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# Transport Mechanisms and Reproductive Success of Fishes in the California Current

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*Abstract* Surface marine observations are used to infer the large-scale seasonal patterns of ocean surface drift near the coast in the California Current. Reproductive strategies of the most successful coastal fishery species show a pattern of correspondence to the major features of surface transport. In the Pacific Northwest, coastal fish species having pelagic larvae tend to spawn during winter when surface wind drift is generally directed toward the coast, rather than during the more productive upwelling season. In the region of vigorous upwelling off northern California, which is characterized by strong offshore surface transport through most of the year, there is a paucity of locally spawning species with epipelagic eggs. The fishes spawning in this region have a wide range of reproductive strategies that reduce the planktonic phase of the early life history. Local coastal stocks comprise a minority of the fish biomass in the region. Rather, the fish stocks that harvest the massive productivity of this region are primarily migrating species that spawn under the more favorable drift

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conditions in the Southern California Bight. Closed gyral circulations in the Southern California Bight and off southern Baja California appear to foster favorable spawning conditions that have led to distinct subpopulations of pelagic fishes.

The apparent dependence of spawning strategies upon surface drift conditions suggests the hypothesis that anomalies in surface drift patterns could be a major cause of the observed wide variations in spawning success of the major fishery species of the California Current region.

Egg and larval transport is a critical process in the life cycle of many marine organisms. Typically, spawning grounds are "upstream" in relation to ocean current flow from nursery grounds. The reproductive strategies of many marine species are adapted to fit the prevailing currents, which are relied upon to bring the largely planktonic larvae to nursery grounds usually found in relatively shallow or inshore waters. In order for survival to be adequate, there must be sufficient food during the larval drift period, and the currents must allow the larvae to arrive at the nursery grounds at the proper time and size (Stevenson, 1962; Parrish and Saville, 1965; Ketchen and Forester, 1966; Cushing, 1967). The potential inshore nursery grounds are limited in the California Current region due to the narrow continental shelf. In addition, during certain seasons the prevailing winds cause seaward drift of surface waters, favoring offshore dispersion and loss of larvae. The segment of coastline from Cape Blanco to Point Conception, in particular, is characterized by minimal shelf area and is subject to intense offshore surface drift through much of the year.

The fish fauna of the California Current region is composed principally of elements of a cold-temperate fauna centered in the Pacific Northwest (i.e., the area north of Cape Blanco) and a subtropical fauna centered in the southern California–Baja California region. The transition region between Cape Blanco and Point Conception contains elements of both faunas. Two other faunal groups are well represented in the California Current region: an offshore assemblage (central water mass forms) and a component of the eastern Pacific tropical fauna, which extends into southern Baja California. Many of the hypotheses discussed here probably do not apply to the offshore and tropical faunas.

The exploitable fish biomass in the California Current System is dominated by a small number of pelagic species (Table 1). The spawning grounds of these stocks are primarily in areas characterized by weak coastal upwelling. These fishes, or very closely related species, dominate the fisheries of the three other major eastern boundary current systems (Bakun and Parrish, 1980). Ryther (1969) pointed out that the fisheries of upwelling regions are dominated by pelagic fishes that have relatively short food chains, whereas the fisheries of higher latitudes are dominated by demersal fishes with somewhat longer food chains. The

**Table 1.**
Peak landings and biomass estimates
(in thousands of metric tons)
of the dominant exploitable fishes spawning
in the California Current region.

| *Species* | *Peak Landings by Region* | | | | *Biomass Estimates* | |
|---|---|---|---|---|---|---|
| | *Total* | *Pacific Northwest* | *Region of Maximum Upwelling* | *Southern California Bight* | *Peak Year* | *Recent* |
| Sardine | 718[a] | 91[a] | 529[a] | 167[a] | 3625[a] | 5[b] |
| Anchovy | 288[c] | — | 21[d] | 284[c] | 7067[e] | NA |
| Hake | 231[f] | 161[g] | 101[g] | — | 3270[h] | 1519[g] |
| Jack Mackerel | 68[i] | 4[g] | 15[j] | 66[d] | 1905[k]* | NA |
| Pacific Mackerel | 66[l] | — | 2[l] | 64[l] | 438[m] | 167[n] |
| Pacific Ocean Perch | 39[o] | 39[o] | — | — | 120[f] | 18[f] |
| Rockfish (other) | 33[f] | 18[f] | 11[f] | 5[f] | NA | NA |
| Sablefish | 17[f] | 7[f] | 6[f] | 4[f] | NA | 61[f] |
| Dover Sole | 16[f] | 7[f] | 10[f] | — | NA | NA |
| Bonito | 16[p] | — | — | 16[p] | NA | NA |
| Saury | — | — | — | — | 266[q]* | NA |
| Shortbelly Rockfish | — | — | — | — | 295[f]* | 295[f]* |

*—minimum estimate
NA—estimates not available

[a] Murphy (1966)
[b] Klingbeil (1974)
[c] Preliminary 1980 Mexican and California catch[1]
[d] California Marine Fisheries Branch (1954)
[e] Vrooman and Smith (1971)
[f] Pacific Fisheries Management Council (1980)
[g] Dark (pers. comm.[2]/
[h] Alverson and Larkins (1969)
[i] Knaggs (1979)
[j] California Bureau of Marine Fisheries (1952)
[k] Blunt (1969)
[l] California Bureau of Commercial Fisheries (1937)
[m] Parrish and MacCall (1978)
[n] Klingbeil (1981)
[o] Gunderson (1977)
[p] Collins et al. (1980)
[q] Smith et al. (1970

California Current System is no exception. Pelagic fishes dominate in the southern part of the system where upwelling occurs throughout the year. The northern portion of the system, where upwelling is highly seasonal, has had extensive demersal fisheries in addition to pelagic fisheries.

The purposes of this paper are (1) to present a simplified, but unified and consistent, description of broad time and space scale characteristics of ocean surface flow in the California Current region, and (2) to point out a gross pattern of correspondence to these features among the reproductive strategies of the most successful coastal fish stocks. We believe that this correspondence offers useful insights into the factors regulating recruitment and exposes fruitful directions for further research.

## Transport Mechanisms

### *Seasonal Flow Patterns*

The two components of near surface ocean flow that are fundamental to our hypotheses are the surface wind drift, which is the water being carried along in the ocean surface layer under the direct action of the wind, and the underlying geostrophic current field. The geostrophic flow is associated with pressure gradients in the ocean. Its contribution to the near surface velocity field can be inferred largely from temperature and salinity structure. Present understanding of surface wind drift is based on Ekman's (1905) theory, in which the total transport (Ekman transport) in the wind-drifted layer is completely determined by the intensity of the wind stress on the sea surface. On the rather large time and space scales involved in the larval drift problem, transport in the surface layers of the ocean may be adequately viewed as a simple linear combination (i.e., vector addition) of contributions due to these two flow components. The conceptual picture is of a thin surface layer of Ekman wind drift that varies in phase with large-scale atmospheric weather patterns superimposed on a deeper, more slowly varying geostrophic flow field. The physical basis for this conceptual model comes from scale analysis of the terms in the hydrodynamic equations (Greenspan, 1968).

