no such correlation was found. Bailey suggests that, since hake larvae tend to be distributed near the top of the thermocline, a deeper surface mixed layer off Baja California could perhaps protect the larvae from offshore transport.

Bailey (MS) constructed an index of yearclass strength from annual trawl surveys by summing the percentages of the total age composition contributed by each cohort over the ages 4-6 years. Over 14 years of available data, January offshore Ekman transport is negatively correlated ($r = 0.73$, significance 0.997) to this year class index; offshore transport during the winter spawning season appears to be detrimental to reproductive success, in agreement with the hypotheses presented by Parrish et al (MS). If larvae spawned off Baja California are indeed relatively protected from offshore transport, and the shift of spawning intensity to the less protected Central California region was indeed caused by the operation of the fishery, this situation presents an additional mechanism by which fishing pressure may adversely affect resilience to environmental perturbation.

Temperature does affect the situation. Bailey (In press) indicates more northward spawning in warm years relative to cold years. In addition egg and larval survival seems to be better in warm years judging from numbers of large larvae found in the spring. Bailey found that when a temperature index was added as a second explanatory variable to the regression of year class strength against Ekman transport, 69% of the variance in year class strength ($r = 0.83$, significance 0.998) is accounted for.

Bonito

The Pacific Bonito, Sarda chiliensis, has been fished commercially in the California Current region since the beginning of this century. Collins and MacCall (1977) have summarized the available information on the population dynamics and biology of the California Current stock.

Historically, the landings have fluctuated widely. The population appears to be centered near Sebastian Vizcaino Bay in central Baja California while much of the exploitation occurs off Southern California. The Southern California fishery apparently operates on two stock segments, one of which migrates annually northward from the population center and the other of which is a transient resident population which becomes established during periods of particularly favorable local conditions. Thus it is difficult to separate fluctuations in stock size from variations in availability to fishing operations.

Collins and MacCall constructed an index of relative recruitment success from estimates of spawning biomass derived from aerial surveys and estimates of recruitment based on catch per unit effort (CPUE) of the partyboat sport fishery (MacCall, Stauffer and Troadec, 1974). They found a positive relationship between this index and the upwelling indices (Bakun, 1973) off northern Baja California averaged over the March-July spawning season. Previous to 1963 no aerial surveys were available. For this period Collins and MacCall used the ratio of CPUE during a given year to the CPUE of the year previous to indicate relative recruitment success and to demonstrate a similar relationship to upwelling index as was found for the later period.

Dover sole

Many of the pleuronectids of the California current region have extended pelagic phases. Dover sole, Microstomus pacificus, which is the dominant commercial flatfish of the region, has larvae which are pelagic for up to a year; it is a late winter - early spring spawner. Off Oregon younger larvae are common both inshore, over the continental shelf, and offshore. Larger larvae are most common in waters outside of the continental shelf but during the winter there is an increase in the largest larvae over the shelf and slope where they settle (Pearcy, et. al., 1977). Hayman (1978) used fishery-based estimates of year-class size of Dover sole to determine the relationship between recruitment and oceanographic conditions. He found that recruitment was associated with reduced offshore Ekman transport during the period of maximum upwelling off Oregon (June-July) and with increased convergence during the Dover soles' settling period (December-January). It appears that increased offshore dispersal, during the period of the year when upwelling prevails off Oregon, is associated with reduced recruitment of the Dover sole and that wind-related features during the winter settling period also affects recruitment.

Rockfish

Little is known about the population fluctuations of rockfish in the California Current, but it seems useful to our discussion of drift responses to present some anecdotal information. In the California

Current region there are nearly 60 separate species of the genus *Sebastes* which are known by the collective term rockfish. The existence of such a variety of species in the very dispersive medium of an upwelling system may be facilitated by their livebearing mode of reproduction which produces young which may be capable of maintaining position relative to very specific ocean depths, bottom types and other conditions. Most of these species release young in the late winter when offshore surface transport is most relaxed (Parrish, et al., Ms). The larvae are pelagic for 4-6 months and the juveniles are observed to congregate in the inshore region in the summer. It is known that occasional good year-classes pass through the fishery; however, until very recently the fishery has not been regularly sampled and the relative sizes of individual year-classes is unknown.

