

TURBULENCE, TRANSPORT, AND PELAGIC FISH IN THE CALIFORNIA AND PERU CURRENT SYSTEMS

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ABSTRACT

The California and Peru Current systems are compared in terms of three environmental processes thought to be likely regulators of reproductive success of pelagic fishes: (1) turbulent mixing, leading to destruction of fine-scale food strata required for successful first feeding of larvae, (2) offshore transport, resulting in loss of reproductive products, and (3) upwelling intensity, as it relates to total productivity of the system. Newly generated climatological distributions of coastal-oceanic temperature contrast, wind-generated turbulent energy production, sea surface wind stress, and surface Ekman transport are presented. A consistent pattern of avoidance of centers of maximum upwelling, which are characterized by intense turbulent mixing and offshore transport, is noted in the reproductive strategies of anchovies. Large stocks tend to occur in regions of low turbulent mixing, downstream of upwelling maxima.

RESUMEN

Se comparan los sistemas de corrientes de California y Perú en relación con los procesos ambientales estimados como reguladores del éxito en la reproducción de los peces pelágicos: (1) la mezcla turbulenta que elimina los estratos conteniendo organismos de talla pequeña, necesarios para un umbral óptimo en la alimentación de las larvas; (2) flujo mar afuera que ocasiona pérdida de gametos y productos de la reproducción; y (3) la intensidad del afloramiento y su relación con la productividad total del sistema. Se discuten las características climatológicas en relación con el contraste en la distribución de la temperatura en la zona oceánica y costera, la turbulencia generada por el viento, la acción del viento sobre la superficie del mar, y el transporte Ekman en aguas de superficie. La estrategia de las anchovetas durante su época de reproducción muestra una característica constante. Así, evitan los centros de afloramiento máximo donde se produce una acción de mezcla intensa y turbulenta, y las zonas de corrientes mar afuera. Las poblaciones tienden a concentrarse en regiones donde la acción de

mezcla y turbulencia es de intensidad baja, en la corriente procedente de las zonas de máxima surgencia.

INTRODUCTION

The four major eastern boundary current systems of the world—the California, Peru, Canary, and Benguela—appear to have similar environmental dynamics and are dominated, in terms of exploitable biomass, by very similar assemblages of pelagic fish species (Table 1). Bakun and Parrish (1980) presented a rationale for interregional comparative studies as a means for developing insights to enhance effectiveness in managing fishery impacts in the face of fluctuating environmental conditions.

The economic importance of the stocks of pelagic fishes in the four principal eastern boundary currents and their apparent tendency to collapse under heavy exploitation make it of great interest to know to what extent we can transfer experience from one system to another, i.e. whether to expect similar outcomes from similar actions. For example, in the Peru Current system a massive anchovy-dominated system has, under heavy exploitation, recently shifted to a sardine-dominated system. The presently expanding exploitation of the central stock of California Current anchovy invites comparison of the two situations. Conversely, extremely heavy exploitation of sardine, jack mackerel, and mackerel resources off Peru and Chile is reminiscent of the heavy exploitation of similar California Current stocks, followed by collapse and subsequent shifting of the system to anchovy dominance several decades ago.

Deducing the environmental factors controlling reproductive success through pattern recognition of environmental-reproductive relationships derived from different eastern boundary current systems is one method to integrate the oceanographic and fishery research that has been carried out in the different regions. Reproduction is singled out as the most significant life-history feature because recruitment variability is considered to be the principal factor responsible for pelagic fish population fluctuations in upwelling regions (Troadek et al. 1980; Csirke 1980; Lasker 1981). Natural selection implies that observed reproductive

TABLE 1
 Dominant Anchovy, Pilchard, Horse Mackerel, Hake, Mackerel, and Bonito in the Four Major Eastern Boundary Currents

California Current	Peru Current	Canary Current	Benguela Current
<i>Engraulis mordax</i>	<i>Engraulis ringens</i>	<i>Engraulis encrasicolus</i>	<i>Engraulis capensis</i>
<i>Sardinops sagax</i>	<i>Sardinops sagax</i>	<i>Sardina pilchardus</i>	<i>Sardinops ocellatus</i>
<i>Trachurus symmetricus</i>	<i>Trachurus symmetricus</i>	<i>Trachurus trachurus</i>	<i>Trachurus trachurus</i>
<i>Merluccius productus</i>	<i>Merluccius gayi</i>	<i>Merluccius merluccius</i>	<i>Merluccius capensis</i>
<i>Scomber japonicus</i>	<i>Scomber japonicus</i>	<i>Scomber japonicus</i>	<i>Scomber japonicus</i>
<i>Sarda chiliensis</i>	<i>Sarda chiliensis</i>	<i>Sarda sarda</i>	<i>Sarda sarda</i>

After Bakun and Parrish 1980.

strategies represent successful accommodation to the most crucial environmental factors. Thus, compelling patterns in seasonal and geographical relationships of reproductive and environmental characteristics suggest important causal linkages over the period during which the reproductive characteristics were generated. The assumption that these same linkages continue to affect reproductive success on a year-to-year basis provides a rational basis for including these factors in empirical modeling efforts.

Recent studies have directed attention toward three classes of environmental processes considered to be likely regulators of pelagic fish reproductive success.

1. Destruction of fine-scale food particle concentrations by wind-generated turbulent mixing has been found detrimental to larval anchovy survival by a series of laboratory and seagoing experiments (Lasker 1975, 1978; Lasker and Smith 1977). Comparative studies of anchovy reproduction in the California Current system versus turbulence and water column stability (Husby and Nelson, this volume) have added corroborative evidence.
2. A comparative study of seasonality and geography of ocean transport and fish reproductive strategies in the California Current (Parrish et al. 1981) has indicated a general pattern of avoidance of intense offshore flow conditions in the reproductive habits of a wide variety of coastal fish stocks. The suggestion is that offshore loss of reproductive products may exert an important control on reproductive success.
3. The major upwelling regions of the oceans are notable for high levels of primary organic production and for particularly massive fish stocks (e.g., Cushing 1969). Recognition of this pattern has led to the widespread belief that fish abundance in these regions is dependent on maintenance of organic production by the upwelling processes, and that long time-scale variations in upwelling intensity may induce fish stock fluctuations. Bakun and Parrish (1980) re-

viewed a number of recent studies in which estimates of variations in upwelling intensity in the California Current system have been related to fish stock variations.

In this paper we focus primarily on the first two hypotheses. The third is considered in terms of the linkage between offshore surface transport and coastal upwelling, the differing effects being distinguished according to the time and space scales on which they operate; for example offshore transport previous to and upstream of spawning activity might enhance larval survival by ensuring adequate food particle concentrations, whereas the same level of offshore transport right at the spawning site could result in offshore loss of eggs and larvae.

