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Comparative studies of coastal pelagic fish reproductive habitats: the Brazilian sardine (*Sardinella aurita*)

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We extend a framework of comparative climatology of reproductive habitats of neritic pelagic fishes, heretofore focused on temperate eastern ocean upwelling systems, by adding a tropical western ocean example. Maritime weather reports off southeastern Brazil are summarized to yield distributions of wind stress, Ekman transport, wind mixing index, insolation, cloud cover and sea surface temperature for two-month segments of the seasonal cycle. These are used to describe seasonal aspects of the oceanography of the region. Vigorous coastal upwelling occurs in the vicinity of Cabo Frio–Cabo São Tomé through most of the year, relaxing only during austral fall. Directly downstream of this upwelling center lies the coastal bight between Cabo Frio and Cabo Santa Marta Grande, within which offshore Ekman transport and wind-induced turbulent mixing fall to coastwise minima. The near-coastal water column within the bight, while vertically homogeneous during winter, becomes stably stratified during summer. We infer a rather enclosed circulation pattern within the bight, with the main Brazil Current flow skirting across the bight opening rather than following the coastline into the bight interior. This coastal bight constitutes the primary reproductive habitat of the Brazilian sardine. Peak spawning activity during summer serves to place larvae into a stable, enriched environment, where they enjoy high likelihood of retention. In the manner of achieving these advantages, the reproductive strategy of this population appears to be a nearly exact analogue to those of sardine populations inhabiting eastern boundary current upwelling systems, in spite of its western ocean boundary location and the fact that a warmer water genus is involved. The conclusion is that this *Sardinella* population is solving similar dominant environmental problems to those faced by the more temperate *Sardinops* and *Sardina* stocks of eastern boundary systems, only at a warmer temperature range. These findings lend support to the idea that our various fragments of experience of environmental effects on fish populations are not unconnected anecdotes, as they are often treated, but are amenable to scientific generalization.

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Introduction

Recruitment variability in fish populations remains the key unsolved problem of fishery science, even after many decades of committed scientific effort. The problem has been extremely difficult to address at the population level via the experimental approach. And the empirical approach, whereby correlations are sought between recruitment time series and time series of environmental variables, has yielded only limited insights (Bakun, 1984; Shepherd *et al.*, 1984).

Because the detailed causal mechanisms are largely unknown, there is presently no way effectively to cope with large-amplitude quasi-random recruitment variability, occurring on the year-to-year time scale, which largely obscures the essential signals needed to foresee the effects of fishery exploitation over longer time scales. These signals include the functional form of the relationship between stock size and expected recruitment, trends in stock productivity, interspecies interactions, effects of climatic variability or habitat alteration, etc. Lacking the ability to resolve these signals, the methodologies of fishery science must rely on arbitrary assumptions concerning the crucial factors involved in projections of the viability of an industry or in the preservation of a resource over multi-year time periods. The oversimplification and non-realism of these controlling assumptions has in many cases resulted in failure of the scientific methodologies, often with severe socio-economic consequences (Glantz, 1984).

Fishery-based data series tend to be too short, and the variability too non-random, for objective filtering techniques to be effective in detecting and allowing for this inter-year noise. Therefore, an improved degree of insight into the actual mechanisms controlling the variability appears to be required in order to identify the underlying signal. As one approach for developing the needed level of insight, Bakun and Parrish (1980) suggested use of interregional comparative studies. Mayr (1982) calls the experimental method and the comparative method "the two great methods of science", and cites the comparative method as being particularly appropriate to situations not amenable to experimental controls; for example, it has been the basis for "nearly all of the revolutionary advances in evolutionary biology".

Parrish et al. (1983) assembled seasonal distributions of ocean surface processes in the California, Peru, Canary, and Benguela Current regions and identified a pattern of simultaneous avoidance of strong offshore-directed transport and of wind-induced turbulent mixing in the spawning habits of the anchovies and sardines inhabiting those temperate eastern ocean boundary upwelling systems. The existence of a consistent interregional pattern suggests that these particular factors may well have exerted major controls on reproductive success during the period over which the observed seasonal and geographical spawning adaptations were developed. Bakun (1985) further elaborated the rationale for using comparative studies of the oceanography of preferred spawning habitats both to identify the environmental factors controlling reproductive success and to build confidence (or detect spuriousness) in empirical findings.

In looking for additional examples which might serve as useful comparative analogs to the temperate eastern boundary pelagic fish stocks, we are faced with two major alternatives: (1) to shift attention to stocks of similar species which inhabit the dynamically quite different western boundary current regions, or (2) to redirect our focus toward closely related tropical genera, such as *Sardinella*, which could be employing similar life cycle strategies, but at a warmer temperature range.

In this study, we take both steps at once and address the western boundary current *Sardinella* population located off the southeastern coast of Brazil (Fig. 1). The Brazil Current is a representative poleward-flowing western boundary current, albeit a less intense flow than the Kuroshio or the Gulf Stream (Stommel, 1966). Olson *et al.* (1988) find the mean latitude of separation of the Brazil Current from the shelf break to be 35.8 ± 1.1°; thus over essentially the entire latitude range addressed in the study, the area to seaward of the 1000 m isobath is dominated by southward or southwestward Brazil Current flow (Fig. 1).

The Brazilian sardine (*Sardinella braziliensis* = *Sardinella aurita*) represents a warmer water counterpart

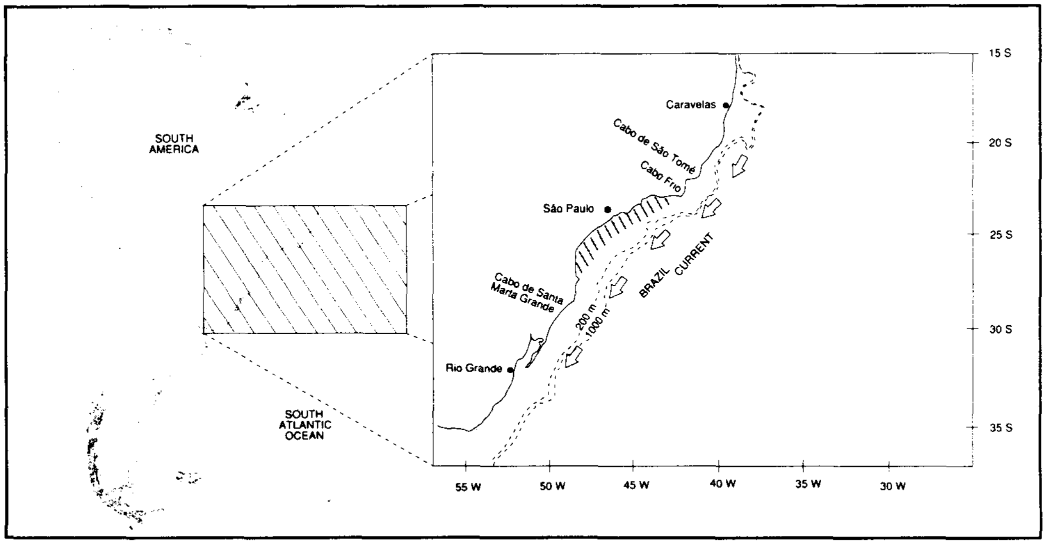

Figure 1. Study region. The area of the Brazilian sardine fishery is indicated in light shading (after Saccardo, 1983). The main spawning grounds (Bakun, MS) are located within the area indicated by diagonal hatching. The large-sçale flow of the Brazil Current generally extends shoreward to the continental shelf break (see text), as indicated by the arrow symbols.

to the sardine species of the genera *Sardinops* and *Sardina*, which have constituted very large populations in coastal upwelling regions along the eastern boundaries of the world's oceans and in the western ocean boundary region near Japan (Parrish *et al.*, 1989). *Sardinella* is rather widely distributed on both sides of the Atlantic as well as in the Indo-Pacific and is one of the dominant genera in terms of total world fishery landings. The recent history of the Brazilian population recalls the scenario which has become familiar in the case of the exploited sardine stocks of eastern boundary currents, with landings growing rapidly to a peak (228 000T in 1973) and falling off to a lower level thereafter (Saccardo, 1983). Most recently, landings have fallen off precipitously and there is concern about the possibility of a population collapse (Y. Matsuura, pers. comm.; S. Saccardo, pers. comm.).