## *Geostrophic Current*

The annual mean geostrophic flow at the sea surface (Figure 1A) was constructed from temperature and salinity summaries produced by Robinson and Bauer (1973), who pooled the available observations within areas defined by 1° increments of latitude and longitude to yield long-term annual mean values at standard depths. Dynamic topographies relative to the 1,000 db level (1,000 m) were computed following La Fond (1951), and a velocity vector for each 1° square was calculated from the gradients defined by dynamic height values in the directly adjacent 1° squares. The result is a rather smooth field in which much of the temporal and spatial detail available in finer scale summaries (Wyllie, 1966) has been filtered out, revealing the large-scale features that provide the basis for our arguments.

The nearshore surface geostrophic flow tends to parallel the coast and, south of Cape Blanco, to be directed equatorward. The general direction of geostrophic flow into the Southern California Bight and toward the coast south of Point Conception is significant to our argument. This is a consistent feature during all seasons, being evident in all of Wyllie's (1966) long-term monthly charts. However, seasonal alongshore surface current features, such as the Davidson Current (Sverdrup et al., 1942), are suppressed in Figure 1.

The pattern of geostrophic flow at 60 m (Figure 1B), constructed by analogous procedures, is similar to that at the surface, but shows a tendency for less southward (more northward) flow near the coast. Thus, the area within 200 km of the coast is characterized by greater vertical shear in the velocity structure in the upper layers of the ocean. This northward tendency in the near coastal subsurface flow relative to the flow at the sea surface is associated with the California Undercurrent (Reid, 1962, 1963; Wooster and Jones, 1970) and continental shelf poleward undercurrent (Smith, 1974; Pedlosky, 1974) phenomena.

## *Surface Wind Drift*

Quarterly distributions of Ekman transport (Figure 2) were computed from Nelson's (1977) stress summaries. Ekman transport is calculated as the ratio of the wind stress magnitude to the local value of the Coriolis parameter and is directed 90° to the right of the wind stress (in the

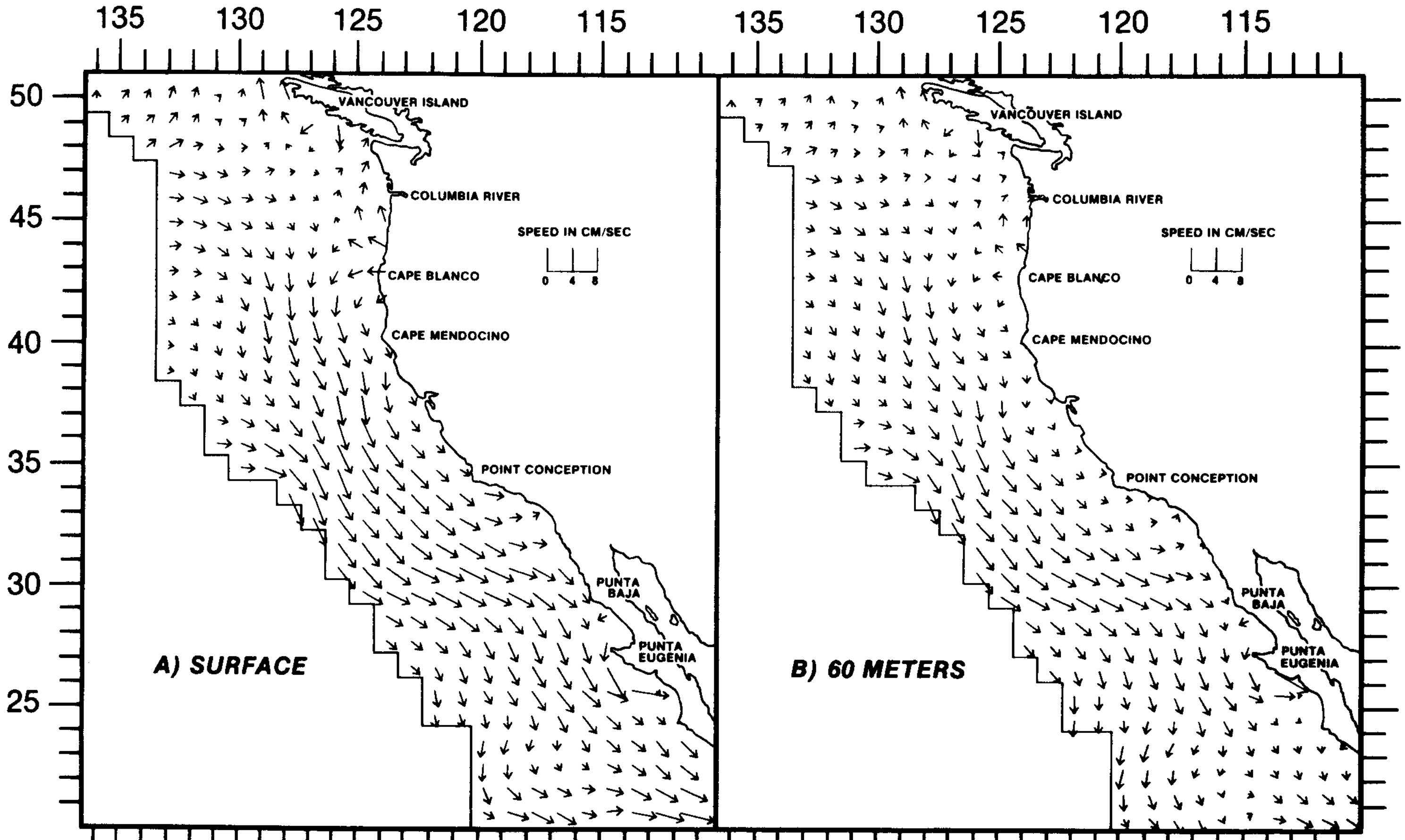

**FIGURE 1.** Mean geostrophic flow: A. at the sea surface (0/1000 db), B. at 60 m (60/1000 db). Vector symbols represent the large-scale, long-term, mean geostrophic currents. Speed is scaled according to the key on the chart.