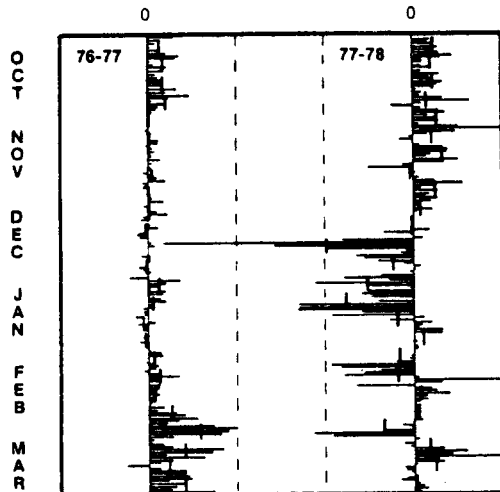


Figure 9. Daily and weekly means of 6-hourly upwelling index computations at 36 degrees N. latitude on the Central California coast. Horizontal lines indicate daily mean values. Values to the right of the zero line indicate offshore transport and upwelling; those to the left indicate onshore transport and downwelling.

Two very anomalous recent winter situations have been the winter of 1976-77, in which the near absence of storms contributed to a serious drought in California, and the winter of 1977-78 in which the drought was broken dramatically by unusually intense winter storm activity. Upwelling index computations (Figure 9) illustrate the contrasting conditions. The winter of 1976-77 is a consistently low energy situation marked by the near absence of periods of transport either toward or away from the coast. This lack of significant transport events is unique in the time series of daily indices which begins in 1967 (Bakun, 1975). During 1977-78 intense storm events followed one another in rapid succession, resulting in a highly fluctuating mixture of strong onshore and offshore transport episodes.

During the summer of 1977 extraordinary concentrations of juvenile rockfish were observed off northern-, central-, and southern California. In contrast, the 1978 year-class appears to be a complete bust, judging from observations of summer juvenile concentrations.

To attribute the apparent differences in larval rockfish survival to the difference in transport conditions, it seems necessary to assume that the ability of larvae to maintain a position relative to the coast throughout the pelagic period is crucial. The extent to which the larvae may be capable of maintaining such a position is undocumented. Parrish, et al. (MS) point out a pattern of correspondence between fish reproductive strategies and transport characteristics which suggest a general difficulty in maintaining resident populations in the region of intense upwelling. If the relative success of the large number of rockfish species in countering this pattern is based on their livebearing mode of reproduction, the required assumption seems the most likely mechanism. It will be interesting to note whether the present very stormy winter, 1979-80, will be followed this coming summer by a scarcity of juvenile rockfish in California coastal waters.

6. Personal communication, Jim Hank, California Dept. of Fish and Game, Monterey, California, 93940.
7. Personal communication, Kenneth Mais, California Dept. of Fish and Game, Long Beach, California, 90801.
8. Personal communication, William H. Lenarz, Southwest Fisheries Center, National Marine Fisheries Service, NOAA, Tiburon, California, 94920.

Dungeness crab

Peterson (1973) found significant correlations indicating increased Dungeness crab landings off Washington, Oregon and Northern California in years following high values of Bakun's (1973) upwelling indices averaged over the spring and summer seasons. The lag times for the correlations were 1/2 year for Washington and 1 1/2 years for Oregon and Northern California. Since the period of growth from larva to recruitment is four years, the upwelling effect on recruitment could not be acting at the larval stages. Peterson suggested that delays in molting during years of low upwelling-related productivity could be the causative mechanism. However, the data do not appear to support this mechanism. Crabs cannot delay their molts indefinitely and one would expect a pattern of increased catches in the year following as the "delayed-molting" crabs reached harvestable size. This pattern is not evident. Rather, multi-year runs of good or poor catches dominate the available time series.

Botsford and Wickham (1975) using slightly different statistical techniques confirmed Peterson's results of significant correlation at lag times near one year. Their cross correlations were positive for lags extending out to the four year growth period, but not significant at the levels required to confidently reject the null hypothesis of no relationship. They hypothesize density dependent biotic factors, such as cannibalism of adults upon juveniles, as mechanisms for the observed long period cyclic variations.

These studies were done using upwelling index data through 1971 reported by Bakun (1973). More recent upwelling index computations have indicated an unprecedented series of very high spring and summer values beginning in 1973 and continuing through 1975. The crab correlation reported by Peterson appears to be continuing to hold with northern California landings rising explosively from 160 MT during the 1973-74 season, to nearly 700 MT in 1974-75, to over 6,000 MT in 1975-76, and to over 11,000 MT in 1976-77 (Orcutt, 1978). A drop to about 6,000 MT in 1977-78 may reflect slightly lessened seasonal upwelling index values for 1976 or perhaps the density dependent biotic factors suggested by Botsford and Wickham.

