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COMPARATIVE STUDIES AND THE RECRUITMENT PROBLEM: SEARCHING FOR GENERALIZATIONS

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ABSTRACT

Empirical attempts to relate recruitment variation to variability in the environment or in the biological community have not been notably successful. This is due in part to the very short data series generally available for empirical analysis. Obviously, we must develop generalizations to provide a basis for unifying the available fragments of experience in a coherent framework.

The ecosystems of the four major subtropical eastern ocean boundary regions, i.e., the California, Peru, Canary, and Benguela current regions, appear to be controlled by similar environmental dynamics (characteristic late spring distributions of coastal temperature anomaly and Ekman transport for the four regional systems, supplementing previously reported winter and summer distributions, are presented). These regions contain very similar assemblages of exploitable pelagic fishes, and exhibit comparable histories of fishery growth and abrupt decline. The similarities suggest that fish communities in these different systems may function alike with respect to their environments and may have reproductive strategies for similar environmental problems. Because natural selection implies that reproductive strategies are responses to the most crucial factors regulating reproductive success, compelling patterns of correspondence among reproductive habits and environmental characteristics are likely to reflect important causal mechanisms. Such findings, which are independent of time series results, furnish a guide for selecting variables for time series modeling in a way that makes improved use of the minimal degrees of freedom that are available.

Beyond comparisons of spawning habitat climatology, it may be fruitful to compare actual time series relationships among similar regional ecosystems (a number of recent studies showing environmental/ biological relationships for eastern boundary pelagic fishery stocks are cited). Under an assumption of analogy, weak empirical relationships having a similar general form in several systems could be assigned greater confidence than otherwise warranted. Conversely, a high correlation found in one system might be questioned if no suggestion of a similar linkage were found in other systems appearing to be analogous. Arraying identically formulated empirical models from different regional systems might yield patterns among model parameters that could provide insights for predicting effects of human actions or natural perturbations on a given system from the record of previous similar events in other systems.

RESUMEN

Los intentos empíricos de relacionar las variaciones en el reclutamiento con variaciones ambientales o en las comunidades biológicas no han sido demasiado exitosos. Ello se debe, en parte, a las series demasiado breves de datos que generalmente se dispone para los análisis empíricos. Es obvio que debemos desarrollar generalizaciones para proveer una base con el fin de unificar los fragmentos de experiencia disponibles en un marco de trabajo coherente.

Los ecosistemas de las cuatro principales regiones de corrientes de margen oriental, i.e., California, Perú, Canarias, y Benguela, parecen estar controlados por esquemas dinámicos semejantes (se presentan las distribuciones primaveral tardía características de anomalías térmicas costeras y transporte de Ekman en los cuatro sistemas regionales, complementando la información previa acerca de las distribuciones invernal y estival). Estas regiones contienen conjuntos de peces explotables muy semejantes e historias similares en lo que se refiere al crecimiento y abrupta declinación de las pesquerías. Estas semejanzas sugieren que las comunidades de peces en estos sistemas diferentes pueden funcionar de manera semejante con respecto a sus ambientes, y pueden tener estrategias reproductivas para problemas ambientales similares. Dado que la selección natural implica que las estrategias reproductivas consistan en respuestas a los factores más importantes que regulan el éxito reproductivo, los obligatoriamente análogos modelos de hábitos reproductivos y de características ambientales pueden reflejar mecanismos causales importantes. Estos hallazgos, que son independientes de los resultados de las series temporales, proveen una guía para seleccionar vari-

ables para modelos de series de tiempo de manera tal que se optimiza el aprovechamiento de la cantidad mínima de grados de libertad disponibles.

Mas allá de la comparación de la climatología de los habitat de desove, puede resultar provechoso comparar las relaciones entre series de tiempo reales entre ecosistemas regionales similares (se mencionan varios estudios recientes que muestran las relaciones ambientales/biológicas en stocks pesqueros pelágicos en áreas de margen oriental). Asumiendo la analogía, podría asignarse mayor confianza a las relaciones empíricas débiles que poseen un formato general semejante en varios sistemas. Recíprocamente, una alta correlación en un sistema podría ser cuestionada si no se encuentra evidencia de una vinculación semejante en otros sistemas que parecen ser análogos al primero. El ordenamiento de modelos empíricos de formulación idéntica provenientes de sistemas regionales diferentes puede brindar patrones entre los parámetros de los models; estos patrones podrían suministrar información útil para predecir los efectos del accionar humano o de las perturbaciones naturales sobre un sistema dado, sobre la base del registro de eventos anteriores semejantes.

INTRODUCTION

The recruitment problem, which has been called the central problem of fish population dynamics (Beyer 1981), remains unsolved after decades of scientific interest and effort. The term "recruitment" refers to *the quantity of younger fish surviving the various egg, larval, juvenile, etc., stages to reach a size at which they become susceptible to fishing gear and thus begin to be sampled by the fishery.* The term therefore integrates the entire period during which the populations are invisible to humans, between the formation of reproductive products in the parental fishes and the later remanifestation of these products as progeny of harvestable size. It thus spans a lengthy continuum of susceptibilities to mortality involving a great range of processes by which the thousands of eggs spawned in the lifetime of a given female must, on average, be reduced to approximately two surviving adult fish.