The seasonal distributions of environmental processes and properties presented herein are based on summaries of the historical record of marine weather reports. By international convention, such weather observations are recorded routinely by a variety of types of ships operating at sea. Observations of wind speed and direction, sea and air temperature, barometric pressure, humidity, and cloud cover included in these reports provide a basis for estimating a number of environmental variables pertinent to the study of ocean variability. The observations are made and collected, albeit at varying densities, in all regions of the world ocean in which maritime commerce takes place. All of the actual measurements are made at or above the sea surface; however, ocean variability is forced primarily at the air–sea interface and data such as these therefore provide a basis for drawing inferences about processes and conditions within the interior of the ocean environment. Thus, if effective comparative frameworks can be deduced from surface maritime data, the habitat of virtually every important exploited fish population in the world would be a potential candidate for comparative study.

In this paper we summarize the historical record of these reports available for the area off southeastern Brazil to construct seasonal distributions of (1) stress of the wind on the sea surface, (2) associated surface Ekman transport, (3) an index of wind-derived mechanical energy available for mixing of the water column, (4) rate of absorption of solar radiation through the sea surface, (5) average fraction of sky obscured by clouds, and (6) sea surface temperature. The first four items are primary forcing agents of seasonal variability in local oceanographic processes. The last two items, particularly sea surface temperature, provide some evidence of the nature and consequences of the indicated seasonal forcing.

Besides being the habitat of the Brazilian sardine, historically Brazil's largest fishery stock, the study area has considerable oceanographic, ecological, and social-economic importance. The adjacent coast is the site of the great urban and industrial centers of Brazil. The local ocean ecosystem is thus potentially subject to particular stress from the impacts of human activities. Thus in addition to supporting comparative evaluation of pelagic fish reproductive strategies, the distributions presented herein may serve as inputs to a variety of marine-oriented scientific studies in the region.

Methods

Maritime reports contained in the US National Climatic Center's file of surface marine observations (Tape Data Family – 11; incorporating data from late 1800s through 1979) were grouped by one-degree latitude/longitude areal quadrangles and by two-month segments of the calendar year. Estimates of the various quantities of interest were produced from each individual report. The average value of all the estimates in each of these groups of reports was taken as the expected value for the location and two-month seasonal segment. The vector quantities, wind stress, and Ekman transport, were averaged by component (vector averaged). The one-degree quadrangles selected for these summaries are centered at intersections of a grid of even whole degrees of latitude and longitude, spanning the interval from 18°S lat to 34°S lat and extending twelve degrees of longitude offshore of the coastal boundary. Editing of the data consisted only of a gross error check to ensure physically possible values. Wind speeds greater than $50\ \mathrm{m\ s^{-1}}$ (~100 knots) were discarded.

The vector quantities (Figs. 2, 3) are displayed as discrete vector symbols, each value being derived from a data set that is independent of all other one-degree quadrangles and two-month seasonal segments. Particularly large standard errors were found to be typical of the estimates in the southern offshore portions of the gridded area, reflecting not only very low available data density in that part of the region but also highly energetic variability in actual conditions. The low degree of coherence among spatially-adjacent values visible in that area of Figures 2 and 3 should thus be regarded as largely reflecting lack of stability of the estimates rather than as indicating real small-scale spatial differences in characteristic value.

In preparing the contoured maps of the scalar quantities (Figs. 4, 5, 6), some minimal spatial smoothing has been applied. A three by three grid point version of the median smoother (Tukey, 1977) was employed to deal with the intense "bull's-eyes" that largely obscured the underlying significant pattern in the more data-poor offshore areas. However, in cases where this procedure may have removed features which were similarly indicated by directly-adjacent independent samples and which were judged to be real after examination of the standard errors of the individual sample means, the contours were subjectively adjusted to re-insert the