Offshore surface transport is adequately represented as Ekman transport (Parrish et al. 1981), except in the immediate vicinity of the equator. Actual transport is the sum of the Ekman and geostrophic components; however, we have not specifically addressed the

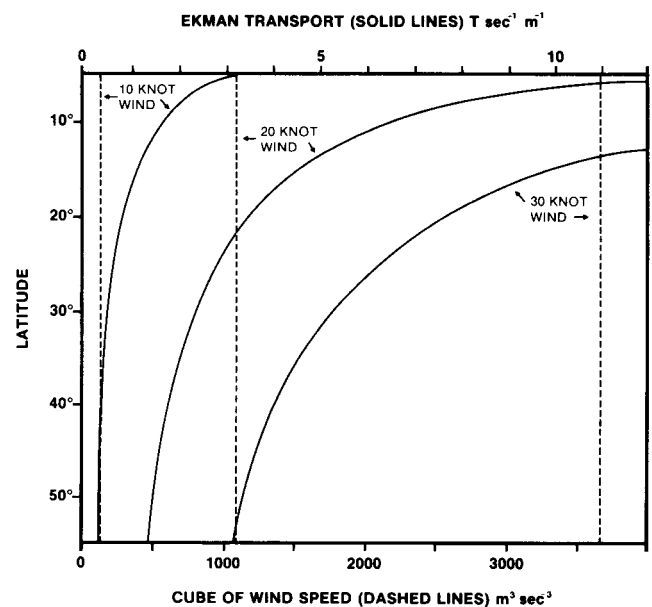


Figure 1. Turbulent mixing energy production (proportional to the third power of the wind speed) vs Ekman transport, for several values of wind speed.

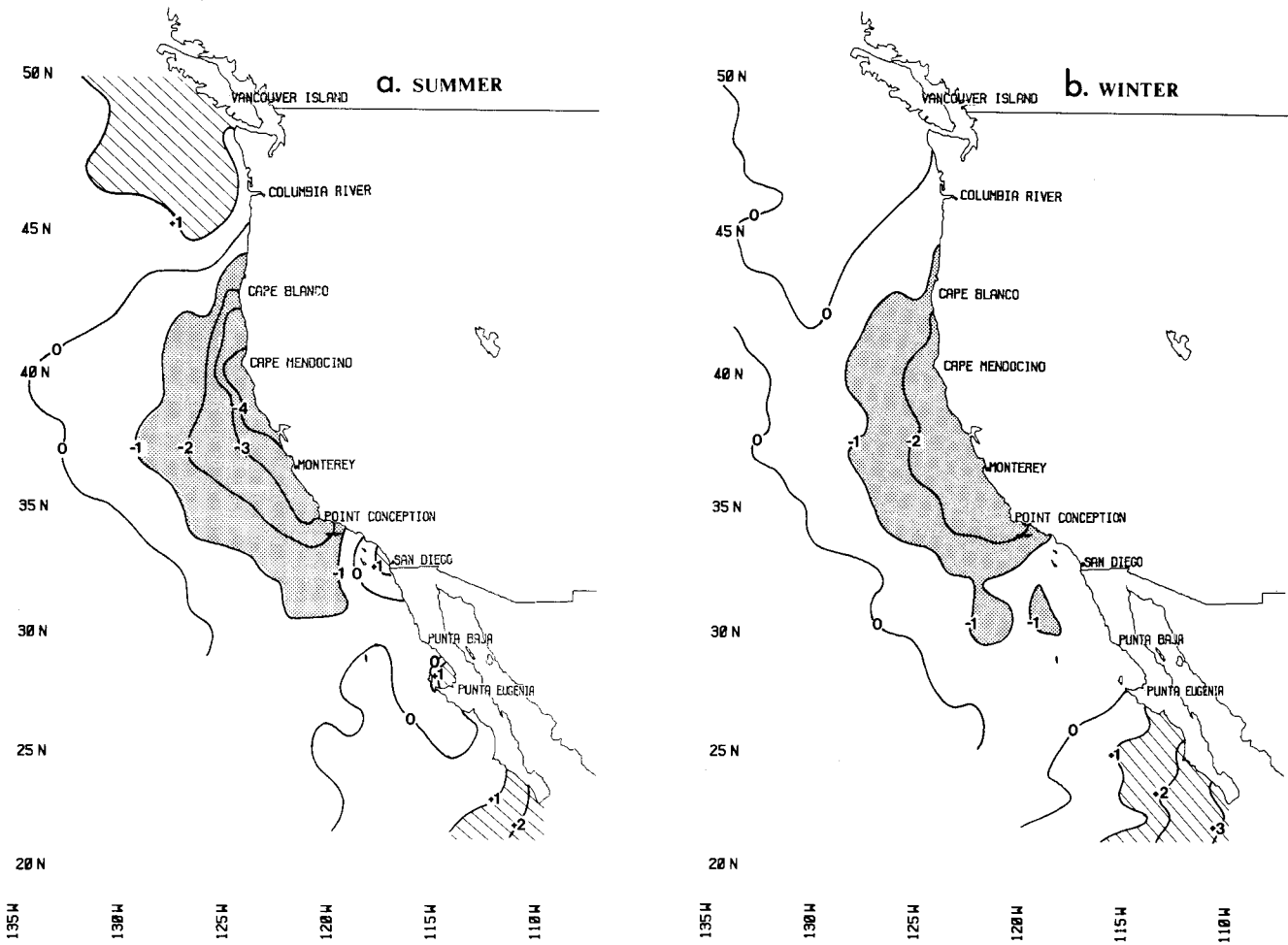


Figure 2. Coastal temperature anomaly (degrees Celsius) computed as the difference between the temperature at each location and a smoothed reference temperature considered to be characteristic of offshore conditions at the same latitude (see text). (a) Summer (May, June, July, Aug.). (b) Winter (Nov., Dec., Jan., Feb.).

geostrophic component because Peru Current flow fields are not yet available on the proper scale. The rate of production of wind-generated turbulent mixing energy varies as the third power, or "cube," of the wind speed (Niiler 1975). Thus for a given wind speed, turbulent mixing energy production is not dependent on latitude, whereas Ekman transport has a strong latitude dependence (Figure 1). This difference is basic to our interregional comparison; for example, a given level of offshore transport would be accompanied by a much lower level of turbulent mixing off Chimbote at 10°S than in the Southern California Bight at 33°N.

SEA SURFACE CLIMATOLOGY

California Current Coastal Temperature Anomaly

Summer and winter distributions of coastal temperature anomaly for the California Current region

(Figure 2) were constructed as follows. All the sea surface temperature observations available in the Fleet Numerical Oceanography Center's version of the National Climatic Centers' File of Marine Surface Observations (TDF-11) for each group of months were averaged by 1-degree latitude and longitude quadrangles. A smoothed offshore temperature reference was constructed by successively applying, at each 1-degree latitude increment, a 5-degree latitude by 3-degree longitude moving-average filter centered at the eleventh 1-degree quadrangular sample westward from the coast. To further minimize sampling irregularities, the three highest and three lowest of the fifteen sample averages covered by the filter at each step were discarded and the remaining nine averaged together; the result is a smoothly varying function of latitude, which we chose as a reference of the offshore oceanic temperature conditions. Finally, the value of this reference at the proper latitude was subtracted