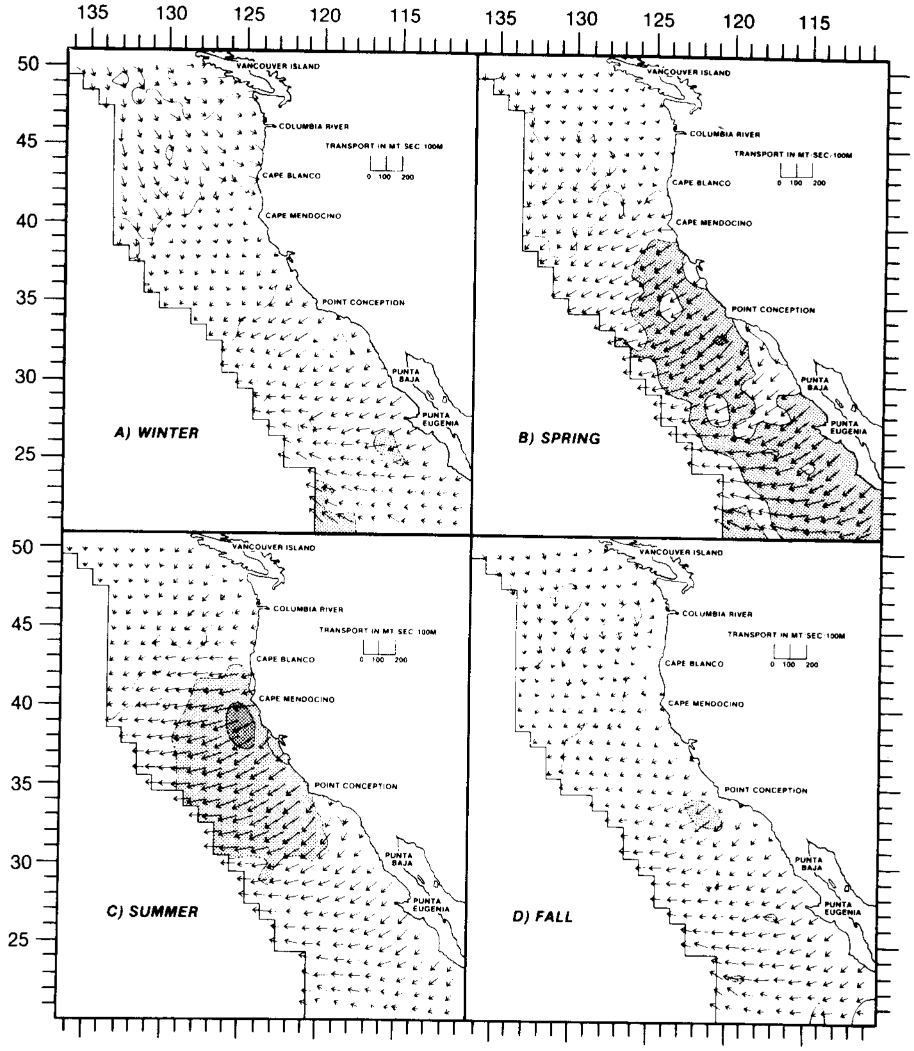

**FIGURE 2.** Surface Ekman transport: A. winter (December through February), B. spring (March through May), C. summer (June through August), D. fall (September through November). The contour interval is 50 t $s^{-1}$ per 100 m width. Areas of transport greater than 100 t $s^{-1}$ per 100 m are shaded.

Northern Hemisphere). The fine-scale vertical structure of the Ekman velocity field depends on vertical eddy viscosity characteristics, which are not well known; however, the total transport of water in the layer between the sea surface and the depth at which the drift velocities become negligible does not depend on these characteristics and can be inferred from the wind stress alone. The depth of negligible Ekman drift velocities is likewise not well known. However, most of the transport probably occurs in the upper 20 to 30 m; no appreciable Ekman drift is likely to penetrate beneath the surface mixed layer into the stratified portion of the water column. Therefore, the movement due to wind drift of aggregates of organisms that are mixed over a depth range as deep as or deeper than the Ekman layer generally corresponds to Ekman transport. The upper portion of the Ekman layer would tend to move in a direction closer to that of the wind stress, and so organisms that can maintain themselves at depths very near the surface might be moved at angles less than the full 90° to the right of the wind (i.e., somewhat to the left of the vectors in Figure 2). However, Ekman theory would have even the very surface of the ocean moving no less than 45° to the right of the wind, and so reference to the Ekman transport vectors will generally provide a sufficiently precise indication of onshore or offshore surface transport.

During winter (Figure 2A), Ekman transport is directed toward the coast in the Pacific Northwest region. South of Cape Mendocino the transport is offshore and increases in strength to a maximum south of Punta Baja, Baja California. By spring (Figure 2B), onshore Ekman transport in the north has relaxed and offshore transport has strengthened along the coasts of California and Baja California. Within the Southern California Bight, there is a local minimum in offshore transport. In summer (Figure 2C), the region of maximum offshore transport shifts north to northern California, and offshore transport occurs throughout the region. Transport off central Baja California has diminished considerably from the spring situation.During fall (Figure 2D), offshore transport relaxes off California. The mean surface drift becomes onshore north of Cape Blanco. The Southern California Bight continues to be an area of reduced offshore wind drift, as it is throughout the year. A discussion of the atmospheric features responsible for these seasonal wind drift patterns can be found in Nelson (1977).

The geostrophic flow data (Figure 1) yield velocities of water motion. However, the Ekman drift computations (Figure 2) yield mass transports averaged over the effective vertical thickness of the Ekman layer. Proper vector addition of the two flow components requires knowledge of the Ekman layer thickness, which is lacking. Equal vector symbol lengths in Figures 1 and 2 would indicate equal velocity contributions, assuming an effective Ekman depth of 25 m, a reasonable (Neumann and Pierson, 1966) but arbitrary choice. For example, Peterson et al. (1979) deduced a thinner Ekman layer of 5 to 15 m from their observations of copepod distributions off Oregon. For a thinner Ekman layer, the velocities corresponding to a given transport value would be proportionately larger, and for a thicker layer proportionately less. The long-term composite geostrophic flow fields (Figure 1) are, of course, highly smoothed representations. Any synoptic distribution would contain much more spatial detail, with local speeds ranging an order of magnitude greater (Wyllie, 1966).

### Shorter Scale Flow Variations

Within the California Current, spawning tends to be distributed in both time and space. In addition, eggs and larvae may drift in the plankton for a considerable period after being spawned. Thus, small-scale flow fluctuations tend to be integrated by the time–space continuum of drifting larvae. The flow variations likely to cause year-class fluctuations by affecting overall reproductive success are those of large enough scale so that their effects are not averaged out. Such large time and space scale variations conform well to the simple Ekman–geostrophic model described in the previous section.

Instantaneous flow in the ocean is turbulent and approaches the Ekman–geostrophic model only in a large-scale mean sense. Any particular flow measurement could well be in complete nonconformity with the model. An appreciation of the scales of actual motion in the California Current can be gained from infrared photographs taken from earth-orbiting satellites, particularly during the upwelling season (Figure 3). Cold upwelled water (light gray shades) adjacent to the coast appears to be swept far offshore in large eddies and plumelike structures of up to several hundred kilometers in width. Sharp contrast with adjacent warmer surface waters (darker gray shades) is maintained over large distances, indicating transport of surface water at much higher speeds than the large-scale averages (Figures 1, 2). The large eddies are relatively deep features embedded in the geostrophic current field (Bernstein et al., 1977).