As might be expected from such a tenuous chain of circumstances, recruitment is notoriously variable. In populations of fishes like anchovies, sardines, and mackerels, the ratio between parental stock size and resulting recruitment typically varies from year to year by factors up to several hundred. Such extreme variability, since it cannot be accounted for mechanistically, introduces a very large noise component into fishery population time series, and largely obscures the signals essential for managing human impacts on the biological system. These signals include evidences of stock-recruitment relationships, multispecies in-

teractions, etc.—knowledge of which could govern fishery development and management strategies. Indeed, the need to account for quasi-random, large-amplitude variations in order to reveal essential mechanisms responding to human alterations of marine biological population structures probably presents, in many cases, a stronger argument for scientific efforts on the recruitment question than does the more often cited need for early prediction of a following year's recruitment. In recognition of the need for progress in this area, an International Recruitment Project (IREP) is the primary focus of the major new international program Ocean Science in Relation to Living Resources, cosponsored by the Intergovernmental Oceanographic Commission and the Food and Agriculture Organization of the United Nations (Anon 1985). For CalCOFI, in particular, the recruitment question could be considered the core scientific issue (Marine Research Committee 1950).

There seems to have been a remarkable lack of progress since the importance of the recruitment problem was recognized early in this century. However, when one considers the nearly total lack of direct information about the fairly complex series of events involving nutrition and associated growth or starvation; predation (which is size-dependent and therefore growth-dependent); transport processes (perturbations of which may disrupt well-tuned adaptations for placing large numbers of individuals in proper habitats for required life-cycle transitions); physiological stresses; etc., the problem's resistance to solution is not so surprising (Table 1). In addition, even where some data are obtainable, difficulties in coping with the interference of strong intrinsic annual periodicities has led to a conventional practice of pooling shorter-scale variations into annual composites; this has further exacerbated the difficulties of empirical analysis by (1) lowering the available signal-to-noise ratios in both environmental and biological time series, (2) severely limiting the number of data points available in reasonably stationary time series, and (3) scrambling together different causal mechanisms controlling different shorter-period survival variations within the same annual composite data point.

Because of the wide variety of possible linkages of environmental fluctuations to recruitment variations (Table 1), and because a variety of oceanographic, meteorological, or other proxy time series may be available to somehow be associated with one or more of these linkages, correlations with short available series of annually composited survival estimates can generally be found and readily justified according to some ecological mechanism. When such a correlation happens to be high enough to meet standard significance

TABLE 1
Some Hypothetical Controls on Survival of
Early Life Stages of Fishes

I. **Starvation hypotheses**
- Turbulent mixing of fine-scale food particle strata
- Low productivity of system
- Wrong type of potential food organisms
- Dispersion of food due to divergent flow pattern
- Mismatch with seasonal food succession caused by anomalies in growth rate

II. **Predation hypotheses**
- Incidence of small planktonic predators
- Incidence of large planktonic predators (coelenterates, etc.)
- Incidence of predatory adult fish
- Incidence of predatory larval fish
- Variations in growth with size-dependent predation

III. **Advection hypotheses**
- Offshore transport (removal of drifting larvae from favorable habitat)
- Onshore transport (exposure of larvae to damage in surf zone, etc.)
- Disruption of normal current patterns to which reproductive habits are tuned

IV. **Physiological stress hypotheses**
- T, S, or [O_2] conditions not within physiological range
- Effects of environmental pollution

V. **Disease hypotheses**
- Infectious outbreaks, etc.

criteria, it becomes publishable as an advance in scientific understanding, whereas slightly weaker correlations do not. This happens even though, given the complexity of the ecological systems involved, it may be quite unreasonable to expect such overwhelming control of survival by any single environmental variable or process as to yield significant (e.g., $P < 0.05$, etc.) nonspurious correlations from the very short data series typically available, particularly since the real degrees of freedom in both environmental or biological time series are often substantially fewer than the number of annual data points because of interyear serial correlation.

Thus, we have the situation that most of the published empirical environment/recruitment relationships are probably (at least to some degree) spurious, with others that may have represented realistic levels of linkage having been discarded as nonsignificant. Tacit recognition of this situation by the fisheries science community has led to a general low opinion of such relationships, with the result that they are not often used in serious decision-making procedures and thus presently are of little practical value.

The following sections of this paper attempt to

illustrate a rationale for interregional comparative studies directed toward (1) providing a framework for systematizing fragmentary information and insights in order to foster useful generalities concerning physical, biological, and (most important for management activities) human impacts on recruitment, and (2) developing a basis for detecting spurious relationships and for increasing confidence in certain weak relationships by comparisons with similar situations in other regional ecosystems. Objections regarding the possibility of discrediting certain valid relationships in situations where the assumption of analogy may be faulty can be answered with the observation that such relationships are essentially useless anyway in a situation where the valid cannot be distinguished from the spurious.

The comparative method and the experimental method are the two great methods of science (Mayr 1982). The comparative method is particularly indicated in situations not amenable to controlled experiments, and it has underlain nearly all the revolutionary advances in evolutionary biology, to cite one example. It seems surprising that the method has not found wider use in the fishery-environmental field, which appears to have been preoccupied with diversity rather than synthesis, and prone to view each local situation as unique.