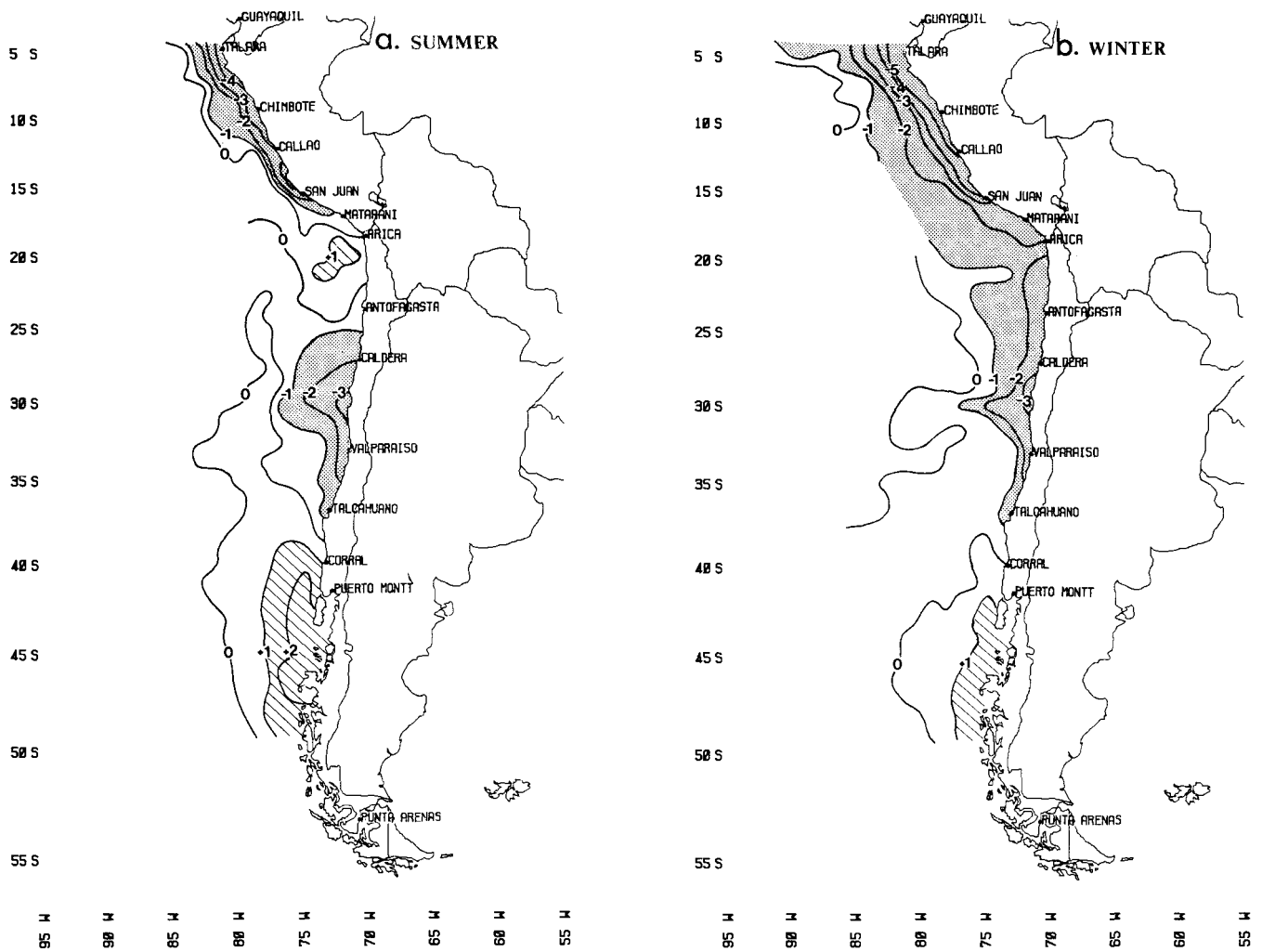


Figure 3. Coastal temperature anomaly (degrees Celsius) computed as the difference between the temperature at each location and a smoothed reference temperature considered to be characteristic of offshore conditions at the same latitude (see text). (a) Summer (Nov., Dec., Jan., Feb.). (b) Winter (May, June, July, Aug.).

from each 1-degree averaged temperature. Coastal temperature anomaly as used herein is therefore the difference between the temperature at each location and the large-scale temperature offshore; it thus filters the global scale equatorward temperature gradient, thereby highlighting local effects.

The area of negative anomaly greater than 1°C (shaded in Figure 2) delineates the area of maximum upwelling that is centered off northern California. The lobe of negative anomaly extending southward from Point Conception appears to be advective in origin, although local Ekman pumping (oceanic upwelling) associated with the strong positive wind stress curl in this location (Nelson 1977) may be a factor. During the summer, positive anomalies greater than 1°C appear in the interior of the Southern California Bight and within Sebastian Vizcaino Bay, north of Punta

Eugenia (Figure 2a). Positive anomalies off the Pacific Northwest appear to be continuous with generalized warm advection into the Gulf of Alaska region. The area off Punta Baja has negative anomalies consistent with an upwelling region, but their magnitude is very low compared to the region north of Point Conception. The winter distribution (Figure 2b) is grossly similar to that for summer, but with a general lessening of gradients.

Peru Current Coastal Temperature Anomaly

The coastal temperature anomaly distribution for southern hemisphere summer (Figure 3a) off Peru and Chile indicates two distinctly separate upwelling maximum regions, one off Peru and the other off north-central Chile centered at about 30°S. These are separated by a region of warm anomaly near Arica.