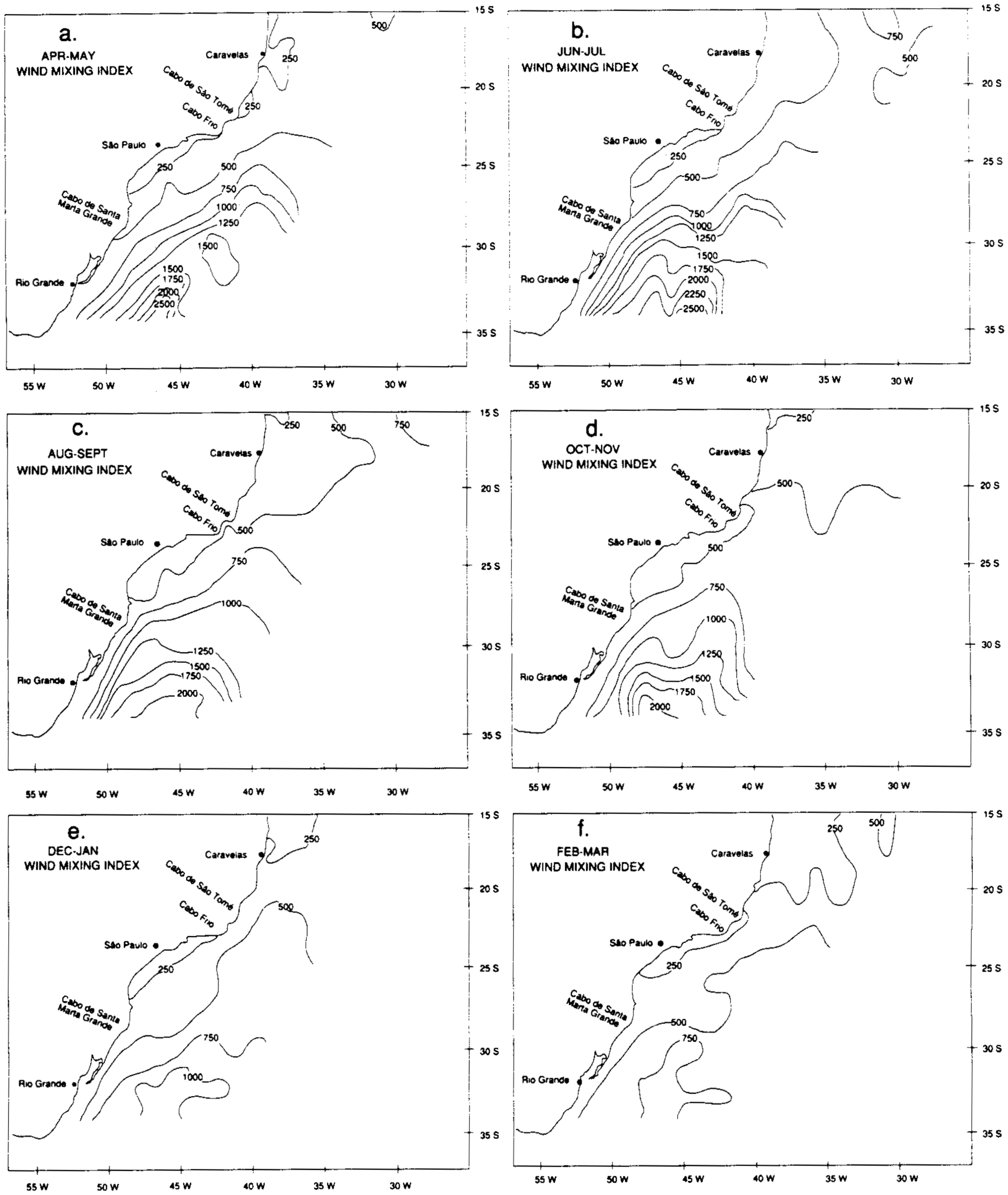

Figure 4. "Wind cubed" index of rate of addition to the ocean, by the wind, of mechanical energy available for turbulent mixing of the upper water column; nominal units are $m^{-3}s^{-3}$. (a) April–May; (b) June–July; (c) August–September; (d) October–November; (e) December–January; (f) February–March.

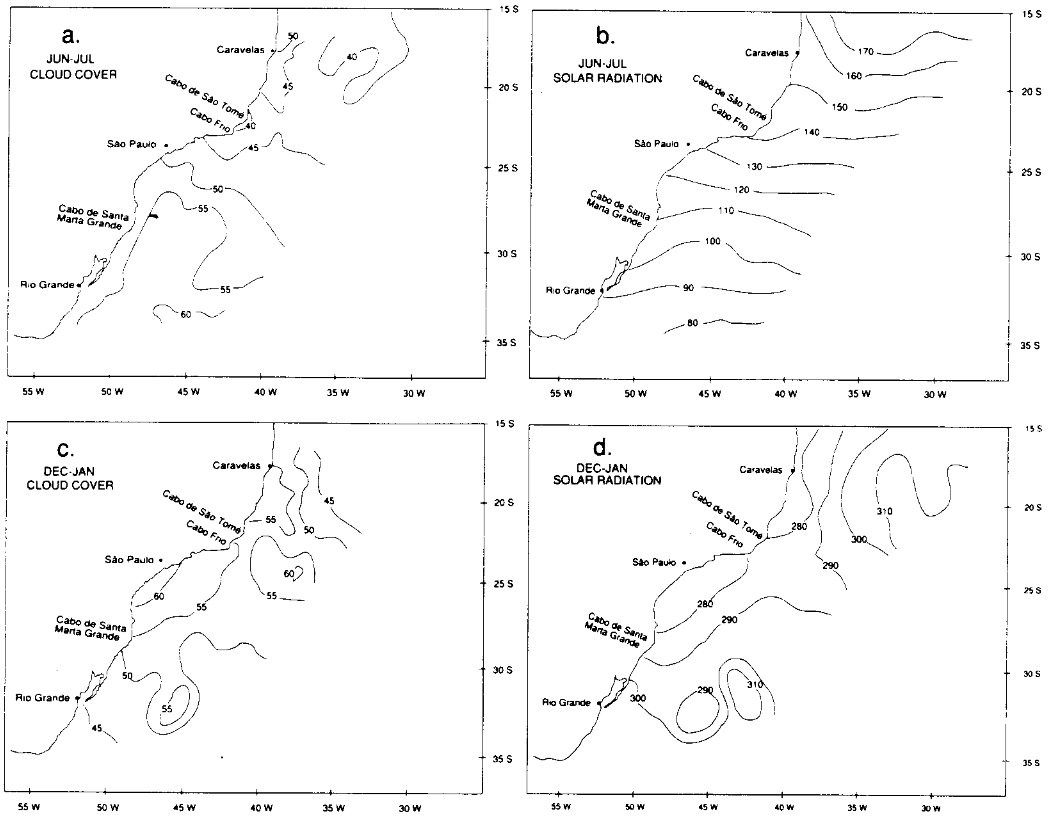

Figure 5. Mean cloud cover and solar radiation. (a) Cloud cover during June–July (austral winter); (b) solar radiation absorbed through the sea surface during June–July; (c) cloud cover during December–January (austral summer); (d) solar radiation absorbed through the sea surface during December–January. Units for cloud cover distributions are percent of sky obscured. Units for solar radiation distributions are watts m^{-2} (to convert to cal cm^{-2} day^{-1}, multiply values by the factor 2.064).

features. The intention has been to avoid showing features that are determined by only a single estimate (i.e. shown only in one of the two-month, one-degree lat/long sample means).

Wind stress

In estimating the stress of the wind on the sea surface we use the same procedure as established by Bakun *et al.* (1974). An estimate of the stress is formed from each wind report according to the standard formulation

$$\vec{\tau} = \rho C_D |\vec{v}| \vec{v} \qquad (1)$$

where $\vec{\tau}$ represents the stress vector, ρ is the density of air (considered constant at 0.00122 gm cm^{-3}), C_D is an empirical drag coefficient (considered constant at 0.0013), $|\vec{v}|$ is the scalar wind speed, and $\vec{v}$ is the vector wind velocity. Reports where the wind direction is coded as "variable" are incorporated as calms (zero wind speed) in the stress summaries (see discussion by Bakun (1987)).

Ekman transport

On the seasonal time scales being addressed, the drift of waters at the sea surface under the direct action of the wind stress is satisfactorily characterized by the simplified idealization known as Ekman transport (Ekman, 1905). The net Ekman transport, $\vec{E}$, integrated over the layer of some several tens of meters beneath the sea surface in which it occurs, is given by

$$\vec{E} = \vec{k} \times \frac{\vec{\tau}}{f} \qquad (2)$$

where $\vec{k}$ is a unit vector directed vertically upward, "×"

denotes the vector ("cross") product, $\vec{\tau}$ is the wind stress vector and f is the Coriolis parameter ($f = 2\omega \sin \phi$) where ω is the angular velocity of the earth's rotation and ϕ is the latitude (negative degrees in the southern hemisphere). Net Ekman transport is thus directed perpendicularly to the left of the wind stress in the southern hemisphere.

Wind mixing index

The rate at which the wind imparts mechanical energy to the ocean to produce turbulent mixing of the upper water column is roughly proportional to the third power, or "cube", of the wind speed (Elsberry and Garwood, 1978). A "wind mixing index", which is simply the mean of the cube of the observed wind speeds in each of the seasonal/areal samples, provides a guide to the variability in this particular process (Bakun and Parrish, 1982). In this case wind reports with the direction coded as "variable" are handled differently than in the stress summaries. Here the wind speed enters as a scalar quantity and directionality is immaterial, and so the wind speed value is incorporated directly as coded in the report.