Even higher frequency variability characterizes the surface wind drift. Spectra of nearshore surface winds show a pronounced diurnal

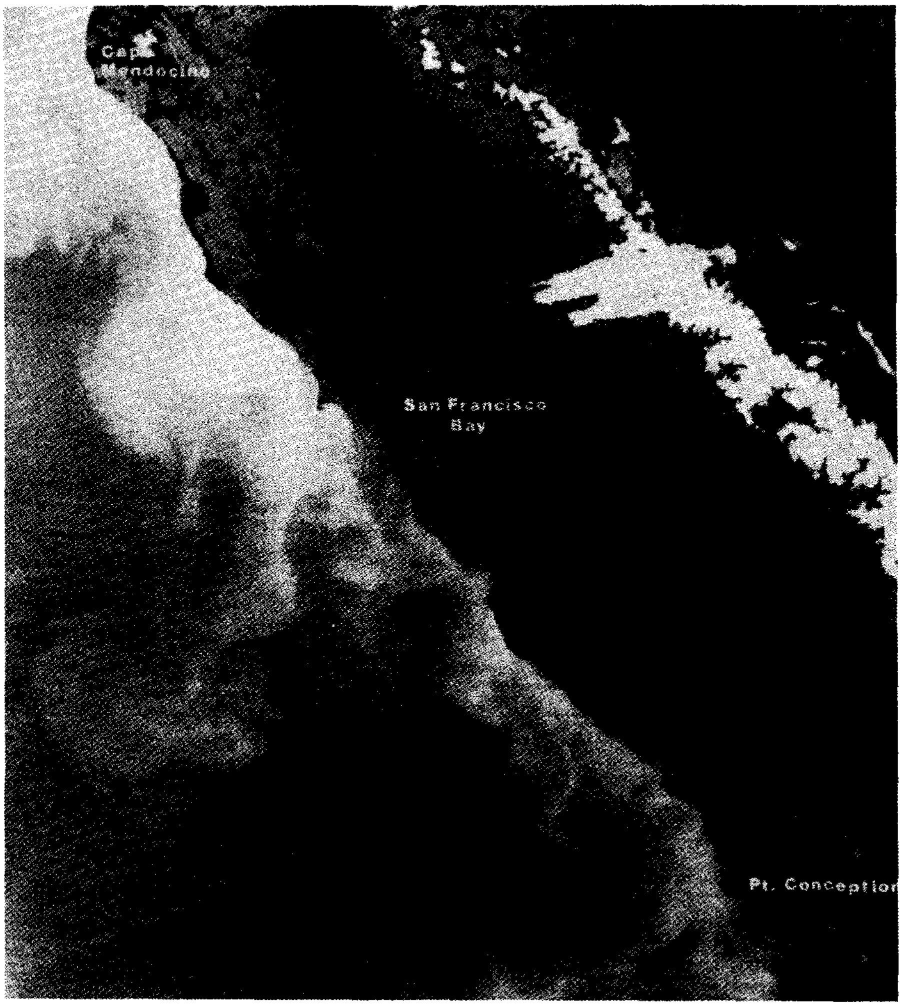

**FIGURE 3.** Infrared photograph of the California coast and the adjacent ocean taken from the NOAA-5 satellite on May 30, 1978. Cooler temperatures are indicated by lighter gray shades, warmer temperatures by darker shades. The filamentous patterns near the coast reflect the sea-surface temperature structure. Other whitish areas in the picture reflect snow on mountain tops and the cold upper surfaces of clouds. Photo supplied by NOAA/NESS Satellite Field Services Station, Redwood City, California.

periodicity and a large amount of variance on the "event" time scale, ranging from two days to several weeks (Bakun and Nelson, 1977). Off the Pacific Northwest, winter is marked by strong onshore-directed wind-driven transport events interspersed with relatively weak offshore transport episodes (Figure 4); relatively weak offshore transport characterizes summer. South of Cape Mendocino, the trend is for progressively less predominance of onshore transport during winter and stronger offshore transport during summer. The most energetic pulses of offshore transport occur off northern California during spring and summer. Off Baja California, a more continuous but less intense level of offshore surface wind drift is maintained throughout the year; here, the maximum tends to be in spring rather than in summer, as is the case farther north.

To the extent that these shorter scales of motion are self-cancelling and do not contribute to the larger scales, their net effect on the distribution of drifting larvae is to spread and mix the distributions in a manner somewhat analogous to turbulent diffusion. In this way, certain individuals could be transported counter to the longer-term displacement of the total larval biomass. Small-scale details of the flow on the continental shelf are lacking in our presentation. It is possible that unresolved features in the shelf circulation would not be self-cancelling on longer time scales. Considerable work near the Oregon coast (Smith, 1974) has indicated rapidly fluctuating alongshore geostrophic flow responding to variations in the local wind. However, the onshore–offshore component of flow is apparently much less energetic and resembles the large-scale Ekman transport.

## *Convergence, Divergence, and Upwelling*

Where the surface wind drift is directed offshore the result is divergence next to the coast, since there is no possibility of a balancing wind drift from the solid continent. To the extent that coastal divergence cannot be compensated by convergence in the other components of horizontal flow, the result is a net loss of surface waters next to the coast. Conservation of mass requires the upward pumping of deeper waters, known as coastal upwelling. The converse process, where coastal convergence due to onshore surface drift leads to a downward intrusion of surface waters, is often referred to as downwelling.