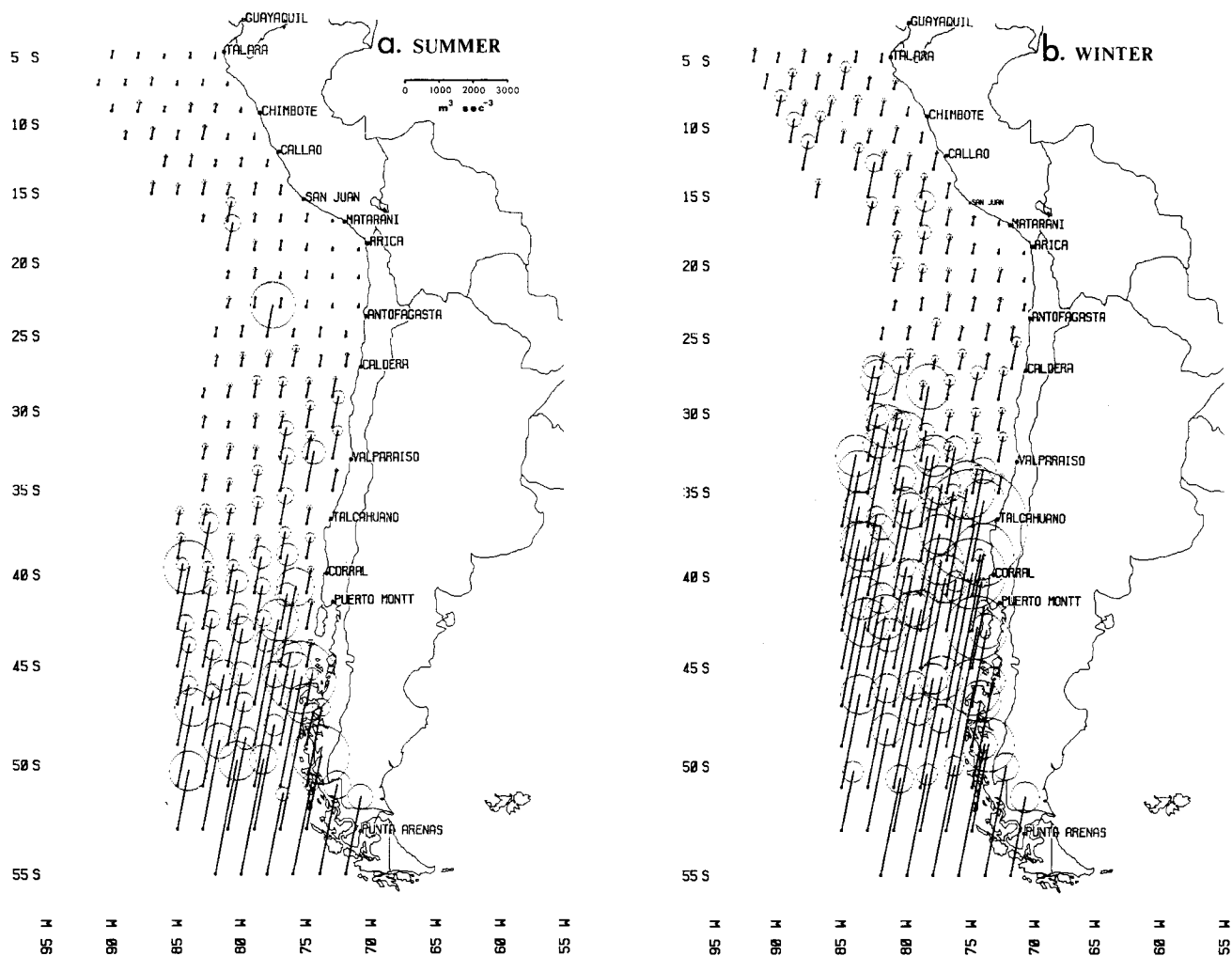


Figure 4. Cube of wind speed ($m^3 sec^{-3}$) indicating rate of turbulent mixing energy production by the wind. Mean magnitude is indicated by length of each symbol; the standard error of each mean magnitude is indicated by the radius of the circle plotted at the top of each symbol (see scale on figure). (a) Summer (Nov., Dec., Jan., Feb.). (b) Winter (May, June, July, Aug.).

Water mass analysis (Cañon 1978) indicates distinctly different source waters for the upwelling occurring in the two regions. South of $40^{\circ}S$ latitude, coastal warming is associated with warm poleward advection resulting from bifurcation of the mid-latitude west wind drift.

During the winter (Figure 3b) the coastal temperature anomaly off Peru is somewhat more intense than in the summer. The area of near-coastal warming off Arica disappears, but a definite minimum in the coastal temperature deficit continues to separate the two upwelling maxima. The negative temperature anomaly in the Chilean upwelling maximum appears to be slightly less intense in winter, as is the coastal warming south of $40^{\circ}S$. This smoothing of gradients in the coastal temperature anomaly distribution during winter relative to those in the summer distribution is

similar to the situation noted for the California Current region (Figure 2).

Peru Current Turbulent Mixing Energy Production

One-degree summaries of wind reports were constructed from the same TDF-11 data file. In order to clarify the presentations in this paper, symbols are plotted only for alternate 1-degree quadrangles in both latitude and longitude coordinates. Thus only one-fourth of the total number of independent samples are shown. The South American coast is too large an area to indicate all the samples on a figure. The complete data set has been examined, and the reduced set shown illustrates the characteristic features. Where a particular sample contains fewer than ten observations, no symbol is plotted.

The distributions of the cube of the wind speed

(Figure 4) show much higher values in the south than in the north, with the region of extremely high values extending farther north in the Southern Hemisphere winter than in the summer. The regions near the coast are generally less turbulent than offshore; a notable exception is the Chilean upwelling maximum region near 30°S during summer. Low turbulence production is characteristic of the coastal region of Peru and of the extreme northern part of Chile, with summer being the least turbulent period. A spatial minimum of wind-generated turbulence is located within the coastal bight near Arica throughout the year.

Peru Current Wind Stress

The resultant stress of the wind on the sea surface is directed equatorward during summer (Figure 5a) along the coasts of Peru and Chile to 40°S. Moderate magnitudes characterize most of the coast of Peru; very low values occur within the coastal bight near Arica. Strong equatorward stress overlies the region of negative coastal temperature anomaly centered near 30°S (Figure 3), which is identified as the Chilean upwelling maximum. South of 40°S strong coastward stress is associated with large-scale westerly airflow.

During winter (Figure 5b) the equatorward stress off Peru strengthens substantially. The bight off Arica continues as a definite minimum in the distribution. The strong resultant stress found in summer near 30°S has disappeared; the offshore region at this latitude is under the influence of the westerly airflow, which has expanded northward. The "roaring forties" (the area south of 40°S) show magnitudes of resultant coastward stress similar to those in summer; however, relatively large standard error ellipses demonstrate stormy, highly variable winter conditions.

Peru Current Ekman Transport

The latitudinal variation in the Coriolis effect (Figure 1) modifies the distributional patterns when the stress distributions (Figure 5) are converted to Ekman Transport (Figure 6). Strong offshore transport is indicated off Peru, particularly in winter. Numerical magnitudes in this case should be viewed with caution because the Ekman transport relationship breaks down at the equator; it is presently unclear how close to the equator Ekman transport continues to acceptably approximate actual transport conditions.

The Chilean upwelling maximum near 30°S is associated with strong offshore-directed Ekman transport during summer (Figure 6a), which relaxes in winter (Figure 6b). Thus the seasonal Ekman transport cycle is similar to that in the Californian upwelling maximum (Parrish et al. 1981), but opposite in phase to that off Peru. The coastal bight near Arica appears as a region of minimal offshore transport, separating

the two upwelling maximum regions and their associated intense offshore transport conditions. South of 40°S the Ekman transport is generally parallel to the coast and equatorward, with a definite onshore component south of about 48°S latitude.

ANCHOVY AND SARDINE STOCKS OF THE CALIFORNIA CURRENT AND PERU CURRENT SYSTEMS

Anchovy

Anchovies are among the most abundant fishes in eastern boundary current regions. In the Peru Current region the dominant anchovy is *Engraulis ringens*; a closely related species, the northern anchovy (*Engraulis mordax*), dominates in the California Current region. Both species are widely distributed; according to Cañon (1978) *E. ringens* ranges from 4°30'S to 42°30'S, and according to Miller and Lea (1972) *E. mordax* extends from 23°N to 53°N. Both species have extended spawning seasons, with some eggs and larvae being taken all year. Eggs and larvae occur over nearly the entire range of both species; however, they are heavily concentrated in distinct spawning grounds.

Meristic, morphometric, and tagging studies suggest that there are at least two major stocks of *E. ringens* (Tsukayama 1966; Rojas de Mendiola 1971; Jordán and Malaga 1972; Serra and Gil 1975). The bulk of the Peruvian fishery was based on a stock centered off northern and central Peru. A smaller stock centered off southern Peru and northern Chile was the basis of the Chilean fishery. Both of these stocks are currently greatly depleted. There is meristic and spawning-pattern evidence for a third stock near Talcahuano (36°S) in central Chile (Brandhorst, et al. 1965; Jordán 1980). A separate fishery has existed on this apparent stock and another pelagic species, *Clupea bentincki* (Serra 1978).

The Peruvian stock has its major spawning grounds located in northern and central Peru from 6°-14°S, and the highest concentrations of eggs occur near Chimbote at about 9°S (Santander 1980). Santander (1981) suggests that the areas and time of maximum spawning do not co-occur with the areas and periods of maximum upwelling; spawning is greatly reduced in the core of maximum upwelling (14°-16°S).