Solar radiation

Net incoming solar radiation Q_s, absorbed by the ocean was estimated from each individual report according to Bakun's (1987) adaptation of Nelson and Husby's (1983) computational procedure. The procedure is based on the standard formation

$$Q_s = (1 - \alpha)Q_0(1 - 0.62C + 0.0019h) \qquad (3)$$

where α is the fraction of incoming radiation reflected from the sea surface, Q_0 is the sum of the direct and diffuse radiation reaching the ground under a cloudless sky, C is the observed total cloud amount in tenths of sky covered, and h is the noon solar altitude. Q_0 is estimated according to the procedures and tables presented by List (1949), using a four-by-four element curvilinear interpolation of the table entries via Bessel's central difference formula and assuming the atmospheric transmission coefficient of 0.7 recommended by Seckel and Beaudry (1973). The linear cloud correction in Equation (3) is as suggested by Reed (1977); Reed's recommendation that no correction be made for cloud amounts less than 0.25 of total sky was followed. Sea surface albedo, α, was extracted from Payne's (1972) tables, following Nelson and Husby's (1983) algorithm which involves entering the tables with the 0.7 atmospheric transmission coefficient, reduced by a factor equal to the cloud correction applied in Equation (3), and with the mean daily solar altitude.

Results

Wind stress

The area of study lies generally between, but definitely under the influence of, the strong steady easterly trade wind circulation which dominates the tropical region to the north and the violently variable westerlies of the "roaring forties" to the south. The degree of influence of these respective systems varies seasonally, particularly so in the case of the westerlies, with the pattern shifting somewhat northward in austral winter (Jun–Sep) and shifting back southward in austral summer (Dec–Mar).

Thus during austral autumn (Fig. 2a) the wind stress in the northern portion of the gridded area is directed toward the coast in conformity with the trade wind circulation which flows in the same direction. In the southern portion, the northward extension of the zone of strong erratic westerlies (eastward stress) is evident. Off Cabo Frio and Cabo São Tomé, the mean stress is weak and directed toward the coast.

As the season progresses, the region of strong easterly (westward) stress expands southward. By late winter (Fig. 2c) strong westward stress is evident in the offshore half of the gridded area as far south as 24°S lat. Nearer the coast, the wind stress is directed generally alongshore toward the southwest, forming an alongshore maximum off Cabo Frio and Cabo São Tomé, parallel to the Brazil Current flow which is indicated in Defant's (1961) charts to be particularly strong at that season of the year. Substantial westerly (eastward) stress extends during this season to well north of 30°S lat (in the offshore portion of the gridded area). Near the coast south of Cabo Santa Marta Grande, the net resultant stress falls to generally low values.

By early summer (Fig. 2e) the stress near the coast is alongshore and poleward for nearly the entire length of the area studied, and by late summer (Fig. 2f) the effect of the westerlies has essentially vanished from the gridded area. However, the alongshore stress of Cabo Frio and Cabo São Tomé remains substantial until its relaxation in late fall.

Throughout the year, the area near the shore within the coastal bight lying between Cabo Frio and Cabo Santa Marta Grande is an area of minimal net average stress. The offshore increase in stress results in a general pattern of cyclonic (clockwise in the southern hemisphere) horizontal shear in the stress pattern. Also there is a general cyclonic curvature to the pattern. The shear and curvature combine to constitute a predominance of cyclonic wind stress curl in the area. In our studies of similar coastal bights in eastern boundary current regions (Bakun, MS), such a predominance of cyclonic wind stress curl has invariably been reflected in a rather enclosed cyclonic gyral circulation. The existence of the poleward flowing Brazil Current seaward of the bight area would tend to reinforce the tendency in this case. Matsuura (1986) and Castro Filho *et al.* (1987) present sample vertical sections which show areas of doming of subsurface structure shoreward of the continental shelf break, suggesting a degree of baroclinically-compensated cyclonic gyral geostrophic flow pattern within the bight.

Ekman transport

The seasonal distributions of Ekman transport corresponding to the wind stress distributions (Fig. 2) are presented in Figure 3. The seasonal cycle of course directly follows the seasonal cycle of wind stress. Of major interest is the offshore-directed Ekman transport in the vicinity of Cabo Frio and Cabo São Tomé, which is relaxed in the austral autumn (Fig. 3a) but intensifies through the early winter (Fig. 3b) to reach a maximum in the late winter and early spring (Fig. 3c, d) which is maintained essentially through the entire austral summer (Fig. 3e, f). This pattern of seasonal offshore Ekman transport is remarkably similar to the patterns which drive the classical seasonal coastal upwellings of the eastern boundary regions (Wooster and Sievers, 1970; Bakun *et al.*, 1974; Wooster *et al.*, 1976; Parrish *et al.*, 1983). Note also that the magnitude of offshore transport continues to increase with distance from the coast, out to more than 200 km from shore (a consequence of the cyclonic wind stress curl cited in the previous section). Thus the coastal upwelling that occurs within several tens of kilometers of the coast will be augmented by additional upward "Ekman pumping" driven by the general divergence of Ekman transport further offshore.

Within the coastal bight south of Cabo Frio there is a local minimum in the general offshore-directed Ekman transport that extends over most of the region during spring and summer (Fig. 3d, e, f).

Wind mixing index

As regards the generation of turbulent energy available for mixing the water column, the effect of the erratically-varying westerlies impinging from the south dramatically outweighs the steadier trade wind circulation affecting the northern portion of the gridded area. The seasonal differences are very large in the southern offshore portion most affected by the westerlies, with the effects being extreme in austral winter (Figs. 4b, c) when wind mixing index values of several thousand $m^3 s^{-3}$ occupy a substantial area, and most relaxed in late summer (Fig. 4f).

In contrast, the coastal bight from Cabo Frio to Cabo Santa Marta Grande appears as an area of very gentle wind-induced turbulent mixing, with average wind mixing index values tending to be less than $250 \, m^3 s^{-3}$ except during late winter and early spring when the values tend to be slightly greater (Fig. 4c, d). By early summer, wind effects within the bight diminish such that the area enclosed by the $250 \, m^3 s^{-3}$ contour covers essentially the entire bight area (Fig. 4e). Castro Filho *et al.* (1987) report little stratification over the inner shelf during winter; however, during summer a two-layer vertical stratification builds up, with a strong thermocline at mid-depths. With the relaxation of coastal upwelling in late summer, even the Cabo Frio–Cabo São Tomé upwelling center falls within the $250 \, m^3 s^{-3}$ contour (Fig. 4a).

Solar radiation and cloud cover

During the austral winter the cloud cover (Fig. 5a) varies from less than 40% of sky obscured on average in some offshore locations at the northern edge of the study area, to greater than 60% at some locations at the southern edge. The upwelling center off Cabo Frio and Cabo São Tomé is marked by a local minimum of cloud cover along the coast, as is the general pattern for upwelling centers in eastern ocean boundary areas (Parrish *et al.*, 1983). The corresponding distribution of solar radiation absorbed (Q_s) during winter (Fig. 5b) shows a strong meridional gradation related to the latitudinally-varying solar angle. The effect of the cloud cover distribution is seen only in deflections of the isopleths from a strictly zonal orientation.