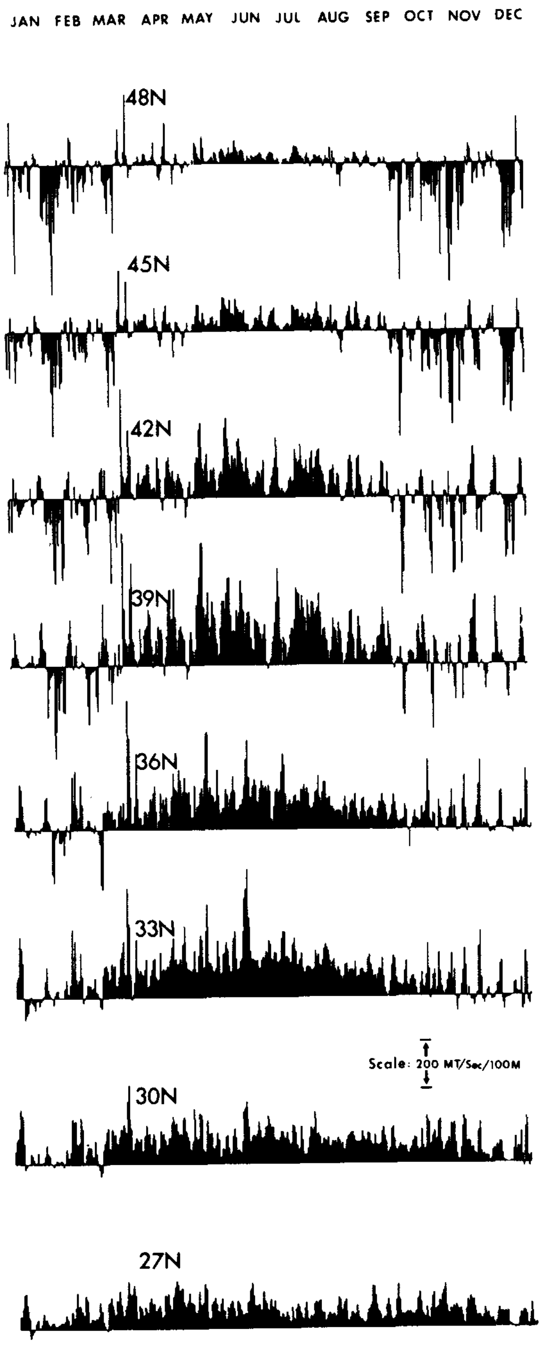

**FIGURE 4.** Daily upwelling indices for 1975 at 3° intervals from the coast of Washington to central Baja California. The magnitude of the offshore Ekman transport is indicated by the length of the bars. The scale is shown on the figure. Units are t $s^{-1}$ per 100 m length of coast. Bars extending upward indicate offshore Ekman transport (coastal upwelling). Those extending downward indicate onshore Ekman transport (coastal downwelling).

The seasonal coastal upwelling cycle is well described by the drift patterns shown in the Ekman transport distributions (Figure 2). Conditions favorable to coastal upwelling continue throughout the year off Baja California; maximum intensity occurs during spring. Off the Pacific Northwest the upwelling season is largely confined to summer; winter is characterized by vigorous downwelling. The apparent effects of coastal upwelling are less obvious in the Southern California Bight than in the regions to the north or to the south (Bakun et al., 1974; Bakun and Nelson, 1977). The offshore extent of the primary coastal upwelling region is on the order of 10 to 20 km (Mooers and Allen, 1973), although under certain circumstances continental shelf topography may cause seaward expansion of this offshore scale (Huyer, 1976). Although the solid coastal boundary obviously affords the condition for the most intense divergence or convergence of surface drift, some convergence and divergence will occur whenever horizontal variation in the wind results in transport gradients along the direction of flow. Offshore areas of surface convergence would tend to concentrate near-surface planktonic material; accumulation of material in fronts and coalescence of patches would be favored. Areas of surface divergence would favor dispersion of planktonic organisms and diffusion of patch structure.

The tendency for convergence or divergence in the surface Ekman layer is controlled by the wind stress curl (Fofonoff, 1963). In the Northern Hemisphere, positive wind stress curl induces Ekman layer divergence; negative wind stress curl induces Ekman layer convergence. Quarterly distributions of wind stress curl (Figure 5) were constructed from Nelson's (1977) monthly distributions. Some of the small-scale detail in these patterns can be attributed to sampling error. However, major features are consistent and certainly significant.

Negative wind stress curl (surface convergence) predominates in the offshore region throughout the year. From this offshore region, a lobe of negative wind stress curl extends shoreward and impinges on the central Baja California coast between Punta Baja and Punta Eugenia. This feature appears consistently during all seasons. In this same area there is a consistent local maximum in the offshore Ekman transport (Bakun and Nelson, 1977). Directly adjacent to the coast the strong coastal boundary effect overrides the weaker surface Ekman convergence related to negative wind stress curl. Thus, coastal divergence and upwelling characterize the coastal boundary zone. However, offshore of the boundary zone surface convergence predominates. The situation from

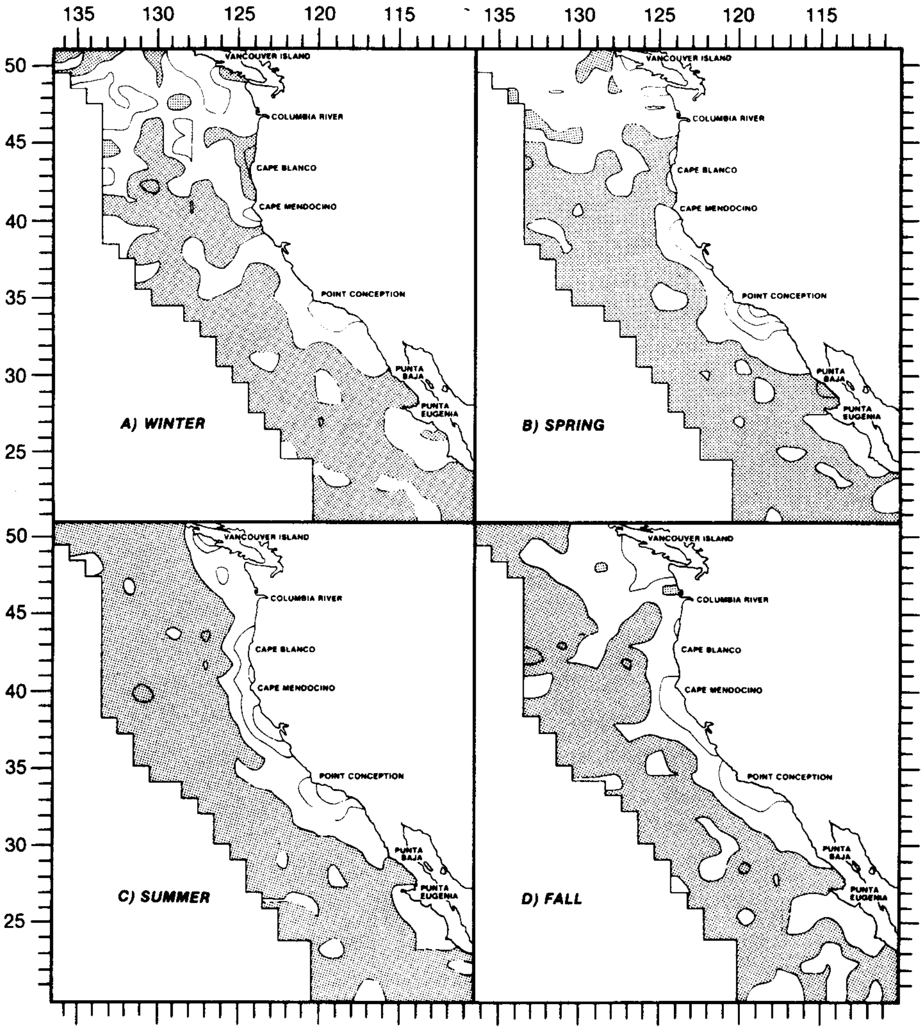

**FIGURE 5.** Wind stress curl: A. winter (December through February), B. spring (March through May), C. summer (June through August), D. fall (September through November). The contour interval is 0.25 dyne $cm^{-2}$ per 100 km. Negative values are shaded and indicate surface Ekman convergence. Unshaded areas indicate surface Ekman divergence.