Cañon (1978) found several centers of spawning for the Peru-Chilean stock in northern Chile, especially near Arica (18-19°S) and Mejillones (22-23°S). However, the available literature does not indicate how far the spawning grounds extend into southern Peru. Anchoveta eggs have been found as far south as 40°S (Cañon 1978), and it is reported (Serra et al. 1979) that the spawning grounds of the potential central

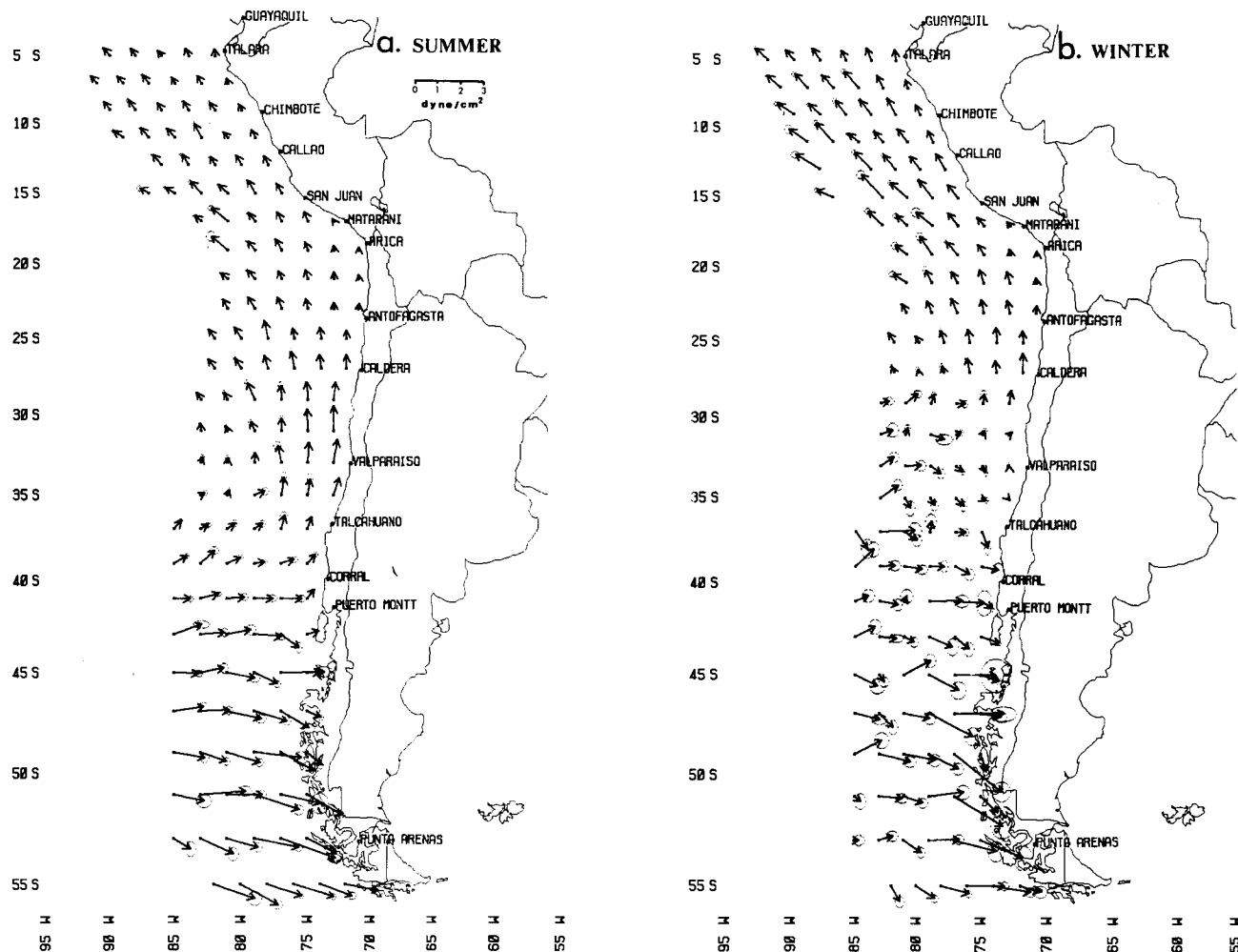


Figure 5. Wind stress on the sea surface (dynes cm^{-2}). Magnitude is indicated by length of symbol (see scale on figure); direction is indicated by orientation of symbol. Standard errors of the means of the meridional and zonal components are indicated by the vertical and horizontal axes of the ellipses plotted at the head of each symbol. Computation of stress is as described by Bakun et al. 1974. (a) Summer (Nov., Dec., Jan., Feb.). (b) Winter (May, June, July, Aug.).

Chilean stock are in the vicinity of the fishery at Talcahuano (36°S).

Meristic, morphometric, electrophoretic, and tagging studies with *E. mordax* suggest that there are at least three stocks in the California Current region (McHugh 1951; Vrooman et al. 1981; Haugen et al. 1969). According to Richardson (1980) the spawning grounds of the northern stock are centered at about 44° - 46°N in the Columbia River plume; spawning occurs in summer, and is highly concentrated in July. The central stock's spawning grounds are principally in the Southern California Bight (30° - 34°N); spawning occurs throughout the year, with a distinct maximum from February to April and a minimum from August to October (Lasker and Smith 1977). Both the Californian and Mexican anchovy fisheries are based on the central stock, which in recent years has been the largest of the three. The spawning grounds of the

southern stock are centered in southern Baja California (25° - 28°N); the peak spawning season is similar to that of the central stock, but slightly earlier in the year. Peak larval abundance occurs from January to March (Smith 1972).

The Peruvian anchoveta stock was by far the largest of the Engraulid stocks of the Peru and California Current regions, and it has supported fisheries at least one order of magnitude greater than any of the other stocks. Landings for the period just before its collapse averaged about 10 million metric tons (MT) per year (Valdivia 1980), and virtual population estimates show that the spawning biomass averaged about 20 MT during the early years of the fishery (Csirke 1980). It is difficult to determine the catches or population size of the Peru-Chilean stock, for it was a minor but undetermined proportion of the Peruvian landings and a major proportion of the Chilean land-