COMPARATIVE SPAWNING HABITAT CLIMATOLOGY

Parrish et al. (1983) presented maps of two-month (Jan.-Feb. and July-Aug.) long-term mean distributions of various environmental characters for the four major eastern boundary regions of the world: the California, Peru, Canary, and Benguela current systems. These maps generally represented seasonal extremes in each system; however, peak upwelling in the temperate areas is generally earlier toward the equator. The summer and winter maps of Parrish et al. are supplemented here by characteristic late spring (May-June, N. Hemisphere; Nov.-Dec., S. Hemisphere) distributions of coastal temperature anomaly (Figure 1) and Ekman transport (Figure 2).

Negative coastal temperature anomalies greater than 2°C (i.e., 2 degrees cooler than at the same latitude some 1,000 km offshore; stippled in Figure 1) delimit the major upwelling centers. Note the definite separation of the two distinct major upwelling regions off South America. Warm anomalies (areas of positive anomaly greater than 1°C are diagonally hatched in Figure 1), or areas where cold anomalies are less intense, often correspond to spawning regions of coastal pelagic fishes (Parrish et al. 1983). Ekman transport vectors illustrate the strong offshore surface transport that must be accommodated in reproductive
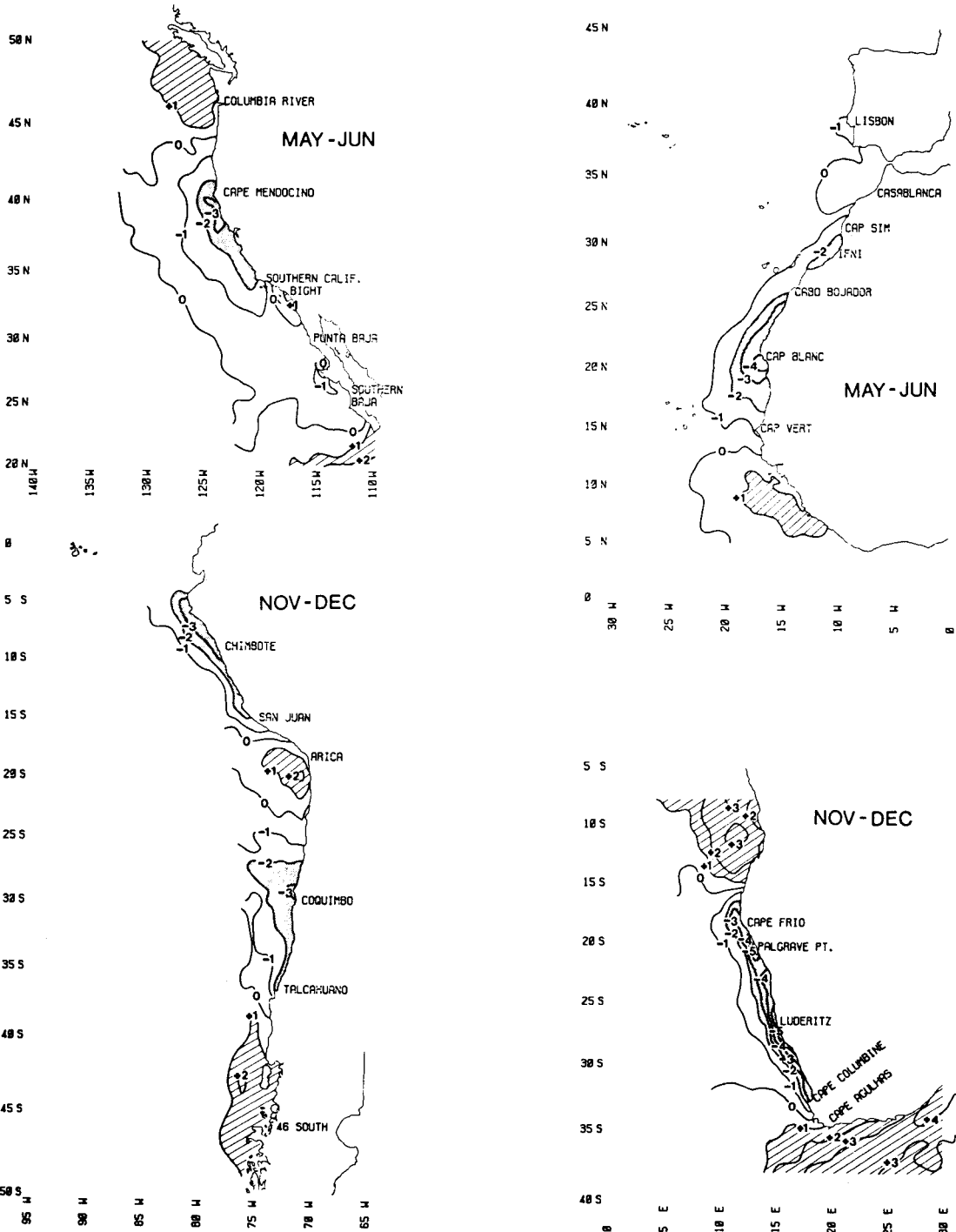
Figure 1. Coastal temperature anomaly (difference from characteristic temperature at similar latitude some ten degrees longitude offshore) distributions in the four major eastern boundary current systems, characterizing late spring conditions in the respective hemispheres. Units are degrees Celsius. Corresponding winter and summer maps, and details of their construction, are presented by Parrish et al. (1983).
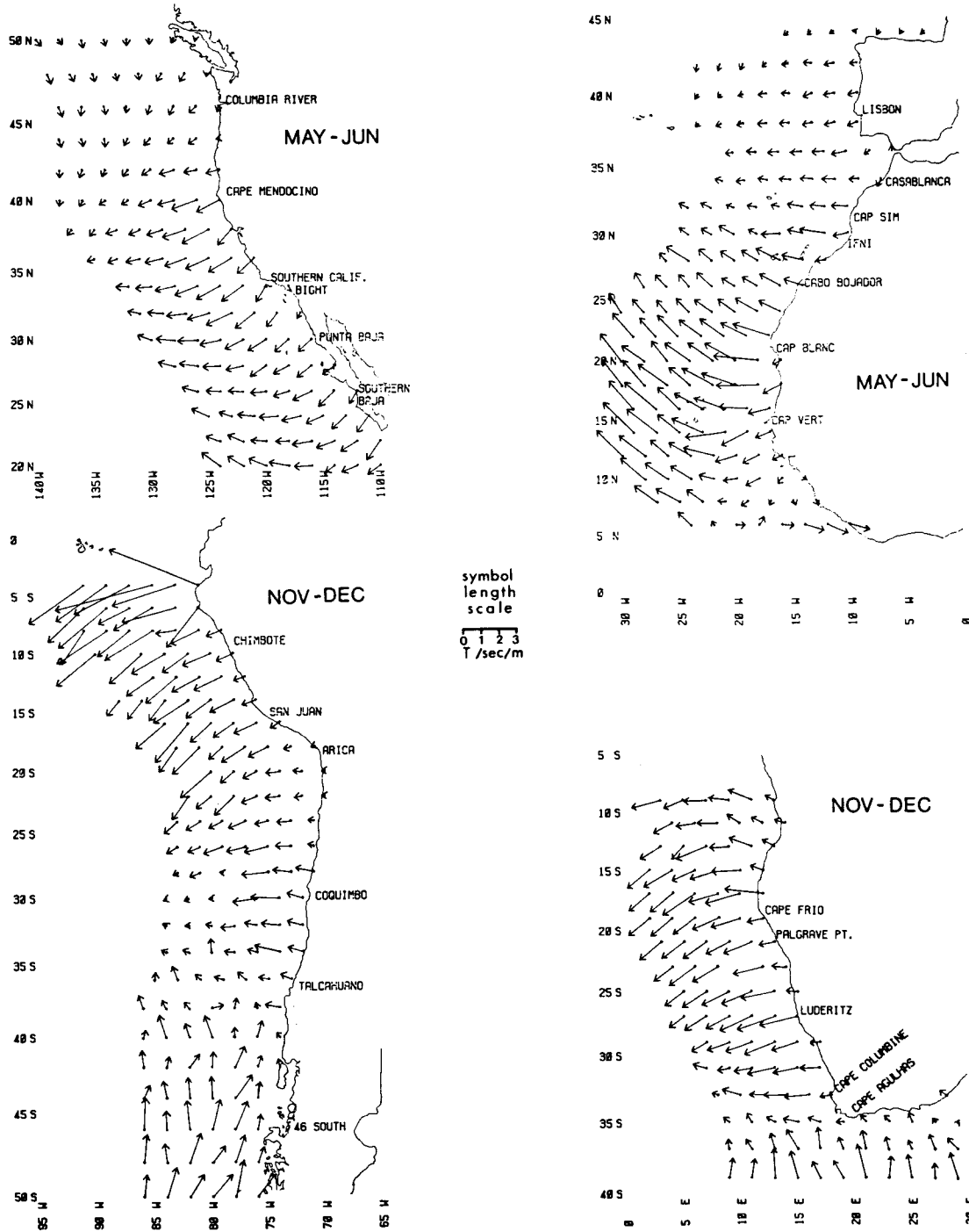
Figure 2. Surface Ekman transport distributions in the four major eastern boundary current systems, characterizing late spring conditions in the respective hemispheres. Transport is proportional to vector symbol length. A symbol length scale is provided; units are metric tons per second across each horizontal meter width. Corresponding winter and summer maps, and details of their construction, are presented by Parrish et al. (1983).