During the austral summer the distribution of cloud cover (Fig. 5c) continues to have a coastwise minimum in the vicinity of Cabo Frio and Cabo São Tomé. The coastal bight immediately to the south contains a relative maximum in cloud cover. At this season the noon position of the sun is nearly directly overhead and the shape of the Q_s isopleths (Fig. 5d) is strongly influenced by the cloud cover distribution. The Cabo Frio–Cabo São Tomé upwelling center represents a local coastwise maximum in solar radiation absorbed. The summer values of Q_s (Fig. 5d), representing energy available for (1) absorption by water molecules, thereby warming the ocean surface layer, or (2) absorption by plant pigments to provide the energy for photosynthetic production of organic matter, tend to be more than twice the winter values (Fig. 5b) both at the upwelling center and within the coastal bight immediately to the south.

Sea surface temperature

Comparison of the sea surface temperature distributions (Fig. 6) with the solar radiation distributions (Fig. 5) shows little correspondence in pattern, except for the global-scale latitudinal gradations in these properties which characterize the oceans as a whole. The other ocean-atmosphere heat exchange components, i.e. long wave back radiation and evaporative and conductive heat fluxes, tend to be small compared to the short wave solar radiation input in such near-tropical regions (e.g.

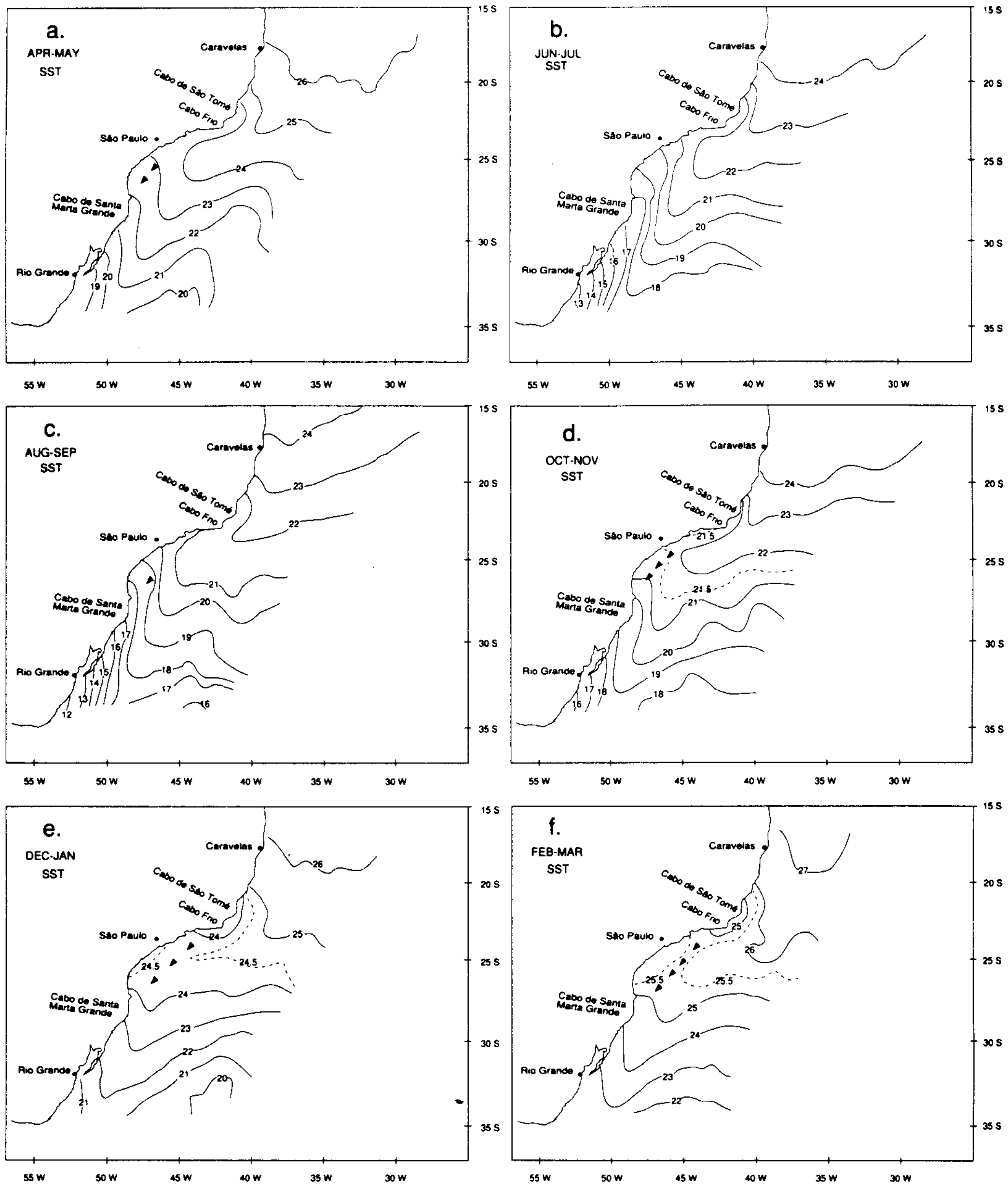

Figure 6. Sea surface temperature distributions for two-month segments of the seasonal cycle. Units are degrees Celsius. (a) April–May; (b) June–July; (c) August–September; (d) October–November; (e) December–January; (f) February–March. Triangular symbols indicate locations of local one-degree lat/long average temperature minimum values occurring offshore, downstream of the Cabo Frio–Cabo São Tomé upwelling center.

Bakun, 1987); also, the long wave back radiation would have a similar pattern to the cloud cover (Fig. 5). Thus features in the sea surface temperature pattern which deviate from the global-scale pattern of zonal isotherms can apparently be ascribed to such dynamic processes as advection, upwelling, and surface cooling due to vertical mixing, rather than to local variations in sea surface heat exchange.

Evidence of the southwestward flow of the Brazil Current, parallel to the large-scale coastline trend, is seen in the strong curvature of the surface isotherms (Fig. 6) into definite tongue-like forms which extend towards the southwest, with axes generally centered some two to three hundred kilometers offshore.

Near the Cabo Frio–Cabo São Tomé upwelling center, relative cooling of the sea surface resulting from the local coastal upwelling is evident. During the fall season of quite relaxed offshore Ekman transport (Fig. 3a), the effect is seen merely as an exaggeration of the tongue-like feature (Fig. 6a). However, by early summer (Fig. 6e) the upwelling core is surrounded by closed isotherms which intersect the coast both to the north and to the south, strikingly similar in form to the closed isotherm distributions seen in similar maritime data summaries for such "classical" eastern boundary upwelling centers as Cape Mendocino in the California Current, San Juan in the Peru Current, Cap Blanc in the Canary Current, and Lüderitz and Cape Frio in the Benguela Current (Parrish *et al.*, 1983).