Punta Baja to Punta Eugenia is thus one of vigorous upwelling very near the coast, with convergence and downwelling beginning 10 to 20 km from the coast and extending to the offshore region.

To the north and south of this lobe of negative curl, regions of positive wind stress curl (surface divergence) extend from the coast to 100 to 300 km offshore. These are also consistent features, appearing in all of Nelson's (1977) monthly distributions. Ekman transport is generally directed offshore in both areas (Figure 2); the coastal boundary zone is characterized by divergence and coastal upwelling. Seaward of the boundary zone a continued level of divergence and upwelling extends offshore to the region where negative curl (convergence) predominates. Particularly strong positive curl characterizes the Southern California Bight. This strong positive curl area expands northward, following the seasonal northward progression of coastal upwelling, to occupy virtually the entire coast during summer. Vigorous coastal upwelling nearshore, accompanied by continued lower intensity upwelling offshore of the narrow coastal boundary zone, appears to be the most typical situation in the California Current.

## Larval Transport and Reproductive Success

The preceding descriptions of the mean geostrophic flow, Ekman transport, and wind stress curl patterns in the California Current System suggest that, for purposes of larval transport, the system can be divided into four regions:

(1) The Pacific Northwest region (i.e., from Vancouver Island to Cape Blanco),
(2) The region of maximum upwelling (i.e., from Cape Blanco to Point Conception),
(3) The Southern California Bight (i.e., from Point Conception to Punta Eugenia),
(4) The southern Baja California region.

These four oceanographic regions are almost identical to the faunal regions described by Dana (1852) on the basis of temperature. The boundaries between the southern three regions correspond well with those used by most of the later biogeographers (Hedgpeth, 1957; Peden and Wilson, 1976; Horn and Allen, 1978). However, the separation of the Pacific Northwest and maximum upwelling regions into distinct faunal regions is not supported by recent zoogeographic studies based on extreme ranges. Horn and Allen (1978), who considered only the California fauna, did not find a faunal break at Cape Blanco, whereas Peden and Wilson (1976), who did not limit their study to fishes recorded in California, found a minor faunal break at Cape Blanco. The fact that the boundaries of these oceanographic regions may or may not agree with faunal breaks established by zoogeographic studies based on extreme ranges of species is not pertinent to this study. We are concerned with the relationships between reproductive strategies and oceanographic conditions on the spawning grounds of the dominant exploitable fishes in the California Current System. Furthermore, distributions of significant reproductive populations are imprecisely measured by zoogeographical regions based on range limits (Steinbeck and Ricketts, 1941:293–297; Peden and Wilson, 1976).

## *The Region of Maximum Upwelling*

The surface circulation in the region between Cape Blanco and Point Conception is a logical explanation for the biological paradox that occurs here; the region is characterized by extensive upwelling, but also by low catches of resident fishes (Table 1). The fisheries and exploitable biomass of this region have been dominated by migratory pelagic stocks (sardine, *Sardinops sagax,* hake, *Merluccius productus,* and jack mackerel, *Trachurus symmetricus),* which spawn in the Southern California Bight. Young sardine, hake, and, to a lesser extent, jack mackerel are most abundant in central California, well south of the upwelling maximum at Cape Mendocino. Older sardine, hake, and jack mackerel are seasonally most abundant in the Pacific Northwest (Murphy, 1966; Alverson and Larkins, 1969; Blunt, 1969). The largest resident group of exploitable fishes in the region of maximum upwelling (*Sebastes*) has a local minimum in abundance near Cape Mendocino; peak abundance occurs in central California and in the Pacific Northwest (Gunderson and Sample, 1980). The largest resident stock in this region, shortbelly rockfish, *Sebastes jordani,* is found in central California. This is a pelagic species that has some life history features similar to clupeids (Lenarz, 1980). Stocks that feed in the region of surface convergence offshore (albacore, *Thunnus alalunga,* saury, *Cololabis saira,* and squids) are also relatively large compared to the resident coastal stocks.

Although the biomass of exploitable fishes is dominated by migratory stocks, the majority of the fish fauna are resident species that have various reproductive strategies that could reduce the advective loss of reproductive products. For example, demersal spawning in protected inshore waters occurs in herring, *Clupea harengus,* lingcod, *Ophiodon elongatus,* cottids, hexagrammids, stichaeids, and most of the other intertidal and littoral fishes of this region. Other strategies include live-bearing (rockfishes and embiotocids), anadromous spawning (salmonids and some osmerids), and deep-water spawning (some pleuronectids and sablefish, *Anoplopoma fimbria*). Another prevalent strategy, which reduces the advective loss of eggs and larvae, is spawning during winter and spring when onshore Ekman transport is most likely to occur in this region. The life history descriptions in Hart (1973) show that the majority of the fishes in the region of maximum upwelling and in the Pacific Northwest have a late winter–early spring spawning season, with peak spawning usually in February and March.[3]

There are fewer published data on larval fish in the region of maximum upwelling than in either the Pacific Northwest or Southern California Bight regions. However, at least in the southern portion of the region of maximum upwelling there appears to be a single peak in the inshore larval fish abundance. Icanberry et al. (1978) showed that maximum larval density occurred in February, and larval densities were high from January to March. This period of larval abundance was associated with low ocean temperatures and the onset of coastal upwelling. The density of larvae inshore declined sharply in March and April as the upwelling season developed.

There are three features in this region that could aid in the inshore retention of pelagic eggs and larvae. The first is the winter occurrence of onshore Ekman transport events, which are related to those that occur in the Pacific Northwest region. These events occur in the northern portion of the region of maximum upwelling, although they are usually of lesser magnitude than in the Pacific Northwest region. In central California the onshore events are less common and of shorter duration (Figure 4; lat. 36° N). The second feature is the shallow nature of the nearshore geostrophic flow in this region. Advection of organisms by both Ekman and geostrophic components of flow is dependent on their depth in the water column. Planktonic eggs and larvae in the upper mixed layer are highly susceptible to dispersion. Deep-water spawning and vertical migration of larvae are likely mechanisms for reducing the advective loss of eggs and larvae. Seliverstov (1974) has shown that larvae of the Atlanto-Scandian herring have diurnal vertical migrations as large as 75 to 100 m, and that regular diurnal migrations begin after the larvae have started feeding, six to nine days after hatching (8.8–10.8 mm). The third feature is the occurrence of eddies (Figure 3), which could return larvae to the inshore region.