TABLE 2
Dominant Anchovy, Sardine, Jack (Horse) Mackerel,
Hake, Mackerel, and Bonito in the Four Major Eastern
Boundary Currents

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

After Bakun and Parrish (1980)

strategies of marine organisms inhabiting these regions (Figure 2). In addition, McLain et al. (1985) and Shelton et al. (1985) show that biological communities, not only in the Pacific systems but apparently also in the Atlantic, must cope with intermittent extreme warm episodes of El Niño-type intensity.

Very similar assemblages of dominant coastal pelagic fish species inhabit the four regions (Table 2). In each region there is a dominant anchovy, sardine, jack mackerel, hake, mackerel, and bonito. In several cases, the same nominal species inhabits more than one of the regions. In other cases, the species are so similar that their difference may be more a matter of assumption than of demonstration (R.H. Parrish, pers. comm.). There have also been similar regional experiences of rapid fishery expansions and precipitous declines (Parrish et al. 1983).

The various environmental and biological similarities suggest that fish communities in these different regional systems may function similarly with respect to their environments and may be solving similar problems in their reproductive strategies. Survival of offspring to the age of reproduction, which often approximates the age of fishery recruitment, is the direct causative factor in the selective process. Thus natural selection demands response to the most crucial mechanisms regulating recruitment. This implies that we can use the observed results of natural selection in terms of geographical and seasonal aspects of reproductive strategies to understand the causes controlling reproductive success. In other words, pervasive patterns of reproduction, with respect to environmental characteristics, may indicate the actual environmental mechanisms regulating recruitment success.

For example, Parrish et al. (1983) found a general pattern in the spawning habits of anchovies and sardines that seemed to point to a simultaneous minimization of both wind-induced turbulent mixing and offshore-directed transport. Thus the starvation hypothesis, as expressed in Lasker's (1981) scenario of turbulent dispersion of fine-scale food strata, and the transport hypothesis, involving detrimental transport of larvae away from favorable proximity to the coast, are implicated as important mechanisms to be considered in modeling and exploratory data analysis. Temperature of spawning showed much less coherent pattern, suggesting that selection of spawning habitat for any particular optimum temperature is less important than minimizing turbulent mixing or offshore transport.

Certain initially puzzling discrepancies from the general patterns have proved enlightening. For example, Bakun and Parrish (1982) reported that the Peruvian anchoveta, by far the largest fish stock on record before its collapse, stood out as an anomaly in that its spawning peak during austral winter occurred at the very season when offshore Ekman transport was most intense (Figure 3; Table 3), rather than when it was relatively weak, as is the general pattern. However, when mixed layer depth climatologies were produced for the various regions (Parrish et al. 1983), the discrepancy was apparently resolved. Seasonal variation of mixed layer depth off Peru proceeds in phase with that of transport but has greater amplitude (Figure 4), with the result that the thinner mixed layer of austral summer is apparently carried offshore some four times as fast as is the deeper winter mixed layer (Figure 5), even though the winter transport (by volume) is nearly twice as large. Thus the spawning season does indeed appear to be tuned to minimize the rate of offshore loss of eggs and larvae within the ocean's upper mixed layer. This resolution of what initially seemed a discrepancy of a single situation from the general pattern has thus pointed out the generality that, in treating the mechanism of offshore loss of reproductive products distributed in the mixed layer, estimates of wind-driven surface (Ekman) transport should ideally be divided by the effective mixed layer depth to yield an *Ekman velocity of the mixed layer*[1]. In this way we are able to combine two environmental variables to yield a

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[1] In the statement that these two variables should ideally be combined, the qualification "ideally" is important. Ekman transport is estimated from relatively abundant surface wind reports, which reflect the fairly large spatial scales of atmospheric variation. Mixed layer depth varies on much shorter oceanic length scales and must be determined from more sparsely distributed subsurface measurements. Thus there may be cases where the effective mixed layer depth is so imprecisely determined that the combined variable yields a less reliable indicator of interyear variation of offshore velocity than would be provided by the interyear variation in the Ekman transport estimate itself.
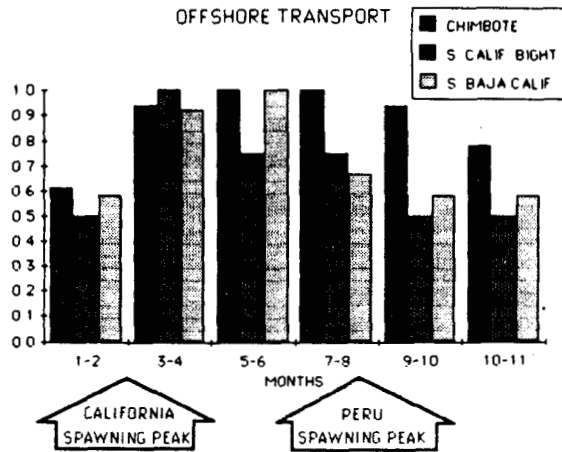
Figure 3. Offshore-directed Ekman transport within the spawning grounds of the Peruvian anchoveta (Chimbote) and within the spawning grounds of the central and southern subpopulations of (California Current) northern anchovy, by 2-month segments of the annual cycle. Units are scaled relative to the seasonal maximum in each area, which is assigned the value 1.0 in all three locations in order to scale them similarly (and thereby to emphasize seasonal timing rather than absolute magnitude). Timing of seasonal peak spawning in the two systems is indicated by the wide arrows. (See Table 3 for unscaled numerical values.)
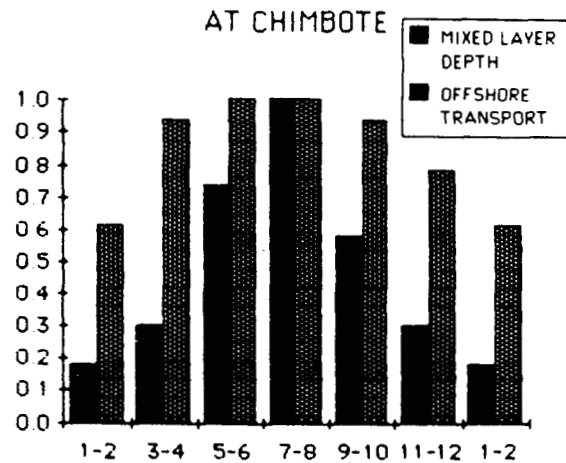

Figure 4. Offshore-directed Ekman transport and mixed layer depth within the spawning grounds of the Peruvian anchoveta, by 2-month segments of the annual cycle. Units are scaled relative to the respective seasonal maxima, which are assigned the value 1.0 in both cases in order to place both on a common scale (and to thereby emphasize seasonal timing rather than absolute magnitude). (See Table 3 for unscaled numerical values.)

single more meaningful variable, thereby conserving degrees of freedom for improving the power of hypothesis tests.