However, the coastal sea surface temperature anomaly (i.e. the difference between the temperature near the coast and the characteristic large-scale offshore temperature at the same latitude) characterizing this particular upwelling center is somewhat less, being of the order of 2°C rather than the 4–6° typical of the most intense eastern boundary upwelling centers. A lesser coastal temperature anomaly is not unexpected, as the offshore Ekman transport which drives the upwelling process is of considerably less strength (Fig. 7) than typically found in the eastern boundary upwelling centers. Also, the alongshore extent of the region of relatively strong upwelling is much less than in the major eastern ocean boundary systems. On the other hand, the strong turbulent mixing that characterizes the offshore area (Fig. 4) relative to the near-coastal area is different from the situation in the eastern boundary upwelling centers, where there tends to be less offshore gradient in wind mixing index values (Parrish *et al.*, 1983); this may work to lessen the relative coastal cooling seen in the sea surface temperature distribution off Cabo Frio–Cabo São Tomé.

It is interesting to note that although appreciable offshore-directed Ekman transport exists well to the north of Cabo São Tomé (to at least 18°S lat) from late winter through the entire summer (Fig. 3c, d, e, f), the marked coastal cooling typical of an upwelling center is not highly evident in the sea surface temperature distributions north of about 20°S lat (Fig. 6), except

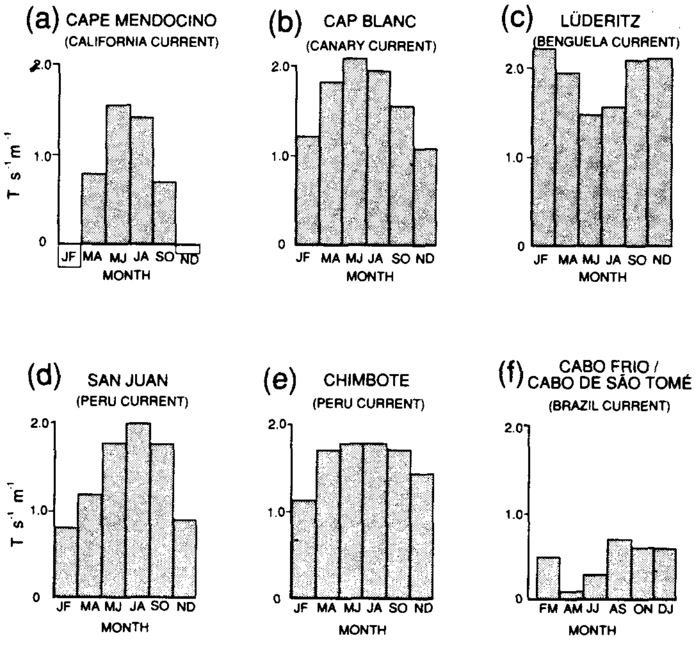

Figure 7. Offshore component of Ekman transport in major coastal upwelling centers by two-month segments of the seasonal cycles. Units are metric t s^{-1} across each meter width. (a) Cape Mendocino, California; (b) Cap Blanc, Mauritania; (c) Lüderitz, Namibia; (d) San Juan, Peru; (e) Chimbote, Peru; (f) Cabo Frio, Brazil.

perhaps in late summer (Fig. 6f). Since coastally-trapped propagation (e.g. Gill and Clarke, 1974) is directed equatorward along western ocean boundaries, the hypothesis that the offshore transport may be replenished by alongshore flow from the upwelling center to the south appears to be untenable since that would imply southward propagation of the forcing signal. Certainly, there are other hypothetical explanations available. For example, friction associated with Brazil Current flow impinging against the Abrolhos Bank (which can be seen in Figure 1 in the major seaward bulge of the isobaths to the east and south of Caravelas) may lead to the flow becoming locally sub-geostrophic, resulting in cross-isobar (shoreward) surface transport which could offset the offshore Ekman transport. However, in this case surface data alone cannot provide a definitive explanation.

A cool core extends to the southwest of the upwelling center across the opening of the coastal bight between Cabo Frio and Cabo Santa Marta Grande. (This is indicated in Fig. 6 by triangular symbols marking the location of the minimum temperature value along each zonally-oriented line of one degree lat/long areal summaries, in cases where the minimum is not at the coast.) This offshore cool core appears to be an advective feature, suggesting that the main current flow must be directly across the open outer edge of the bight rather than following the curvature of the shoreline into the interior of the bight. Warmer surface water exists along the coast shoreward of this cool core, strengthening the impression of a rather enclosed cyclonic gyral circulation within the bight, which was inferred earlier from the wind stress pattern. Matsuura (1986) shows a very narrow band of less saline surface water confined directly against the coast; this would tend to raise the sea height at the coast, promoting northeastward geostrophic flow adjacent to the coast within the bight to close the gyral circulation pattern. In fact, without such a flow to provide a combination of Coriolis and centrifugal forces to balance the horizontal pressure gradient implied by the band of fresher water, it is difficult to envision dynamics that could allow the band to remain confined to the coast in the manner observed.

It is possible that the cool core denoted by the triangle symbols could also be interpreted as being at least partially due to northeastward advection of cooler coastal waters from south of the bight, particularly during the fall through spring seasons (Fig. 6a, b, c, d). The vertical sections presented by Castro Filho *et al.* (1987) are somewhat complex and do show the doming of the density structure to be largely confined to the outer half of the bight during winter. In any case it is clear that the large-scale Brazil Current flow does not sweep directly through the bight interior, but rather skirts across the seaward edge of the bight opening. Thus the interior of the bight must be characterized by one or more semi-enclosed gyral circulation patterns.

Discussion

Several hypotheses concerning environmental effects on the reproductive strategies of small coastal pelagic fishes have been the object of particular recent scientific interest among researchers working in the California Current system and in other eastern boundary current systems:

1. Lasker (1975, 1981a, 1981b) has suggested that wind-induced turbulent mixing could destroy fine-scale food particle aggregations required for successful first-feeding of newly hatched larvae; Peterman and Bradford (1987) demonstrate a time series relationship between early survival of anchovy larvae (*Engraulis mordax*) in the Southern California Bight and the frequency of periods of weak winds of sufficient duration to allow formation of aggregations of food organisms.
2. Parrish *et al.* (1981) survey the diverse reproductive habits of a wide variety of California Current fishes. They identify a common pattern of avoidance of placing pelagic eggs and larvae into circumstances where they would be rapidly transported and dispersed offshore. In particular, they point out that adult coastal pelagic fishes of that region migrate long distances between feeding and spawning grounds, with the result that spawning occurs under the favorable conditions of the Southern California Bight, where offshore Ekman transport is minimal and a closed gyral circulation pattern may serve to retain drifting larvae within the bight.
3. Parrish *et al.* (1983) show that in eastern boundary current regions large stocks of sardines and anchovies tend to spawn in coastal bights downstream (with respect to the large-scale boundary current flow) of major upwelling centers; Bakun and Parrish (1980) show a correlation, at a temporal lag appropriate to the advective transit time, between interyear variability in upwelling intensity at the major upwelling center near Cape Mendocino and interyear recruitment variability of California sardine (*Sardinops sagax*) spawning more than 500 km downstream in the Southern California Bight.

The reproductive strategy of the Brazilian sardine appears to be in close conformity with all three classes of hypotheses. The population is largely resident within the coastal bight between Cabo Frio and Cabo Santa Marta Grande, although adults may leave the bight to feed near the Cabo Frio–Cabo São Tomé upwelling center. Spawning is confined to the bight (Fig. 1) and peaks during summer, particularly during the months of December and January (Matsuura, 1979; Saccardo, 1983). Reproductive activity appears to cease entirely during fall and winter (April to September).