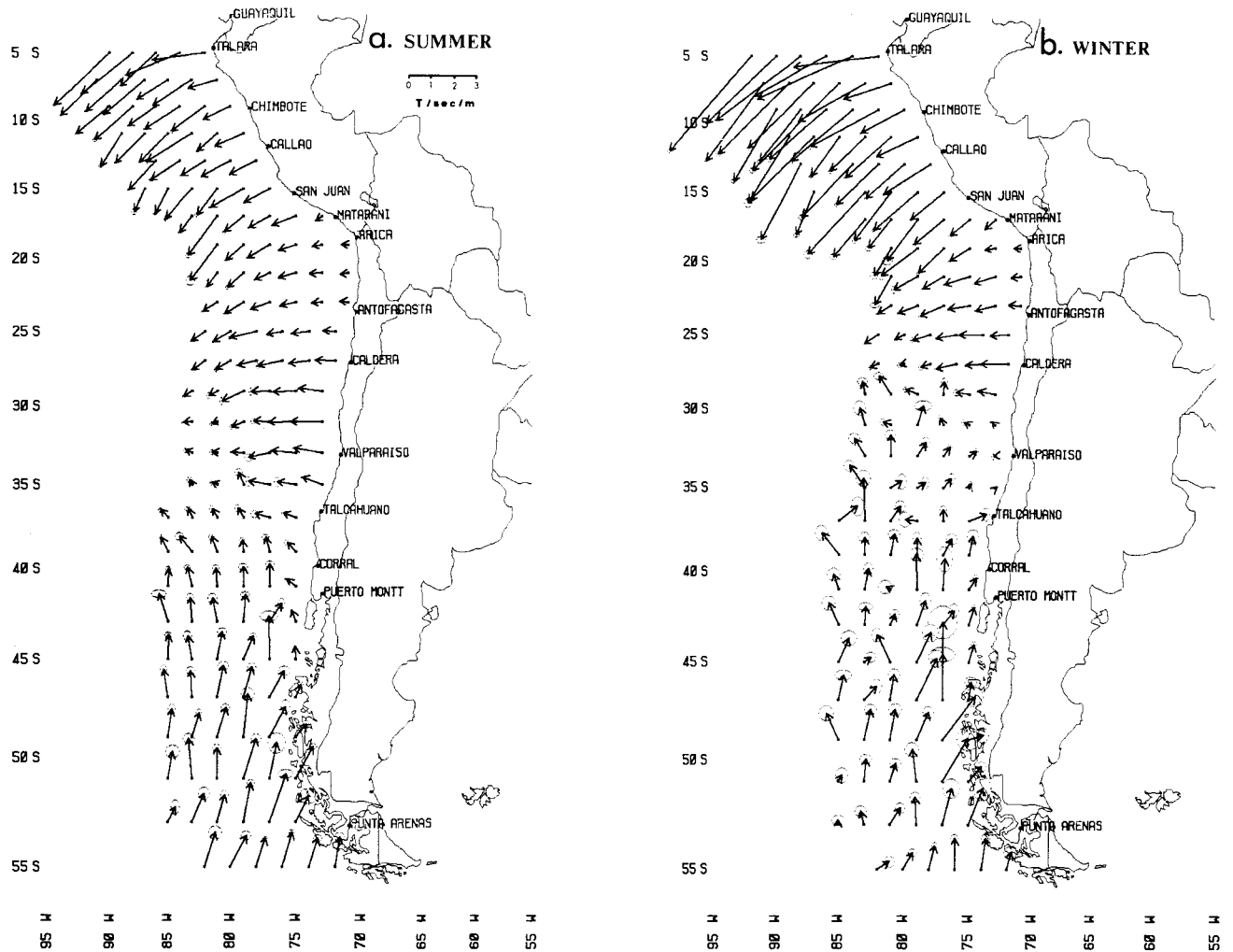


Figure 6. Surface Ekman transport (metric tons per second per meter) computed from the wind stress vectors shown in Figure 5. (a) Summer (Nov., Dec., Jan., Feb.). (b) Winter (May, June, July, Aug.).

ings. The peak Chilean landings of anchoveta were just under 1 MT (Boré and Martínez 1981), the great majority of which was apparently from the Peru-Chilean stock, since the landings from the Talcahuano region, which did not separate *Clupea* and *Engraulis*, had a maximum of just less than 0.2 MT.

The central stock is the only one of the three California Current stocks that has been extensively fished. Combined catches of the Mexican and Californian fisheries on this stock have recently reached 0.3 MT. Peak landings would have undoubtedly been larger than this if the California fishery had not commenced under intense regulation. Spawning biomass estimates based on larval surveys are available for the three California Current stocks. Estimates for the northern stock, based on two years of surveys and several different methods of calculating spawning biomass, vary between 0.14 MT and 1.0 MT

(Richardson 1980). Larval surveys during the 1960s suggested that the spawning biomass of the central stock was from 3 to 4 MT, and the southern stock averaged about 1 MT (Vrooman and Smith 1972). Recent spawning biomass estimates based on egg surveys and Hunter and Goldberg's (1980) and Hunter and Macewicz's (1980) recent findings on the reproductive physiology of the northern anchovy suggest that the biomass estimates based on larval surveys were too large (Stauffer and Piquelle 1981).

The available evidence suggests that the virgin biomass of the Peruvian *Engraulis* stock was about 20 MT; the Peru-Chilean and Southern California Bight stocks were about 1-4 MT, with the Peru-Chilean stock probably the larger of the two. The stocks spawning near Talcahuano, in the Columbia River plume, and off of southern Baja California were both probably less than 0.5 MT.

Sardine

Radovich (1981) reviewed the available information on the sardine *Sardinops sagax* in the California Current region and concluded that there was good evidence for three stocks and sufficient evidence to hypothesize a fourth stock. Two of the stocks occurred together with the southern and central stocks of anchovy, respectively. The Gulf of California stock has no anchovy counterpart, and the hypothesized fourth stock would be a counterpart to the northern stock of anchovy. During the peak of the sardine fishery, landings varied from about 0.5 MT to 0.8 MT. Landings from the Southern California Bight were only 0.1 to 0.2 MT, with the rest coming from central California, which was the major fishing area, and from the Oregon to British Columbia region. Landings in central California and possibly those in the Oregon to British Columbia areas, were derived from sardines that used the upwelling region as feeding grounds and that migrated to the Southern California Bight for spawning.

The fishery for the sardine *Sardinops sagax* in the Peru Current system is quite recent, and therefore there is little published information on the population structure. The information presented below is primarily from Santander (1981) in the case of Peru and from the Chilean Fisheries Resource Catalogue (Boré and Martínez 1981) in the case of Chile. In Peru the area in which eggs and larvae of sardine were found has expanded considerably since 1972, when eggs were largely limited to northern Peru and were primarily located farther offshore than the anchoveta eggs and larvae. Since 1972 the co-occurrence of anchoveta and sardine eggs and larvae has increased, and sardine eggs and larvae are common all along the Peruvian coast; however, the area of most intense spawning is still in northern Peru (i.e., 5°-11°S). In Chile there is extensive spawning in the area between Arica and Antofagasta (18°-23°S), and eggs have been found as far south as Isla Mocha (38°S. B.J.R. Serra, pers. comm.). The fishery is the most intense in the Arica to Coquimbo area (18°-30°S); however, since 1978 there have been substantial catches in the Talcahuano area (37°S). Chilean sardine landings reached 1.6 MT in 1979.

TRANSPORT, TURBULENCE, AND REPRODUCTION

The same data used to produce the 4-month seasonal distributions (Figures 4, 5, 6) were subdivided into 2-month sets in order to plot the seasonal progression of turbulent mixing and offshore transport conditions (Figure 7) and of turbulence and alongshore stress conditions (Figure 8) for the spawning centers

and other significant areas. Characteristic 2-month values of the cube of wind speed for selected locations in the California Current region were assembled from the distributions presented by Husby and Nelson (this volume); corresponding estimates of alongshore stress and offshore Ekman transport were assembled from Nelson's (1977) charts.