The Dungeness crab fishery in central California was appreciable through the 1960's but catches dropped to a low value in 1962 and have remained near that value ever since (Orcutt, 1978). Attempts to link the collapse to pollutants derived from human activities have been inconclusive (Wild, Hauger, and Horn, 1978). Wild and Haugen (1977) have shown a significant correlation between sea level values during the fall and winter and crab landings three years later. This is the proper season and time lag for the relationship to reflect an effect on spawning success, possibly through the linkage of sea level to temperature. Laboratory studies have shown deterioration of egg masses at warmer temperatures (Wild, Hagen and Horn, 1978). The period analyzed in the regression covers the collapse of the fishery and a period of secular rise in sea level, although the authors point out that the highest correlations found are at the expected season and time lag rather than at all seasons and lags as would be expected if the correlations were controlled by the long term trends. This analysis is one in which a test of the correlation after high pass filtering of both the catches and sea level values would seem to be very helpful for interpretation.

Coho salmon

Gunsolus (1978) has indicated a relationship between seasonal upwelling index values off Oregon and both survival of juvenile coho salmon in their first year and the ultimate size of adults present that same year. Both survival rates and growth increase with indication of increased upwelling.

Further work by Zirges⁹ suggests that the date of transition from the winter situation of generally negative daily values (Bakun, 1975) off Oregon to the positive values characteristic of spring and summer may be more directly related to survival than the seasonal average of the index values. The effect of upwelling on the direction of the local alongshore current flow could be the causative factor: after transition the predominant flow switches abruptly from poleward to equatorward (Huyer, Sobey and Smith, 1979). Another possible mechanism is that early transition would allow a larger fraction of the smolts leaving the rivers to experience the higher food particle concentrations resulting from upwelling-related primary production.

9. Personal communication, Mac Zirges, Oregon Department of Fish and Wildlife, Newport, Oregon, 97365.

This result is pertinent to a controversy over the growing number of private salmon hatcheries being established in the region. If the indicated relationship reflects some sort of food-limited carrying capacity for salmon smolts in the ocean, then additional production should perhaps be discouraged. However, if the indicated relationship represents a control of the proportion of smelts surviving, rather than on the absolute numbers surviving, a limitation of production at present levels would not be warranted. Such a proportional control would be more likely if the effect of current direction were predominant or alternatively, if the linkage to upwelling were through size-dependent mortality interacting with growth rates dependent on upwelling-produced particle concentrations.

SUMMARY AND CONCLUSIONS

In defining the effect of the environment on fishery stocks we must deal with a space-time continuum of processes; the necessary coverage is generally not available from research vessel operations. Recently progress has been made using routinely collected maritime and shore station data to produce indicators of variations in important environmental processes. These have led to empirical studies of recruitment variations in certain California Current fishery stocks.

The studies have shed a certain amount of light on processes controlling fish stock fluctuations but have been information-limited. The empirical models based on the studies are not expected to be extraordinarily reliable or skillful in detailed prediction and simulation. However, they at least provide some indication of the tendencies created by environmental variability; they allow simulations of management strategies to at least incorporate a realistic spectrum of environmental variance.

Fishery management science is far from an exact science at this time. Present methods to incorporate environmental effects share this lack of exactness. However, experience has shown that ignoring the problem is no answer. Certainly, it would make little sense to attempt to manage the Peruvian anchoveta fishery without reference to El Nino occurrences. Even as basic a fishery management concept as surplus production can become pretty nebulous in the face of major environmental perturbation; for example, Clark (1977) has suggested the possibility that the collapse of the anchoveta stock, which coincided with the 1972 El Nino, could have been due to insufficient fishing in 1971 as well as to excessive fishing in 1972.

The requirements for further progress are easily stated. We need more independent data points to provide additional degrees of freedom for the empirical approach and/or we need a better understanding of the processes linking fish stocks to their environment for advances via the rational approach. The two approaches are in many ways complementary. A better rational understanding would allow us to predetermine the shape and properties of the function which will be fitted to the available data points. More data points will allow a better and more detailed fit which would reveal more aspects of the functional relationship and thereby lead to increased understanding of the actual processes involved.