The major point to be made is that such findings, which are based on patterns in the long-term composite averages, are independent of any results based on examination of the available time series data. Thus the findings provide a guide to selecting variables for time series analysis so that the selection process itself does not deplete the scarce degrees of freedom. One could say that the observed characteristic seasonality and geography of reproductive strategies results from a large number of "trial-and-error experiments" performed by the population over the period of development. Moreover, natural selection ensures that this observed result is the "most correct" one for the fish, at least in the long term (providing that we are observing truly long-term adaptations).

TABLE 3
Actual (Unscaled) Values Used to Construct Figures 3, 4, and 5

	Transport (T sec^{-1} m^{-1})					
Months	1-2	3-4	5-6	7-8	9-10	11-12
Chimbote	1.1	1.7	1.8	1.8	1.7	1.4
S. Calif. Bight	0.2	0.4	0.3	0.3	0.2	0.2
S. Baja Calif.	0.7	1.1	1.2	0.8	0.7	0.7
	Mixed Layer Depth (m)					
Months	1-2	3-4	5-6	7-8	9-10	11-12
Chimbote	7	12	29	40	23	12
S. Calif. Bight	37	25	11	10	14	20
S. Baja Calif.	45	23	18	9	20	34
	Net Offshore Velocity of Mixed Layer (km day^{-1})					
Months	1-2	3-4	5-6	7-8	9-10	11-12
Chimbote	13.6	12.2	5.4	3.9	6.4	10.1
S. Calif. Bight	0.5	1.4	2.4	2.6	1.2	0.9
S. Baja Calif.	1.3	4.1	5.8	7.7	3.0	1.8

Transport and mixed layer depth climatologies taken from Parrish et al. (1983); offshore velocities computed as the quotient of the two.
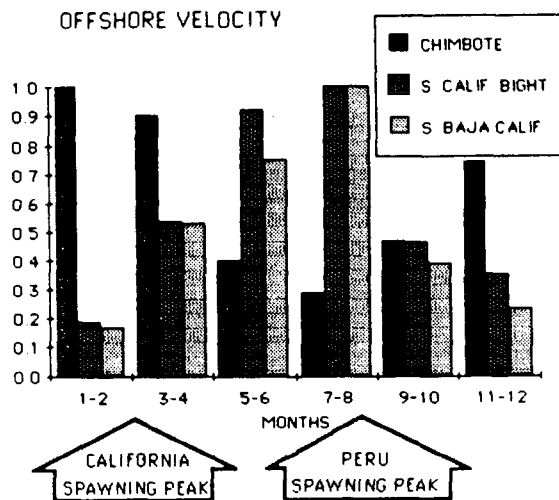
OFFSHORE VELOCITY

Figure 5. Offshore-directed velocity of the surface mixed layer (Ekman transport divided by mixed layer depth) within the spawning grounds of the Peruvian anchoveta (Chimbote) and of the central and southern subpopulations of (California Current) northern anchovy, by 2-month segments of the annual cycle. Units are scaled relative to the seasonal maximum in each area, which is assigned the value 1.0 in all three locations in order to scale them similarly (and thereby to emphasize seasonal timing rather than absolute magnitude). Timing of seasonal peak spawning in the two systems is indicated by the wide arrows. (See Table 3 for unscaled numerical values.)

Thus any empirical relationship based on short time series of recent data on reproductive success and on variations in some environmental characteristic, not corroborated by any apparent reproductive accommodation to that characteristic, might be of questionable validity. Conversely, an empirical relationship reflected in what seems to be an obvious adaptation in characteristic reproductive habits could be assigned increased confidence. This line of reasoning seems applicable even to a unique situation where no assumed analogues are available for comparison, but the comparative aspect introduces a more powerful test. For example, an apparent adaptation may be mere happenstance in a single situation. However, given the regional diversity introduced by varying coastline orientations, atmospheric regimes, advected characteristics, etc., it is unlikely that strong interregional correspondence of reproductive habits with environmental characteristics is due merely to happenstance. Therefore, recognition of such an interregional pattern provides much stronger confirmation of real mechanistic linkage. And, as noted in the Introduction, the present need in recruitment research is for any substantial error to be on the side of undue conservatism and rigor, if results are to be applicable to real problems.

At Pacific Environmental Group we are presently entertaining the notion that the coastal pelagic fishes of the more tropical eastern boundary areas (the sardinellas, etc.) may be playing the same basic survival "game" as those (sardines, anchovies, etc.) in the temperate zones, but at a warmer temperature range. If this is even partially true, the Angola, Guinea, and Costa Rica Dome coastal regions, the Ivory Coast-Ghana upwelling region, the Malabar Coast of India, etc., would provide another set of spawning habitat seasonalities and geographies with which to sharpen these interpretations. Other possibilities for instructive analogues include such western ocean boundary stocks as the Brazilian sardinella and the Japanese sardine; in these cases, basic differences in the environmental dynamics of the systems should be carefully evaluated.