The area off Chimbote, which is the spawning center of the major anchoveta stock, is low in average wind-generated turbulence throughout the year. However, offshore Ekman transport is large (Figure 7), particularly during the winter, when it is the maximum plotted for all areas. Because of Chimbote's proximity to the equator it is possible that Ekman transport overestimates the actual transport; when plotted in terms of alongshore stress (Figure 8), which avoids addressing the effect of rapid decrease of Coriolis near the equator, the cycle at Chimbote shifts toward the origin. One might hypothesize that the spawning of anchoveta during the season of largest alongshore stress (offshore transport) may be related to avoidance of detrimental effects of intermittent El Niño events, which occur most intensely during the Southern Hemisphere summer.

The seasonal pattern in the Southern California Bight, which is the principal spawning ground for the pelagic fishes of the California Current, including the central subpopulation of northern anchovy, is near the origin in both diagrams (Figures 7 and 8). However, it may be noted that the lowest average turbulence is encountered in the summer and fall, whereas spawning is most common in the spring and also in the winter in the case of anchovy. One may hypothesize that the relationship to the upwelling cycle may be the factor that determines spawning seasonality given the low turbulence and offshore transport conditions within the bight throughout the year.

The area off Arica near 18°S is consistently very low in both wind-generated turbulence and offshore transport. This area resembles the Southern California Bight in this and in several other respects, including warm coastal temperature anomalies during summer and location directly downstream from maximum upwelling regions. We need more information about the extent of spawning to properly evaluate its comparative significance.

In comparison to the three largest anchovy stocks of the eastern Pacific, the three smaller stocks appear to spawn in regions of somewhat higher turbulence. The southern Baja California stock spawns in an area where turbulence and offshore transport are moderate throughout the year, with values somewhat higher in the winter-spring transition than during the rest of the year. The high-latitude stocks (the northern stock of

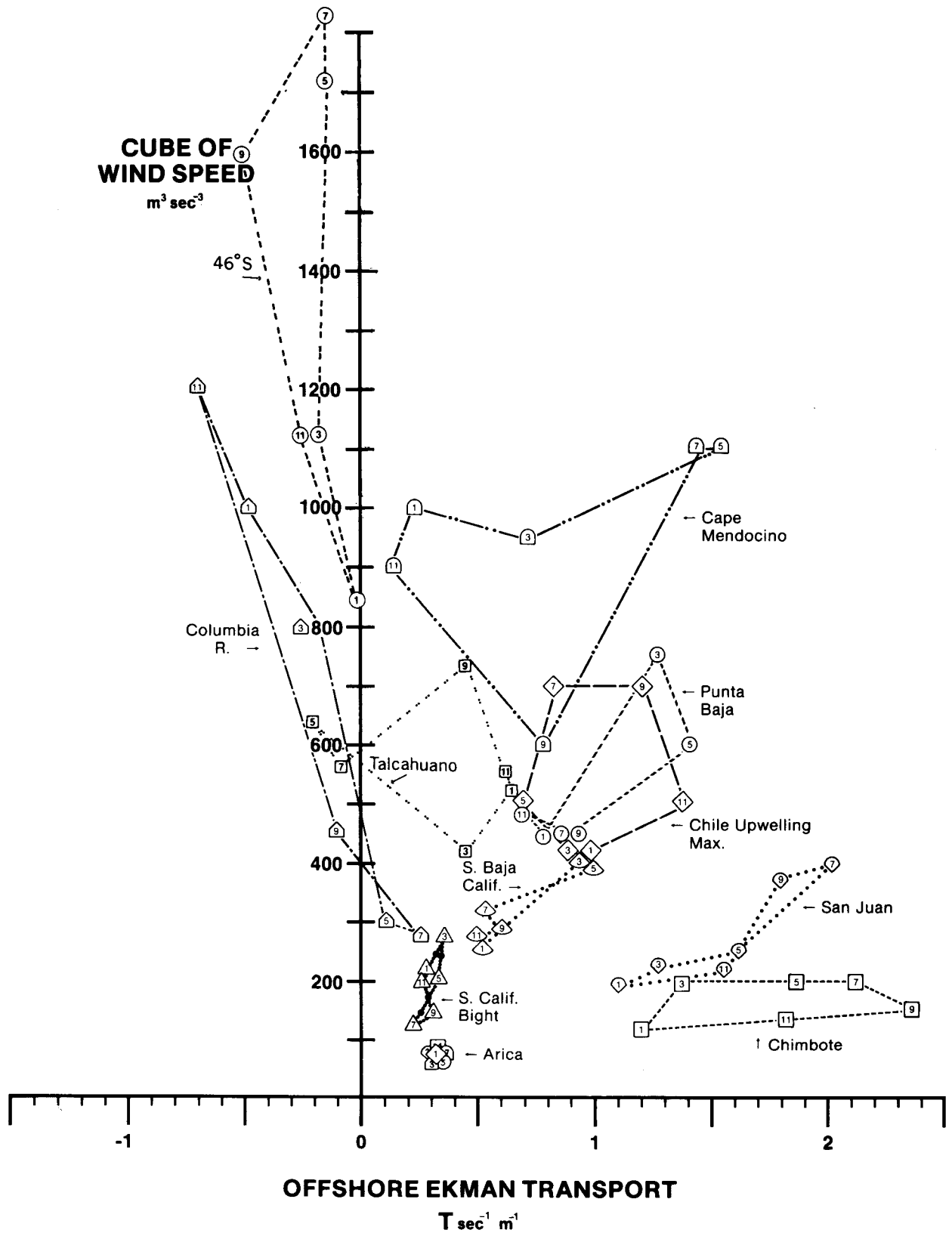


Figure 7. Characteristic seasonal relationships of turbulent mixing energy production (proportional to cube of wind speed) and offshore-directed Ekman transport for various locations off the west coasts of North and South America. Each numbered symbol represents a 2-month sample, with the number corresponding to the first month of the two (e.g., 1 represents Jan.-Feb., 3 represents Mar.-Apr., etc.).