Spawning in the summer serves to place the larvae within an enriched environment directly downstream (with respect to Brazil Current flow) from the Cabo Frio–Cabo São Tomé upwelling center. The timing is such that this occurs during a period of continued rather vigorous upwelling, slightly lagging the seasonal upwelling peak (as appropriate to allow time for upwelling-enriched "planktonic food web" effects to be advected toward, and diffused into, the bight area to enhance the availability of minute food particles needed by the larvae). This is the season when extremely low production of turbulent mixing energy characterizes the entire interior of the coastal bight where spawning occurs (Fig. 4e). This also corresponds to the seasonal peak of solar radiation entering the ocean (Fig. 5d), when energy available for photosynthesis is at a maximum and when a strong tendency for stratification of the upper water column would tend to inhibit destruction of fine-scale structure of food particles by turbulent mixing. In addition, offshore Ekman transport relaxes to a local minimum within the coastal bight (Fig. 3e) and we have inferred a rather closed geostrophic circulation pattern which would also tend to retain larvae and oppose their offshore dispersal and loss from the coastal habitat.

The degree of similarity to the seasonal and geographical reproductive adaptations exhibited by the California sardine stock is remarkable. In addition to spawning habits, the similarity to the California stock also includes the migration of larger adults, out of the coastal bight which serves as reproductive habitat, to feed in the highly productive but more turbulent and dispersive upstream region near the upwelling center.

Thus the seasonal and locational adaptations in the spawning habits of the *sardinella* of southeastern Brazil appear to be tuned in an identical manner, to solve a very similar set of environmental problems, as are those of the sardine which spawns in the Southern California Bight. This is in spite of the very different environmental contexts (i.e. tropical versus temperate, and western boundary current versus eastern boundary current, settings) and of the fact that different genera (*Sardinella* versus *Sardinops*) are involved. Parrish *et al.* (1983) have indicated strong analogies in life-history strategy between the Southern California sardine stock and other eastern boundary current sardine stocks which choose spawning habitats within coastal bights downstream of upwelling centers. Thus the Brazilian population would also appear to be quite analogous, with respect to environmental/life-history linkages, to such other important sardine stocks as the Peru Current stock spawning in the large coastal bight centered near Africa, Chile, and the Canary Current stocks spawning in coastal indentations near Casablanca, and near Sidi Ifni, Morocco.

This represents an encouraging finding in several respects. It supports the hypothesis that insights into the nature and mechanisms of recruitment variability gained from relatively well-studied coastal pelagic fish stocks, such as those of the California and Peru Current systems, may have utility for a wider variety of coastal pelagic stocks around the world. It provides support for an assumption of analogy among multiple regional systems which may aid (1) in recognizing informative patterns of biological–physical interaction and (2) in building confidence in weak empirical relationships that exhibit interregional consistency (Bakun, 1985). It also implies that process-oriented field activities addressing the mechanisms controlling recruitment variation at the population level, which tend to present substantial operational problems, may reasonably be sited in settings selected for special amenability to the particular operational design, with the expectation that results may be applicable to a number of other settings with important fishery management and industrial concerns.

The peak size of the Brazilian population has been only a fraction of that of the major eastern boundary sardine populations, which have all yielded maximum annual landings approaching or exceeding a million tons. A plausible hypothesis for the difference is the smaller magnitude of the Brazilian coastal upwelling system, both in intensity of the offshore Ekman transport of surface waters (Fig. 7f) which constitutes the local driving mechanism for the upwelling and in the size (i.e. alongshore extent) of the upwelling center. In addition, whereas in eastern boundary current situations advection is from the sub-polar regions towards the tropics, in western boundary systems such as the Brazil Current, the alongshore flow is from the tropics toward the poles; thus the water advected horizontally into the system might be expected to be less rich in dissolved nutrient salts, and also in "seed populations" of organisms adaptable to the conditions and capable of utilizing the enrichment associated with an upwelling center.

Assuming that the recent abrupt decline in catches does not portend the final, most unfortunate analogy to the case of the California sardine, i.e. total long-term population collapse, the moderate size of the Brazilian population and its relatively confined habitat located near major ports and scientific institutions may serve to make it a particularly amenable setting for population-level recruitment studies such as the "SARP"-type exercises (Anon., 1987) being promoted under the International Recruitment Programme (IREP) within the IOC–FAO Programme of Ocean Science in Relation to Living Resources (OSLR). Our conclusions tend to support the idea that a well-posed program of scientific study of even a single example such as the Brazilian sardine might produce insights that could be beneficially applied to other important stocks around the world.

Concluding remarks

In concluding this paper we should acknowledge our recognition of the "pitfalls" inherent in any oversimplistic and overoptimistic "leap" to a conclusion of analogy among diverse fish populations, biological communities, and ocean habitats. Admittedly, the results presented here are suggestive rather than conclusive. However, science generally progresses by making assumptions which lead to conceptual frameworks within which the various available data can be categorized and arrayed for examination; these frameworks are generally discarded only after they have supported progress to the extent that it becomes clear they are no longer adequate.

The recruitment question has proven to be very resistant to scientific solution when addressed, in the conventional manner, in the context of any single autonomous fish stock and habitat. Well-posed field studies at the population level are difficult and expensive. The idea that a few process-oriented experimental efforts mounted in particularly amenable population and habitat settings could support and progressively advance a broadly-based framework of comparative scientific insight has considerable attraction (Bakun, in press). The alternative of having to repeat each step, separately and in the same way, for every important fish population in the world is a daunting prospect which is far beyond the resources that are presently available for the purpose. The true situation probably lies somewhere between these alternatives. In such a case it would seem that the most economical and effective approach would be to begin to attempt to structure scientific effort on the basis of the more optimistic assumption, as long as the fact that it remains an assumption continues to be well recognized. Even if the assumption were totally in error the detriment to having employed it would be slight. However, in the much more likely event that it is correct to some substantial degree to miss the opportunities afforded would be unfortunate indeed.

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References

Anon. 1987. IOC-FAO Guiding Group of Experts on the Programme of Ocean Science in Relation to Living Resources, Second Session. Reports of Meetings of Experts and Equivalent Bodies SC-87/WS/41. Intergovernmental Oceanographic Commission, Unesco, Paris, 37 pp.

Bakun, A. 1984. Report of the Working Group on Environmental Studies and Monitoring. *In* Reports of the Expert Consultation to Examine Changes in Abundance and Species Composition of Neritic Fish Resources, pp. 41–54. Ed. by G. D. Sharp and J. Csirke. FOA Fish. Rep., 291(1), 102 pp.

Bakun, A. 1985. Comparative studies and the recruitment problem: Searching for generalizations. CalCOFI Rep., 26: 30–40.

Bakun, A. 1987. Monthly variability in the ocean habitat off Peru as deduced from maritime observations, 1953–84. *In* The Peruvian Anchoveta and its Upwelling Ecosystem: Three Decades of Change, pp. 46–74. Ed. by D. Pauly and I. Tsukayama. ICLARM Studies and Reviews 15. Instituto del Mar del Peru (IMARPE), Callao, Peru; Deutsche Gesselschaft für Technische Zusammenarbeit (GTZ), GmbH, Eschborn, Federal Republic of Germany; and International Center for Living Aquatic Resources Management (ICLARM), Manila, Philippines. 351 pp.