COMPARATIVE TIME SERIES MODELING

Beyond comparisons of long-term mean characteristics of spawning habitats and biological consequences, it may be fruitful to compare empirical (time series) models among similar regional systems. There have been a number of published suggestions of environmental/biological relationships. (Some of the more recent examples for eastern boundary coastal pelagic fishery stocks are cited in Table 4.) Formulations and points of view have differed greatly among researchers concerned with the different regional systems. For example, I believe that Boyd's (1979) formulation in terms of sea-temperature variance, the results of which suggest Lasker's (1981) mechanism of turbulent dispersion of fine-scale food concentrations, has not been tried in the California Current or the other systems.

Systematic comparisons of identical empirical model formulations for all available "analogous" situations might yield suggestive patterns among model parameters to provide new insights into the processes controlling the biological systems. The comparisons could also yield information about the validity of attempts to transfer "experience" among systems (e.g., predicting consequences of human actions or natural perturbations in one system from the record of similar events in other systems, etc.). Under an assumption of analogy, empirical relationships having a similar general form in more than one system might be correctly afforded greater interest and confidence than otherwise warranted. Conversely, a correlation found in one system might be considered questionable if no suggestion of similar linkage were found in other systems appearing, in other respects, to function analogously.

For example, consider the following set of formulations (the variables illustrated in this example are perhaps most suitable to anchovies)

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$$\log (R_i/S_i) = a_{1,i} + B_{1,i}S_i^c \qquad 0 \le c \le 1$$
$$\log (R_i/S_i) = a_{2,i} + B_{2,i}u_i$$
$$\log (R_i/S_i) = a_{3,i} + B_{3,i}\bar{u}_i$$
$$\log (R_i/S_i) = a_{4,i} + B_{4,i}W_i$$
$$\log (R_i/S_i) = a_{5,i} + B_{5,i}T_i$$
$$\log (R_i/S_i) = a_{6,i} + B_{6,i}\tau_i$$

. . . .
. . . .
. . . .

$$\log (R_i/S_i) = a_{m,i} + B_{j,i}S_i^c + B_{k,i}u_i$$
$$\log (R_i/S_i) = a_{m+1,i} + B_{j+1,i}S_i^c + B_{k+1,i}u_i$$

. . . .
. . . .
. . . .

$$\log (R_i/S_i) = a_{p,i} + B_{q,i}S_i^c + B_{r,i}u_i + B_{s,i}\bar{u}$$

. . . .
. . . .
. . . . etc.

where R_i is recruitment to a given fish stock "i",
  S_i is adult stock size,

u_i is upwelling index coincident in time and space with spawning (we might generally expect strong upwelling to be a detrimental factor, involving loss of eggs and larvae via offshore transport),

$\bar{u}_i$ is a properly space- and time-lagged upwelling index that would reflect longer time-scale nutrient inputs to the system at upstream upwelling centers,

W_i is wind-generated turbulence input to the larval habitat (motivation for the choice of variables u_i, $\bar{u}_i$, and w_i can be found in Bakun and Parrish 1980),

T_i is an index of characteristic temperature,

τ_i is temperature variance as used by Boyd (1979), etc.

The dots indicate that other hypothesized factors and combinations of factors would also be considered.

The log (R/S) formulation simply connotes a multiplicative effect of the explanatory vari-

TABLE 4

Examples of Recent Studies Indicating Environmental/Biological Relationships for Eastern Boundary Current Pelagic Fishery Stocks

California Current	Canary Current
Lasker (1981)—northern **anchovy** (*Engraulis mordax*)—negative effect of wind-generated turbulence (wind cubed index) during spawning season.	Belveze and Erzini (1983)—**sardine** (Moroccan central zone; *Sardina pilchardus*)—positive relation of catches to upwelling (index) averaged over the three previous spawning seasons (catch is composed of one- two-, and three-year-olds).—**mixed small pelagics** (Moroccan northern zone; mostly *S. pilchardus*)—high catches in low-rainfall years.
Parrish and MacCall (1978)—Pacific **mackerel** (*Scomber japonicus*)—positive effect of upwelling (index) at spawning ground previous to spawning (one-month lag).	
Bakun and Parrish (1980)—Pacific **sardine** (*Sardinops sagax*)—positive effect of upwelling (index) in upwelling maximum region upstream of spawning grounds (800-km spatial lag) integrated over previous calendar year (2- to 14-month spatial lag).	Freón (1983)—**sardinella** (Senegal)—positive relation of CPUE to wind speed during upwelling season (previous winter); author suggests autocorrelation in wind series as explaining a recruitment effect.
Bailey (1981)—Pacific **hake** (*Merluccius productus*)—negative effect of offshore transport (upwelling index) during planktonic larval period.	Guinea Current
Collins and MacCall (1977)—Pacific **bonito** (*Sarda chiliensis*)—positive effect of upwelling (index) during spawning season.	Bakun (1978)—Ghanain **herring** (**Sardinella** *aurita*)—negative relation of catch to rainfall and sea-surface temperature (related to upwelling).
Peru Current	Binet (1982)—**sardinella** (Ivory Coast and Ghana; *S. maderensis* and *S. aurita*)—positive effect of upwelling (temperature index) and negative effect of coastal runoff on catch.
Various authors—**anchoveta** (*Engraulis ringens*)—negative effect of El Niño (often attributed to lowered primary productivity).	
Benguela Current	Cury and Roy*—**sardinella** (Ivory Coast and Ghana; *S maderensis* and *S. aurita*)—positive effect on catch and on reproductive success of local upwelling (temperature index), which is related to remote forcing by wind stress variations in the western equatorial Atlantic (i.e., off Brazil).
Boyd (1979)—Southwest African **anchovy** (*Engraulis capensis*)—negative effect of sea-surface temperature variance during spawning season.	