Since independent estimates of year-class strength of a given stock are available only once per year, increase of data points is a slow process. Substantial improvement in statistical significance comes only when degrees of freedom are at least doubled or tripled. Thus, in cases where we have several decades of information, simply waiting for more data to accumulate is not a useful response to present needs. However, where we may have only several years of data or no data at all, significant empirical advances would be possible in a reasonable time frame. In any case, when monitoring activities are needed, the best time to begin is immediately. Of course, our conception of what characteristics need to be monitored is always based on our rational understanding of the processes involved; thus substantial data accumulations are always based on a previous conception which is often altered as the data yield improved insight.

One development which may be capable of dramatically increasing the number of independent data points for larval survival processes is the technique of counting daily growth rings on larval otoliths

(Methot and Kramer, 1979). If larvae collected at sea can be effectively aged and their birthdates precisely fixed, the condition and abundance of larvae can be related to short term environmental conditions occurring between birth and collection. Thus, multiple independent data points on larval survival might be established in a single year. The technique appears to be quite labor-intensive, but expenditure in such a pertinent area may be preferable to dissipation of an equivalent amount of effort on activities which, although less tedious, may be less central to the management problem.

Substantial progress in the rational understanding sector likewise does not come easily. It is incredibly difficult to reproduce actual ocean conditions in laboratory experiments. Experiments at sea are also fraught with difficulties. The mixture of scales of motion at sea make it impossible to observe time-dependent aspects of any defined "parcel" of organisms and associated environment without artificially confining it somehow, which represents a fundamental alteration of conditions. Likewise, the actual processes tend to occur on such small space scales that it may be nearly impossible to make observations without perturbing the process being observed. However, the work of Lasker, Hunter, Theilacker and others, on larval anchovy survival processes, has shown that a well-conceived and painstakingly executed series of laboratory and field experiments can yield exciting breakthroughs.

Sometimes this process can be shortcut to yield certain limited results by simply comparing seasonal and geographic features of fish reproductive strategies with corresponding seasonality and geography of environmental processes. When a pattern is recognized, deductions can be made as to which processes appear to control reproductive success. Parrish et al (MS), for example, assembled seasonal transport and wind curl distributions on a finer scale than hitherto available and noted a striking pattern of avoidance of offshore transport in the spawning habits of the most successful coastal fish stocks of the California Current region. This provides a rational basis for empirical attempts to relate anomalous offshore transport to decreased reproductive success.

Dynamic modelling is undoubtedly useful in clarifying conceptual understanding. Mathematical models provide the necessary "bookkeeping" to test whether a given set of assumptions can lead to results which resemble reality. However they cannot generate, nor are they a substitute for, observational data. Their results can only reflect the information and assumptions which are put into their formulation. Mathematics cannot, for example, by itself inform us how far offshore larvae must be transported for their contribution to eventual recruitment to be seriously impaired.

The concept of comparative studies can perhaps be profitably extended to detailed comparisons among the major eastern boundary current regions. Similarities and differences in seasonality and geography of analogous environmental and biological features may lead to pattern recognition which will enhance our understanding of the controlling relationships. Of course such comparisons must be made with great care and be based on a commonality of data types. Because of the continuity of space-time coverage required, the environmental features must probably be defined largely by maritime and other routinely collected data. Specialized research cruises and experiments can illuminate certain aspects within limited time-space "windows". The setting of these "windows" within the larger seasonal-geographical framework is critical. For example, the recent CUEA studies need to be interpreted carefully when used to compare gross aspects of the three eastern boundary current regions in which they were made. In many ways the location off Oregon where the CUE-1 and CUE-2 experiments were made is probably an analog to the area off Portugal (Wooster, et al., 1976) rather than to Cape Blanc where JOINT-I was situated. Cap Blanc may be a better analog to Cape Mendocino (Bakun, et al., 1974) in the California Current. The JOINT-II location off Peru shares certain aspects, such as apparent nonlocal generation of upwelling characteristics (Smith, 1978), with the upwelling region in the Gulf of Guinea (Bakun, 1977). Such comparative studies can also be thought of as relieving the problem of limited degrees of freedom. Empirical models of environment - fish stock interactions among analogous stocks in the various regions can be compared for similarities and differences. If close enough analogies are indicated, statistical confidence would increase for the relationships in each of the regions; for example, in the theoretical case of perfect analogs the degrees of freedom could be considered to be directly additive.