## *The Pacific Northwest Region*

In comparison with the region of maximum upwelling, offshore Ekman transport is weaker and of shorter duration in the Pacific Northwest region. Advective loss of reproductive products from the inshore region would therefore not be expected to be as severe as in the region of maximum upwelling. The faunas of the two regions are similar, with the exception that the Pacific Northwest has stocks of anchovy, *Engraulis mordax,* and hake, which reproduce within the region. The northern stock of anchovy spawns during the peak of the upwelling season (June and July), and its spawning area lies about 50 to 80 km offshore between lat. 44°N and 47°N. This spawning ground lies in an area of relative stability associated with the Columbia River plume (Richardson, 1973). This is also a region of relatively weak mean geostrophic flow (Figure 1) that lies to the north of the region of maximum upwelling (Figure 2C).

In their analysis of coastal and oceanic fish larvae over the Oregon continental shelf, Richardson and Pearcy (1977) delineated inshore and offshore larval assemblages. The inshore assemblage was dominated by spring spawners, particularly the osmerids, which spawn demersal eggs in very shallow water, and pleuronectids. Osmerid larvae primarily occurred near the bottom (100 to 150 m) by day and night, a feature that would reduce advective loss by surface transport. Offshore Ekman transport is minimal directly adjacent to a coastal boundary, and thus fishes that spawn in extreme inshore areas may be less subject to offshore transport. The offshore assemblage was dominated by livebearing rockfishes *(Sebastes)* and by midwater fish larvae. The rockfish spawn primarily in the late winter and early spring when onshore transport prevails. Midwater fish larvae are not expected to conform to the hypotheses presented here.

Pearcy et al. (1977) have shown that at least two northwest flatfish, Dover sole, *Microstomus pacificus,* and rex sole, *Glyptocephalus zachirus,* have larvae that are planktonic for a full year. Both of these fish are late winter–early spring spawners. Smaller larvae are found both inshore and offshore, but larger larvae are most common in waters beyond the continental shelf. During winter there is an increase in the proportion of the largest larvae over the shelf and slope where they will settle. When viewed from the perspective of the present work, the results of Pearcy et al. (1977) suggest that Dover and rex sole larvae are transported offshore during the upwelling season and are then returned onshore during winter when transient winter storms result in strong pulses of onshore transport. This hypothesis is strengthened by the work of Hayman (1978), who compared a wide range of environmental factors with year-class size in Dover sole and found that recruitment was best described by two wind-related indices. Increased recruitment was associated with reduced offshore Ekman transport during the upwelling maximum in June and July and with weak divergence, or convergence, during the December and January settling period.

## *The Southern California Bight*

The Southern California Bight is characterized by minimal offshore Ekman transport (Figure 2) overlying a geostrophic flow pattern that features a closed gyral circulation near the coast (Reid et al., 1958) and an onshore component of flow farther offshore (Figure 1); seaward dispersion of reproductive products would appear to be minimized. The dominant pelagic fishes of the California Current (i.e., those that have supported large fisheries) all spawn in this region. The sardine, hake, jack mackerel, and, to a lesser extent, the Pacific mackerel, *Scomber japonicus,* and bonito, *Sarda chiliensis,* migrate into the region of maximum upwelling off central and northern California and into the Pacific Northwest for feeding. Because of limited swimming ability associated with small size, the central stock of northern anchovy is principally resident within the Southern California Bight, although tagging studies show that a small portion of the stock migrates as far north as central California (Messersmith, 1969).

The Southern California Bight differs from the regions to the north in that standing stocks of zooplankton are much smaller (Smith, 1978). Given favorable transport conditions, food limitation during critical larval stages may regulate reproductive success. Anchovy and hake have peak spawning in late winter (January to March). In this region the winds are normally much weaker in the winter than in the spring or summer. Lasker (1975, 1978) has suggested that successful feeding of early anchovy larvae is dependent on chlorophyll maximum layers, which only exist in the absence of storm-driven turbulence. Sardine, Pacific mackerel, jack mackerel, bonito, and barracuda, *Sphyraena argentea,* have peak spawning seasons during the period of maximum upwelling (May and June). Arthur (1976) has shown that the diet of anchovy larvae is dominated by phytoplankton (dinoflagellates) and early copepod stages, but that larval sardines and larval jack mackerel feed almost exclusively on the early stages of copepods. The other species that spawn during the upwelling maximum probably also have larval feeding preferences for copepods. The development of concentrations of forage for the early fish larvae would therefore be largely dependent upon upwelling-related meteorological conditions prior to and during the spawning periods. Upwelling prior to the spawning period would increase primary productivity and result in copepod reproduction. Upwelling during the spawning peak would disperse both fish larvae and forage.

Parrish and MacCall (1978) have related recruitment in the Pacific mackerel stock to upwelling. Their model, which includes offshore Ekman transport, wind stress curl, and a Ricker density function, accounts for 76% of the variation in recruitment from 1946 to 1968. Upwelling one month prior to spawning was much better correlated with recruitment than was upwelling during the spawning period. The one-month lag may represent the time scale for the development of a copepod bloom following increased nutrient enrichment.

Arthur's (1977) description of the microcopepods of the California Current System shows that the zone of maximum nauplii concentration is seaward of the Channel Islands, about 100 to 300 km off the coast. He states that the average nauplii maximum approaches the coast south of

San Diego and is adjacent to the coast in northern Baja California. We suggest that this zone of maximum nauplii is associated with maximum geostrophic flow (i.e., nutrient-and plankton-rich water from the north) and the inner edge of the negative wind stress curl region (i.e., concentration of plankton by surface convergence).

### *The Southern Baja California Region*

The lobe of negative wind stress curl that impinges on the coast between Punta Baja and Punta Eugenia (Figure 5) separates distinct oceanographic regimes. Off southern Baja California a cyclonic gyre appears during fall, when upwelling is most relaxed. During spring the upwelling-induced southward flow tends to obscure this circulation (Bakun and Nelson, 1977). Due to this seasonality, the feature is not strongly evident in the annual mean geostrophic flow pattern (Figure 1). The southern Baja California region is also separated from the Southern California Bight region by the central Baja California upwelling maximum, which is centered near Punta Baja and extends south of Punta Eugenia. A number of pelagic fishes have subpopulations off southern Baja California that are distinct from those in the Southern California Bight region. These include sardine (Clark, 1947), Pacific mackerel (Roedel, 1952), and northern anchovy (Vrooman and Smith, 1971)

Warm water advection near the coast associated with cyclonic circulation and the proximity to the warm Gulf of California results in a large tropical component in the fauna. The most obvious pelagic form is the galatheid, *Pleuroncodes planipes,* which is extremely numerous in this region (Longhurst, 1967). Tropical clupeids, engraulids, and carangids are also common (i.e., thread herring, *Opisthonema medirastre,* anchoveta, *Cetengraulis mysticetus,* and Mexican scad, *Decapterus hypodus*). Much of this tropical fauna does not extend to the region of strong upwelling near Punta Baja, and the faunal "front" between the tropical and subtropical faunas occurs in the vicinity of Magdalena Bay (Ahlstrom, pers. comm.[4])

## Discussion

A general pattern of correspondence between reproductive strategies and ocean flow characteristics has emerged. The indication is that the necessity for minimization of offshore loss of reproductive products by seaward transport processes must have exerted a particularly strong control on the development of seasonal and geographical spawning characteristics. This, in turn, implies an important effect of transport conditions upon reproductive success, leading directly to the hypothesis that deviations from ''normal'' transport conditions, to which reproductive strategies are adapted, may be a cause of the very large recruitment variations observed in the important coastal fisheries of the California Current.