*Cury, P., and C. Roy. MS. Modelisation de l'abondance des especes pelagiques cotieres de Cote d'Ivoire integrant l'effort de peche et un indice d'upwelling ORSTOM, 24 Rue Bayard, 75008 Paris, France.

ables; i.e., if an increase of a given variable were to double predicted survival per unit spawning biomass, then an equal decrease would halve predicted survival rather than reduce it to zero, as would be required by an additive (i.e., nonlogarithmic) formulation. The exponent c represents MacCall's (1980) suggestion for the incorporation of variable habitat dimension in a density-dependent mechanism such as adult cannibalism (where if $c = 1$, there is no habitat size variation and the result is a normal Ricker curve; if $c = 0$, the habitat size is proportional to stock size and therefore density does not increase with abundance, so that there is no stock-size dependence through the density-dependent mechanism; $0 < c < 1$ implies the less-than-proportional increase of habitat volume with stock size, which fits observation).

The set of formulations would then be fitted to the available data for various "analogous" stocks in similar environmental settings. Thus we fit univariate regressions, and then various multiple regression combinations of the selected explanatory variables, for each stock and spawning habitat. Then we array the total set of model parameters for the various stocks and look for informative patterns.

Obviously, among a large number of models like this, a certain number of fits satisfying significance criteria will always appear, if only by chance correspondence of unrelated variations. For example, if one does not find at least one fit at the $P = 0.05$ significance level out of twenty attempts, one is simply unlucky. But even if each researcher were limited scrupulously to a prior choice of a single formulation, it would not necessarily improve the utility of published results; we have no idea of how many unpublished failures to meet significance criteria may have occurred for each publishable success. In fact, given the multitude of possible interactions with growth, predation, transport processes, physiological stress, etc., at various life stages, it seems almost inconceivable that any one mechanism could so dominate total survival as to yield a strong univariate relationship that was not to some degree spurious. Thus, searching for "significant" empirical relationships may be an exercise in self-delusion. If the weaker relationships that may represent realistic levels of control by particular mechanistic linkages are to be usable, ways must be found to cull out the larger number of spurious chance fits resulting from relaxed significance criteria. If one finds patterns of similar form among relationships, similar signs of model parameters, etc., for analogous

situations, even though the relationships are too weak individually to meet ordinary significance criteria, valuable insight may have been gained. If nothing is found but chaos suggesting unrelated random combinations, one might conclude that little confidence should be placed in any such models based on the really inadequate degrees of freedom represented by short autocorrelated recruitment time series.

CONCLUDING REMARKS

This paper is intended to serve as the convener's introduction to the invited papers for the Symposium on Comparative Studies of Eastern Ocean Boundary Systems at the 1984 CalCOFI Conference. Certain of these introductory remarks may seem negative; their purpose is to indicate that at this stage in the development of fisheries/environmental science, the likelihood that there is no such thing as an exact analogy among large marine ecosystems does not rule out interregional comparison as a useful deductive tool. In using interregional comparison as a gauge for validity of findings, inconsistency with an interregional pattern is of course no proof of spuriousness; however, interregional consistency may provide otherwise unavailable support for a statistically weak but potentially useful result.

In view of the great resources required for experiments covering the range of time and space in recruitment variability of a fish stock, the cost-effectiveness of the comparative approach deserves mention. In many cases the observational investment will already have been made. Maritime reports (such as those used in the construction of all the figures in this paper) are available, at varying density, for all the oceans of the world. Some fishery research studies will have been made in any area containing a substantial exploited fish stock. Thus the costs of a rudimentary comparative study may be little more than those involved in acquiring existing data and arraying them in similar formats.

Fishery/environmental science clearly needs generalities and unifying principles with broad applicability. Consider, for example, the situation at the FAO Technical Consultation to Examine Changes in Abundance and Species Composition of Neritic Resources (held in Costa Rica in 1983) where, at a major gathering of fishery scientists from all over the world, no consensus could be found (e.g., Bakun 1983) as to the probable consequences of continuing to take record sardine catches off northern Chile in the presence of the 1982-83 El Niño, even then recognized as the strongest environmental anomaly in the eastern Pacific for at least fifty years. We certainly expect that valid generalities do exist in the fishery/environmental

field, as in other branches of science. Identifying them and making them available for fishery management and industrial decision making should be given high priority.

The following symposium papers present selected comparative aspects of the four major eastern ocean boundary ecosystems of the world and their associated fisheries. No attempt has been made to assemble a comprehensive and coherent comparative treatment. Our purpose is to provide some examples of ongoing comparative research, some useful insights into the degree of analogy presented by these four similar systems, and some basic information to aid comparative interpretation and deduction. Most important, we hope to stimulate fisheries scientists to maintain a comparative focus in their research efforts.

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