Bakun, A. Recruitment and its relationship to environment: accessible pathways to greater insight. *In* Simposio Internacional Sobre Recursos Vivos y Pesquerías en el Pacífico Sudeste. Ed. by R. Jordon S. Comisión Permanente de Pacífico Sur, Bogatá, Columbia. (In press.)

Bakun, A. (MS) Eastern ocean regional vorticity balance, poleward coastal counterflows, and control of seasonal surface flow pattern by the horizontal gradient of wind stress curl: an interregional comparative approach.

Bakun, A., McLain, D. R., and Mayo, F. V. 1974. The mean annual cycle of coastal upwelling off western North America as observed from surface measurements. Fish. Bull., US, 72(3): 843–844.

Bakun, A., and Parrish, R. H. 1980. Environmental inputs to fishery population models for eastern boundary current regions. *In* Workshop on the Effects of Environmental Variation on the Survival of Larval Pelagic Fishes, pp. 67–104. Ed. by G. D. Sharp. Lima, Peru, 20 Apr–5 May, 1980. IOC Workshop Rep., 28: 323 pp.

Bakun, A., and Parrish, R. H. 1982. Turbulence, transport, and pelagic fish in the California and Peru Current systems. CalCOFI Rep., 23: 99–112.

Castro Filho, B. M. de, de Miranda, L. B., and Miyao, S. Y. 1987. Condições hidrograficas na platforma continental ao largo de Ubatuba: variação sazonaiss e em média escale. Bolm Inst. Oceanogr., S. Paulo, 35(2): 135–151.

Defant, A. 1961. Physical oceanography. Pergamon Press, London.

Ekman, V. W. 1905. On the influence of the earth's rotation on ocean currents. Ark. Mat. Astron. Fys. 2(11): 1–55 (reprinted in J. Cons. Explor. Mer, 20(2), 1954).

Elsberry, R. L., and Garwood, R. W., Jr. 1978. Sea-surface temperature anomaly generation in relation to atmospheric storms. Bull. Am. Meteorol. Soc., 59: 786–789.

Gill, A. E., and Clarke, A. J. 1974. Wind-induced upwelling, coastal currents, and sea level changes. Deep-Sea Res., 21: 325–345.

Glantz, M. H. 1984. Report of the Working Group on Societal Implications of Varying Fishery Resources. *In* Reports of the Expert Consultation to Examine Changes in Abundance and Species Composition of Neritic Fish Resources, pp. 55–66. Ed. by G. D. Sharp and J. Csirke. FAO Fish. Rep., 291(1). 102 pp.

Lasker, R. 1975. Field criteria for survival of anchovy larvae: the relation between inshore chlorophyll maximum layers and successful first feeding. Fish. Bull., US, 73: 453–462.

Lasker, R. 1981a. Factors contributing to variable recruitment of the northern anchovy (*Engraulis mordax*) in the California

Current: Contrasting years 1975 through 1978. Rapp. P.-v. Réun. Cons. int. Explor. Mer, 178: 375–388.

Lasker, R. 1981b. The role of a stable ocean in larval fish survival and subsequent recruitment. *In* Marine fish larvae: morphology, ecology and relation to fisheries, pp. 80–87. Ed. by R. Lasker. Univ. Washington Press, Seattle. 131 pp.

List, R. J. 1949. Smithsonian meteorological tables. 6th ed. Smithson. Misc. Collect. 114. Smithsonian Institution Press, Wash. DC. 572 pp.

Matsuura, Y. 1979. Distribution and abundance of eggs and larval of the Brazilian sardine, *Sardinella braziliensis*, during 1974–1975 and 1975–1976 seasons. Bull. Jap. Soc. Fish. Oceanogr., 34: 1–12.

Matsuura, Y. 1986. Contribuição ao estudo da estrutura oceanografica da região sudeste entra Cabo Frio (RJ) e Cabo de Santa Marta Grande (SC). Ciência e Cultura, 38: 1439–1450.

Mayr, E. 1982. The growth of biological thought. Harvard Univ. Press, Cambridge, Mass. 974 pp.

Nelson, C. S., and Husby, D. M. 1983. Climatology of surface heat fluxes over the California Current region. US Dep. Commer. NOAA Tech. Rep. NMFS SSRF-763. 155 pp.

Olson, D. B., Podestá, G. P., Evans, R. H., and Brown, O. B. 1988. Temporal variations in the separation of Brazil and Malvinas Currents. Deep-Sea Res., 35: 1971–1990.

Parrish, R. H., Bakun, A., Husby, D. M., and Nelson, C. S. 1983. Comparative climatology of selected environmental processes in relation to eastern boundary current pelagic fish reproduction. *In* Proceedings of the Expert Consultation to Examine Changes in Abundance and Species Composition of Neritic Fish Resources, pp. 731–778. Ed. by G. D. Sharp and J. Csirke. FAO Fish. Rep., 291. 1224 pp.

Parrish, R. H., Nelson, C. S., and Bakun, A. 1981. Transport mechanisms and reproductive success of fishes in the California Current. Biol. Oceanogr., 1(2): 175–203.

Parrish, R. H., Serra, R., and Grant, W. S. 1989. The monotypic sardines *Sardina* and *Sardinops:* their taxonomy, distribution, stock structure and zoogeography. Can. J. Fish. Aquat. Sci., 46(11): 2019–2036.

Payne, R. E. 1972. Albedo of the sea surface. J. Atmos. Sci., 29: 959–970.

Peterman, R. M., and Bradford, M. J. 1987. Wind speed and mortality rate of a marine fish, the northern anchovy (*Engraulis mordax*). Science, 235: 354–356.

Reed, R. K., 1977. On estimating insolation over the ocean. J. Phys. Oceanogr., 7: 482–485.

Saccardo, S. A. 1983. Biología y disponibilidad de sardina (*Sardinella braziliensis*, Steindachneer, 1879) en la costa sudeste del Brasil. *In* Proceedings of the Expert Consultation to Examine Changes in Abundance and Species Composition of Neritic Fish Resources, pp. 449–464. Ed. by G. D. Sharp and J. Csirke. FAO Fish. Rep., 291. 1224 pp.

Seckel, G. R., and Beaudry, F. H. 1973. The radiation from sun and sky over the North Pacific Ocean. (Abstr. O33.) EOS, Trans. Am. Geophys. Un., 54: 1114.

Shepherd, J. G., Pope, J. G., and Cousens, R. D. 1984. Variations in fish stocks and hypotheses concerning their links with climate. Rapp. P.-v. Réun. Cons. int. Explor. Mer, 185: 255–267.

Stommel, H. 1966. The Gulf Stream (Second Edition). Univ. California Press, Berkeley and Los Angeles; Cambridge Univ. Press, London. 248 pp.

Tukey, J. W. 1977. Exploratory data analysis. Addison-Wesley, Reading, Mass. 506 pp.

Wooster, W. S., Bakun, A., and McLain, D. R. 1976. The seasonal upwelling cycle along the eastern boundary of the North Atlantic. J. Mar. Res., 34(2): 131–141.

Wooster, W. S., and Sievers, H. A. 1970. Seasonal variations of temperature, drift, and heat exchange in surface waters off the west coast of South America. Limnol. Oceanogr., 15: 595–605.