Large deviations from mean seasonal surface transport conditions are known to occur. Charts of geostrophic currents computed from oceanographic surveys (e.g., Wyllie, 1966) show definite inter-year differences, although methods for quantifying the effects on biological scales are not yet well developed. However, in situations where the geostrophic flow tends to parallel the coast, it is less important in terms of this particular hypothesis than the surface Ekman transport. Offshore transport is more likely to be unfavorable to larval survival than alongshore transport, because the habitat changes more rapidly in the offshore direction than in the alongshore plane. In addition, surface Ekman transport has greatest variability in the onshore–offshore component. Bakun's (1973, 1975) upwelling indices are one attempt at quantifying this effect. At any given location, general seasonal characteristics are maintained from year to year; however, large inter-year differences in seasonal onset, intensity, duration, and properties of short-scale fluctuations are apparent.

Upwelling is also a major mechanism for surface nutrient replacement, which makes the California Current a productive region. Upwelling, therefore, can have favorable and unfavorable aspects. If upwelling events occur prior to a species spawning period it is likely to aid larval survival. If it occurs during the peak of spawning its effects are more likely to be detrimental.

The effects of upwelling on larval survival may also differ geographically. In the region of maximum upwelling between Cape Blanco and Point Conception, larval survival seems more likely to be transport limited than food limited. Conversely, in the upwelling minimum within the Southern California Bight, larval survival may be more likely to be food limited.

Analysis of varved sediments in the Southern California Bight (Soutar and Isaacs, 1974) has shown that the biomass of the major pelagic spawning stocks and, indeed, the total biomass of the combined stocks are subject to large, long-term fluctuations. The two species most likely to be in competition as adults (anchovy and sardine) show no relationship between their stock sizes over a 200-year period. The two species most likely to be in competition as larvae, the sardine and the Pacific mackerel, show considerable similarity in their population fluctuations (Smith, 1978).

Short-term environmental variations or longer-term climatic trends could favor winter spawners (hake and anchovy), spring spawners (sardine and the mackerels), both, or neither. Anchovy might capitalize on good conditions whenever they occur due to its low level, year-round spawning. Individual years with reduced upwelling, such as 1967 (Bakun, 1975), undoubtedly lower the productivity of the system and would therefore affect the adults of all the pelagic species. However, the reduced vertical circulation would result in stability of the water column, which has been associated with good reproductive success of anchovy (Lasker, 1978). Reduced vertical circulation might therefore be expected to produce moderate stocks of anchovy (and perhaps hake, which has peak spawning at essentially the same time as anchovy). A scenario might be: series of years with reduced upwelling in the Southern California Bight region, such as 1964–1968 (Bakun, 1973), would be expected to result in a sharp decrease in the total standing stock of the spring spawners due to poor recruitment. Adult growth of winter spawners would be poor, but recruitment might be favorable due to stability during their spawning season. The anchovy and hake stocks would therefore be expected to be at moderate levels following a run of years such as that occurring in 1964–1968. This is consistent with analyses of scales deposited in sediments, which show that populations of anchovy and hake are much less variable than those of sardine and Pacific mackerel (Smith, 1978).

If population size is largely determined by a highly variable larval survival rate, the conclusion is that the adult population seldom reaches a food-limited carrying capacity. If the stocks were originally near adult carrying capacity, there should be a compensatory alteration in growth and reproductive rates when the stocks are reduced by fishing. Four extensively studied stocks (sardine, Pacific mackerel, anchovy, and Pacific ocean perch, *Sebastes alutus*) have had extensive fluctuations in population size. Knaggs and Parrish (1973) have shown that there were no significant changes in the growth of Pacific mackerel associated with stock size. In the sardine stock the 0-age group, which was largely confined to the relatively plankton poor Southern California Bight, showed increased growth associated with smaller stock size (Iles, 1973). The older fish that made feeding migrations into the region of maximum upwelling and the Pacific Northwest region showed no significant changes in length associated with stock size; changes in the condition factor (relative fatness) have been associated with stock size (MacGregor, 1959). No changes in growth rates have been found in the numerous studies that have been published on the northern anchovy and Pacific ocean perch. There are some indications of density-dependent changes in reproduction. The proportion of sardines that spawn at age two and the proportion of Pacific mackerel that spawn at age one increased as the stocks declined (Murphy, 1966; Parrish and MacCall, 1978). However, stock-recruitment relationships for sardine (MacCall, 1979) and Pacific mackerel (Parrish and MacCall, 1978) show large variations with very little density dependence. Gunderson (1977) has suggested that Pacific ocean perch have a relatively flat spawner-recruit curve. MacCall's (1980) logistic growth-rate curve for the central anchovy stock is quite flat, and MacCall suggests that abundance in any given year is determined more by natural variations in recruitment than by the fishery. The minor nature of the observed density-dependent changes in growth and reproductive rates strengthens the suggestion that carrying capacity for adults is seldom a limiting factor in the major fish stocks of the California Current.

A major problem in defining the environmental-biological relations that are required to construct useful predictive models for fishery management is that there are generally only short time series with which to work. Fishery data characteristically yield one data point per year, and the period over which the time series can be considered homogeneous does not normally exceed 10 to 20 years. To sort out a multitude of possible environmental effects from a series with 10 to 20 data points is obviously a statistically impossible task. Therefore, it is necessary either to find the means to reduce the environmental factors to one, or at most several, indices of integrated environmental state, or to hope that one, or perhaps two, environmental factors will have such a dominant effect as to be discernible through the "noise level" generated by the other environmental effects. The considerations presented in this paper suggest that surface drift during the early egg and larval period may be such a dominant environmental factor for some of the major coastal fishery species of the California Current.

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## Notes

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2. Personal Communication, T. Dark, Northwest and Alaska Fisheries Center, National Marine Fisheries Service, NOAA, Seattle, Washington 98115.

3. This same suite of reproductive strategies occurs in tropical marine fishes associated with coral reef, mangrove, and tropical seagrass communities (Johannes, 1978).

4. Personal communication, E. H. Ahlstrom (deceased), Southwest Fisheries Center, National Marine Fisheries Service, NOAA, La Jolla, California 92037.

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