REFERENCES

- AHLSTROM, E.H.
1966. Distribution and abundance of sardine and anchovy larvae in the California Current region off California and Baja California, 1951-64: a summary. U.S. Fish. Wildl. Ser. Spec. Rep. Fish 534, 71 p.
- BAILEY, K.M.
In press. Recent changes in the distribution of hake larvae: causes and consequences. MS. Larval transport and recruitment of Pacific hake.
- BAKUN, A.
1973. Coastal upwelling indices, west coast of North America, 1946-71. U.S. Dep. Commer., NOAA Tech. Rep. NMFS SSRF-671, 103 p.
1975. Daily and weekly upwelling indices, west coast of North America, 1967-73. U.S. Dep. Commer., NOAA Tech. Rep. NMFS SSRF-693, 114 p.
1978. Guinea Current upwelling. *Nature*, 271: 147-150.
- BAKUN, A., D.R. McLAIN, and F.V. MAYO
1974. The mean annual cycle of coastal upwelling off western North America as observed from surface measurements. *Fish. Bull.*, U.S., 72: 843-844.
- BAKUN, A. and C.S. NELSON
1977. Climatology of upwelling related processes off Baja California. *Calif. Coop. Oceanic Fish. Invest. Rept.* 19: 107-127.
- BAUMGARTNER, T.R., N. CHRISTENSEN, JR., L. FOK-PUM, and W.H. QUINN
1979. Sources of interannual climatic variation in the Gulf of California and evidence for the biological response. Abstract. Annual Conference, Calif. Coop. Oceanic Fish. Invest., University of Southern California Conference Center, Idyllwild, California.
- BEARDSLEY, R.C., and B. BUTMAN
1974. Circulation on the New England continental shelf: response to strong winter storms. *Geophys. Res. Letters* 1(4): 181-184.
- BEAUCHAMP, J.J. and J.S. OLSON
1973. Corrections for bias in regression estimates after logarithmic transformation. *Ecology* 54: 1403-1407.
- BEVERTON, R.J.H. and S.J. HOLT
1957. On the dynamics of exploited fish populations. *Fishery Invest. Lond. Ser. 2* (19), 533 pp.
- BEYER J.B. and G.C. LAURENCE
In press. Modelling growth and mortality of larval herring (*Clupea harengus*). ICES/Early Life History Symposium 1979, Woods Hole.
- BJERKNES, J.
1969. Atmospheric teleconnections from the Equatorial Pacific. *Mon. Wea. Rev.*, 97(3): 163-172.
- BOTSFORD, L.W. and D.E. WICKHAM
1975. Correlation of upwelling index and Dungeness crab catch. *Fish. Bull.*, U.S., 73(4): 901-907.
- CHELTON, D.B.
1980. Low frequency sea level variability along the west coast of North America. Ph.D. Thesis. University of California, San Diego.
-

- CHRISTENSEN, N., JR., R. de la PAZ V., and G. GUTIERREA V.
1979. On the dynamics of coastal currents off Baja California, Mexico. Paper presented at CalCOFI Conference, Idyllwild, California, October 25, 1979.
- CLARK, COLIN W.
1974. Possible effects of schooling on the dynamics of exploited fish populations. J. Cons. Perm. Int. Explor. Mer. 36 (1): 7-14.
- CLARK, F.N.
1947. Analysis of the populations of the Pacific sardine on the basis of vertebrae counts. Calif. Dep. Fish and Game, Fish. Bull. 65, 26 p.
- CLARK, F.N. and J.C. MARR
1955. Population dynamics of the Pacific sardine. Calif. Coop. Ocean. Fish. Invest. Progress Rept: 11-48.
- COLLINS, R.A. and A.D. MACCAL
1977. California Pacific bonito resource, its status and management. Calif. Dep. Fish and Game, Mar. Res. Tech. Rep. 35, 39p.
- CUSHING, D.H.
1969. Upwelling and fish production. FAO Fish. Tech. Pap., 84, 40 p.

1971. The dependence of recruitment on parent stock in different groups of fishes. J. Cons. Perm. Int. Explor. Mer. 33: 340-362.