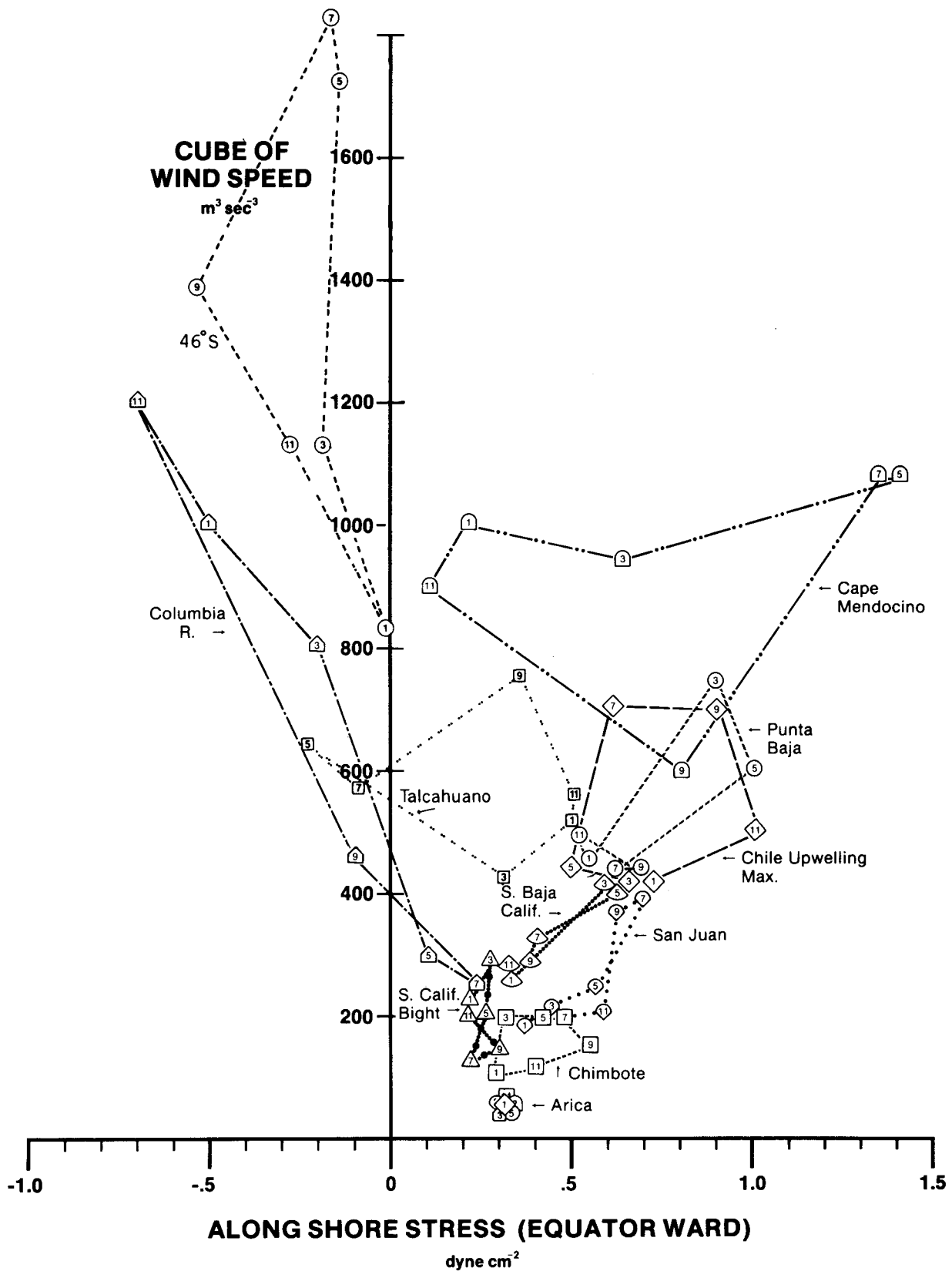


Figure 8. Characteristic seasonal relationships of turbulent mixing energy production (proportional to cube of wind speed) and alongshore wind stress (positive equatorward) for various locations off the west coasts of North and South America. Each numbered symbol represents a 2-month sample, with the number corresponding to the first month of the two (e.g., 1 represents Jan.-Feb., 3 represents Mar.-Apr., etc.).

anchovy, which spawns in the Columbia River plume, and the Talcahuano anchoveta stock) spawn in areas where turbulence is considerably higher than in the other spawning centers and where Ekman transport varies seasonally from onshore to offshore. The stock spawning in the Columbia River plume does so only in the summer, when the seasonal progression enters the space in the diagrams where the other stocks spawn. The Talcahuano stock (if it is a separate stock) is reported as spawning mainly in embayments protected from the higher levels of turbulence occurring off the coast (F.L.E. Robles, pers. comm.).

In the diagrams, the space occupied by the upwelling centers within the regions of maximum upwelling tends to be displaced toward the upper right of the space occupied by the spawning areas: e.g., Cape Mendocino (39°N), San Juan (15°S), and the Chilean upwelling maximum (30°S). This is also the case for the Punta Baja (30°N) area, which is a secondary upwelling region. The seasonal progression at 46°S latitude has a similar shape and orientation to that off the Columbia River at 46°N but is situated at a substantially higher turbulence level, never entering the areas in the diagrams occupied by the spawning regions. We would therefore not expect an extreme southern stock to be able to reproduce successfully enough to maintain a significant population at this latitude in the South American system.

In this connection, it is recognized that the meteorological and oceanographic "equators" are located to the north of the geographical equator, and thus a strict correspondence in latitude might not be expected; i.e., analogous features might be closer to the equator in the Southern Hemisphere than in the Northern Hemisphere. However, note that very much the same space is occupied in the diagrams by the Chilean upwelling maximum at 30°S and by the upwelling center at Punta Baja at 30°N; even the march through the annual cycle is in the same sense, although of course 6 months out of phase.

In concluding our discussion of the diagrams (Figures 7 and 8), we must comment on the precision of the displayed estimates. Available marine surface data are particularly sparse in certain coastal regions off South America, so sampling variability is a problem. Also, gradients in real distributions occur on small scales, which are not well resolved by our summaries. Thus, while we are confident in the general relationships of the spaces displayed, certain smaller details are less certain. For example, the indication of stronger offshore transport off Chimbote during September-October than during July-August may not be reliable; note that because of Chimbote's proximity to the equator the horizontal axis of its seasonal pattern in the

transport diagram (Figure 7) is greatly expanded relative to that in the stress diagram (Figure 8).

CONCLUDING REMARKS

This paper represents only a "first cut" through the information available in the collected marine observations and accumulated knowledge of spawning habits. We are convinced that comparative studies are (1) useful for understanding linkages between fish stocks and environmental processes that are often extremely difficult to investigate experimentally, and (2) very cost-effective when making use of data for which the investment has already been made.

Figures 7 and 8 represent two potential dimensions of a multivariate "reproductive habitat space." To the extent that the other crucial dimensions can be isolated and the favorable intervals defined, the excursions by various spawning sites into and out of the favorable space can perhaps be monitored, providing a basis for formulating empirical models that could be used to predict and simulate effects of management actions.

In adopting this view it is important to recognize the differences in scale, both of time and space, on which the various environmental processes affect eventual recruitment. For example, the critical time scale for turbulence to induce mortality by dissipating food concentrations may be several days at most. The effects of transport of larvae are expected to act on scales of a month or more, with consequences extending into the juvenile stage. Upwelling variations on seasonal and interannual time scales may affect the average background concentration of food organisms, which underlies the patterns altered by the short-scale turbulence mechanism. Likewise, upwelling and its associated offshore transport may be a favorable factor on long time scales and broad space scales, i.e. previous to the spawning season and upstream of spawning grounds, and an unfavorable factor when acting at the precise time and location that larvae may be present. We have noted a pattern of avoidance of upwelling maximum regions and areas of high turbulence in the spawning strategy of engraulids. An exception is the situation off north-central Peru, where an enormous engraulid population has existed in what we are calling an upwelling maximum region. In this case the steadiness of the upwelling process and the low turbulent mixing, which is unique to this region, could be a factor. Smaller-scale upwelling centers, e.g., the area near San Juan, which exist within the larger-scale upwelling maximum region, appear to be avoided in spawning habits (Santander 1981).

One preliminary comparative result with direct management implications is worth noting. The recent alternations between anchovy domination and

sardine-mackerel domination in the two systems have yielded the consistent experience that the exploitable biomass in a sardine- and mackerel-dominated system is located poleward compared to that in an anchovy-dominated system. Thus the shifts in species composition have resulted in a spatial shift of the patterns of exploitation across national boundaries, where they appear to have a tendency to remain. The possibility of shifting the exploitable component of the organic production of a shared system to another nation's waters presents a particularly strong argument to a self-interested nation against overexploitation of the resources off its own coast.

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