1975. Marine ecology and fisheries. Cambridge University Press, Cambridge-New York. 124 p.

1979. Climate variation and marine fisheries. World Climate Conference Overview Paper 22. World Meteorological Organization.
- ELSBERY R.L., and R.W. GARWOOD, JR.
1978. Sea-surface temperature anomaly generation in relation to atmospheric storms. Bull. Amer. Meteor. Soc., 59 (7): 786-789.
- EMERY, W.J.
1975. Dynamic height from temperature profiles. J. Phys. Oceanogr., 6: 613-617.
- FAVORITE, F., and J.A. INGRAHAM
1978. Sunspot activity and oceanic conditions in the northern North Pacific Ocean. In: Ocean Variability: Effects on U.S. Marine Fishery Resources -1975. NOAA Tech. Rep. NMFS Circular 416: 191-196.
- FOFONOFF, N.P.
1963. Dynamics of ocean currents. In: M.N. Hill (editor) The Sea. Inter science Pub., N.Y., 1: 325-395.
- GREENSPAN, H.P.
1968. The theory of rotating fluids. Cambridge Univ. Press, Cambridge, 327 p.
- HAYMAN, R.A.
1978. Environmental fluctuation and cohort strength of Dover sole (Microstomus pacificus) and English sole (Parophrys vetulus). Ph.D. Thesis. Oregon State Univ.
- HICKEY, B.M.
1979. The California Current System - hypotheses and facts. Progress in Oceanography, Vol 8 (4): 191-279.
-

- HOLL, M.M. and B.R. MENDENHALL
1972. Fields by information blending, sea level pressure version. Fleet Numerical Weather Central Tech. Note 72-2, Monterey, California, 66 p.
- HUNTER, J.R. and S.R. GOLDBERG
1980. Spawning incidence and batch fecundity in northern anchovy, Engraulis mordax. Fish. Bull., U.S. 77 (3): 641-652.
- HUNTER, J.R. and C.A. KIMBRELL
In press. Egg cannibalism in the northern anchovy, Engraulis mordax. Fish. Bull. U.S.
- HUYER, A.
1976. A comparison of upwelling events in two locations: Oregon and Northwest Africa. J. Mar. Res. 34: 5310-546.
- HUYER, A., E.J.C. SOBEY, and R.L. SMITH
1979. The spring transition in currents over the Oregon continental Shelf. J. Geophys. Res. 84 (C11): 6995-7011.
- LAEVASTU, T. and I. HELA
1970. Fisheries Oceanography. Fishing News (Books) Ltd., London. 238 p.
- LASKER, R.
1975. Field criteria for survival of anchovy larvae: the relation between inshore chlorophyll maximum layers and successful first feeding. Fish. Bull., U.S., 73: 453-462.

1978. The relation between oceanographic conditions and larval anchovy food in the California Current: identification of factors leading to recruitment failure. Rapp. P.-v. Reun. Cons. int. Explor. Mer., 173: 212-230.
- LASKER, R. and P.E. SMITH
1977. Estimation of the effects of environmental variations on the eggs and larvae of the northern anchovy. Calif. Coop. Oceanic Fish. Invest. Rept. 19: 128-137.
- LASKER, R. and J.R. ZWEIFEL.
1978. Growth and survival of first-feeding northern anchovy (Engraulis mordax) in patches containing different proportions of large and small prey, p. 329-354. In Spatial Pattern in Plankton Communities, J.S. Steele (ed.), Plenum Publ. Corp., New York, 470 p.
- LEWIS, J.M. and T.H. GRAYSON
1972. The adjustment of surface wind and pressure by Sasaki's variational matching technique. Tech. Note No. 72-1. Fleet Numerical Weather Central, Monterey, California.
- MacCALL, A.D.
1979. Population estimates for the waning years of the Pacific sardine fishery. Calif. Coop. Oceanic Fish. Invest. Rept. 20: 72-82.

In press. Population models for the northern anchovy (Engraulis mordax). Symposium on the biological basis of pelagic fish stock management, Paper No. 19.
- MacCALL, A.D., G.D. STAUFFER, and J.-P. TROADEC
1974. Stock Assessments for Southern California Recreational and commercial marine fisheries. Southwest Fisheries Center Admin. Rep. No. LJ-74-24, 144 p.
- MacGREGOR, J.S.
1959. Relation between fish condition and population size in the sardine (Sardinops caerulea). Fish. Bull., U.S. (166): 215-230.
-

- MADSEN, O.S.
1977. A realistic model of the wind induced Ekman boundary layer. *J. Phys. Ocean.* 7 (2): 248-255.
- MARTHALER, J.G.
1976. Comparison of sea level and currents off the Oregon coast using mean monthly data. MS thesis Oregon State Univ., Corvallis, Oregon. 64 p.
- McLAIN, D.R.
1978. Anomalies of coastal sea surface temperatures along the west coast of North America. In: *Ocean Variability: Effects on U.S. Marine Fishery Resources - 1975*. NOAA Tech. Rep. NMFS Circular 416: 127-140.
- METHOT, R.D. and D. KRAMER
1979. Growth of northern anchovy, (*Engraulis mordax*), larvae in the sea. *Fish. Bull., U.S.* 77 (2): 413-423.
- MONTGOMERY, R.B., and E.D. STROUP
1962. Equatorial waters and currents at 150° W in July - August 1952. The Johns Hopkins Press, Baltimore, 66 p.
- MOOERS, C.N.K. and J.S. ALLEN
1973. Final report of the Coastal Upwelling Ecosystems Analysis Summer 1973 Theoretical Workshop. School of Oceanography, Oregon State Univ., Corvallis, Oregon.
- MURPHY, G.I.
1966. Population biology of the Pacific sardine (*Sardinops caerulea*). *Proc. Calif. Acad. Sciences*, 34 (1): 1-84.

1972. Fisheries in upwelling region with special reference to Peruvian waters. *Geoforum* 11: 63-71.

1977. Clupeoids. In J.A. Gulland (ed.) *Fish Population Dynamics*. John Wiley & Sons, New York.
- NELSON, C.S.
1977. Wind stress and wind stress curl over the California Current. U.S. Dep. Commer., NOAA Tech. Rep. NMFS SSRF-714, 87 p.
- NELSON, W.R., M.C. INGHAM, and W.E. SCHAAF
1977. Larval transport and year-class strength of Atlantic menhaden, *Brevoortia tyrannus*. *Fish. Bull., U.S.*, 75 (1): 23-42.
- ORCUTT, H.G.
1978. Introduction. In *Dungeness Crab Research Program, Report for the Year 1978*. Calif. Dep. Fish. Game Admin. Rep. 78-16: 1-5.
- PARRISH, R.H., C.S. NELSON, and A. BAKUN
MS. Larval transport and reproductive success of fishes in the California Current.
- PARRISH, R.H., and A.D. MacCALL
1978. Climatic variations and exploitation in the Pacific mackerel fishery. *Calif. Dep. Fish. Game, Fish. Bull.* 167, 109 p.
- PAULIK, G.
1970. The anchoveta fishery of Peru. *Quant. Science Paper No. 13*. Center for Quant. Sci. in Forestry Fisheries and Wildlife. Univ. of Washington Seattle WA Processed 79 pp.

1971. Anchovies, birds, and fishermen in the Peru current. In W.W. Murdock (ed), *Environment, Resources, Pollution and Society*, Smauer Ass. Inc. Stanford Conn. 156-185 p.
-

- PEARCY, W.G., M.H. HOSIE, and S.L. RICHARDSON
1977. Distribution and duration of pelagic life of larvae of Dover sole, Microstomus pacificus; rex sole, Glyptocephalus zachirus; and petrale sole, Eopsetta jordani, in waters off Oregon. Fish. Bull. U.S. 75 (1): 173-183.
- PETERSON, W.T.
1973. Upwelling indices and annual catches of Dungeness crab, Cancer magister along the west coast of the United States. Fish. Bull. U.S., 71 (3): 902-910.
- PREISENDORFER, R.
1977. Empirical orthogonal functions in the diagnosis and prediction of climate fluctuations. In: Proceedings of the second Annual NOAA Climate Diagnostics Workshop. U.S. Dept. of Commerce.
- QUINN, W.H.
1978. Equatorial Pacific anomalies and El Nino. In: Ocean Variability: Effects on U.S. Marine Fishery Resources U.S. Dep. Commer. NOAA Tech. Rep. Circular 416: 179-190.
- REID, J.L., and A.W. MANTYLA
1976. The effect of the geostrophic flow upon coastal sea elevations in the northern North Pacific Ocean. J. Geophys. Res. 81 (18): 3100-3110.
- RICKER, W.E.
1975. Computation and interpretation of biological statistics of fish populations. Bull. Fish. Res. Board Can. 191: 382 p.
- ROBINSON, M.K. and R.A. BAUR
1973. Report on the production of the Baur-Robinson Northern Hemisphere numerical atlas. Fleet Numerical Weather Central, Monterey, Calif., 10 p.
- ROEDEL, P.M.
1952. A racial study of the Pacific mackerel. Calif. Dep. Fish. and Game, Fish. Bull., 84, 53 p.
- ROYER, T.C.
1979. On the effect of precipitation and runoff on coastal circulation in the Gulf of Alaska. J. Phys. Ocean. 9 (3): 555-563.
- SAUR, J.F.T.
1972. Monthly sea level differences between the Hawaiian Islands and the California coast. Fish. Bull., U.S. 70 (3): 619-636.
- SCOTT, J.T., G.E. MYER, R. STEWART, and E.G. WALTHER
1969. On the mechanism of Langmuir circulations and their role in epilimnion mixing. Limnol. Oceanog. 14 (4): 493-503.
- SISSEWINE, MICHAEL P.
1974. Variability in recruitment and equilibrium catch of the southern New England yellowtail flounder fishery. J. Cons. Int. Explor. Mer. 36 (1): 15-26.
- SMITH, P.E.
1975. Pacific hake larval distribution and abundance - 1951 to 1975. Southwest Fisheries Center Admin. Rep. No. LJ-75-83, 12 p.
1978. Biological effects of ocean variability; Time and space scales of biological response. Rapp. P.-v. Reun. Cons. int. Explor. Mer. 173: 117-127.
-

- SMITH, P.E. and R. LASKER
1978. Position of larval fish in an ecosystem. *Rapp. P.-v. Reun. Cons. int. Explor. Mer.*, 173: 77-84.
- SMITH, R.L.
1974. A description of current, wind and sea level variations during coastal upwelling off the Oregon coast, July - August 1972. *J. Geophys. Res.* 79 (3): 435-443.

1978. Poleward propagating perturbations in currents and sea levels along the Peru coast. *J. Geophys. Res.*, 83 (C12): 6083-6092.

1980. A comparison of the structure and variability of the flow field in three coastal upwelling regions: Oregon, Northwest Africa, and Peru. *Abstract. IDOE International Symposium on Coastal Upwelling. University of Southern California. Los Angeles.*
- STOMMEL, H.
1949. Horizontal diffusion due to oceanic turbulence. *J. Mar. Res.* 8 (3): 199-225.
- SUTCLIFFE, W.R., R.H. LOUCKS, and K.F. DRINKWATER
1976. Coastal circulation and physical oceanography of the Scotian Shelf and Gulf of Maine. *J. Fish. Res. Board Can.*, 33: 98-115.
- SVERDRUP, H.V., M.W. JOHNSON, and R.H. FLEMING.
1942. *The oceans; their physics, chemistry, and general biology.* Prentice-Hall, New York, 1087 p.
- VALDIVIA, J.E.
1978. The anchoveta and El Nino. *Rapp. P.-v Reun. Cons. Int Explor mer.* 173: 196-202.
- VROOMAN, A.M., and P.E. SMITH
1971. Biomass of the subpopulations of northern anchovy Engraulus mordax Girard. *Calif. Coop. Oceanic Fish. Invest., Prog. Rep.* 15: 49-51.
- VLYMEN, W.J.
1977. A mathematical model of the relationship between larval anchovy. (E. mordax) growth, prey distribution and larval behavior. *Env. Biol. Fish.* 2 (3): 211-233.
- WALSH, J.J.
1977. A biological sketchbook for an eastern boundary current. In: *The sea*, Vol. 6, E.D. Goldberg, I.N. McCave, J.J. O'Brien, J.H. Steele, editors. Interscience, New York: 923-968.
- WEARE, B.C., A.R. NAVATO and R.E. NEWELL
1976. Empirical orthogonal analysis of Pacific sea surface temperatures. *J. Phys. Ocean.*, 6: 671-678.
- WILD, P.W. and C.W. HAUGEN
1977. Crab environment project studies. In: *Dungeness Crab Research Program, Report for the year 1977.* Calif. Dep. Fish. Game Admin. Rep. 77-21: 29-48.
- WILD, P.W., C.W. HAUGEN and R.P. HORN
1978. Crab environment project studies. In *Dungeness Crab Research Program, Report for the Year 1978.* Calif. Dep. Fish. Game Admin. Rep. 78-16: 1-5.
- WOOSTER, W.S. and J.L. REID, JR.
1963. Eastern boundary currents. In, *The Sea*, M.N. Hill, ed. Interscience Pub., New York, 2: 253-280.
- WOOSTER, W.S., A. BAKUN, and D.R. McLAIN
1976. The seasonal upwelling cycle along the eastern boundary of the North Atlantic. *J. Mar. Res.*, 34 (2): 131-141.
-

WYLLIE, J.G.

1966. Geostrophic flow of the California Current at the surface and at 200 m. Calif. Coop. Oceanic Fish. Invest., Atlas No. 4, xii p, 288 charts.

WYRTKI, K.

1974. Sea level and the seasonal fluctuations of the equatorial currents in the western Pacific Ocean. J. Phys. Ocean. 4 (1): 91-103.
