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Large scale pattern of recruitment by the labrid, *Semicossyphus pulcher:* Causes and implications

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ABSTRACT

The pattern of recruitment of sheephead, *Semicossyphus pulcher,* is described throughout a major portion of its range over a period of 7–9 years. The relative recruitment success was determined using both field transects and age-structure data. The observed pattern of recruitment was compared to both spatial and year-to-year variations in the current regime within the region using both average flow data (CalCOFI data base) and satellite imagery. It was found that in areas with larval sources to the north and south, recruitment occurred consistently from year-to-year. However, in areas where there was no larval sources "upstream" of the typical current direction, recruitment was highly variable and dependent upon anomalous events in the current flow. These anomalous events are considered on two levels: low-level events, which last from days to weeks, thereby affecting recruitment of only one or a few species, and high-level events, which last from months to years (e.g. El Niño events), affecting recruitment of many species. A positive relationship is found between frequency of recruitment events and density of adult populations. In addition, the persistence of populations is dependent upon recruitment frequency and the longevity of the individuals. The interaction between recruitment frequency, population density and persistence is considered to be important in determining the northern distribution limit of sheephead at Point Conception (also a major break for many other species). In the past, this faunal break has typically been attributed to temperature differences and inferred physiological constraints. It is concluded, from the findings in this study, that the faunal break at Point Conception is heavily influenced by hydrographic constraints on dispersal.

1. Introduction

Recruitment of fish populations has been of interest to fishery biologists for many years (e.g., Hjort, 1926). This interest has been not only in the influence of variable year class success on important fisheries, but also in what are the causes of such variability. More recently, variability of recruitment has been implicated as an important component structuring coral reef fish assemblages (see review by Sale, 1980) and intertidal communities (Underwood, 1979). In these systems, fluctuations in recruitment have been studied over relatively small spatial and temporal scales (up to 1–2 km and year-to-year; Williams and Sale, 1981; Williams, 1983; and others). However, to completely understand the relationship between recruitment and commu-

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nity structure, the pattern of recruitment and the factors which influence the variation of recruitment must be examined over a variety of scales (Williams and Sale, 1981; Dayton and Tegner, 1984; Williams *et al.*, 1984).

The biological and physical processes which influence both spatial and temporal patterns of juvenile recruitment to nearshore habitats may be considered on three scales. First, there are large scale factors that contribute to the overall pattern of larval availability. This category comprises the biological and physical mechanisms that interact to affect the dispersal of the larvae and, hence, the final pattern of larval availability throughout the species range. Second, there are small scale factors which influence the actual settlement of the larvae. An understanding of these factors involves the study of the physical mechanisms of transport onshore of the "available" larvae and the required behavioral responses of the larvae to utilize those mechanisms, as well as reef to reef differences in availability of suitable settlement sites. Third, there are factors mediating the survival of the larvae once they have settled. These include competition and predation pressures associated with early life on the reef as well as physical processes. All of the above processes may interact on all scales to produce a complicated pattern of recruitment variability to nearshore reefs, a pattern not entirely explainable by local events.

Most nearshore marine fishes have planktonic eggs and/or larvae, hence their dispersal is closely tied to currents (Johannes, 1978; Barlow, 1981; Doherty *et al.*, 1985). The timing of reproduction, placement of eggs and/or larvae and length of time in the plankton all contribute to their negative susceptibility to currents (Sale, 1969; Johannes, 1978; Lobel, 1978). Nearshore current patterns, that are probably important in the transport of eggs and larvae, can be influenced by bottom topography, seasonal wind changes and even sporadic, climatic anomalies (e.g. "El Niño" events; Chelton *et al.*, 1982; and others). Inshore and offshore patterns of larval fish abundances have been described in relation to observed current regimes (Leis and Miller, 1976; Richardson *et al.*, 1980; Loeb *et al.*, 1983), but the consequent influences on distribution and population structure of adult forms have not been investigated. On a smaller scale, surface slicks associated with shoreward moving internal waves are thought to transport larval fish and invertebrates shoreward (Zeldis and Jillet, 1982; Shanks, 1983). A variety of behavioral mechanisms have been demonstrated for invertebrate larvae which would enable the larvae to utilize these slicks (Thorson, 1964; Rice, 1966; Ennis, 1975); moreover, the fish larvae concentrated in the slicks presumably use similar behavioral responses (Shanks, 1983).

Few attempts have been made to demonstrate large scale patterns of recruitment in relation to current flow. Parrish *et al.* (1981) have related the spawning strategies (in both space and time) of coastal pelagic fishes to the large scale seasonal pattern of surface drift in the California Current. They suggested that anomalies in the surface drift patterns may account for the variable spawning success of these fishes (see also Nelson *et al.*, 1977; and Yoder, 1983, for similar studies in the western Atlantic

Ocean). Others have tried to relate local eddies to the retainment of planktonic fish larvae and the timing of larval recruitment to island populations (Sale, 1970; Watson and Leis, 1974; Leis and Miller, 1976; Johannes, 1978; Lobel and Robinson, 1983) and to the maintenance of stock integrity (Iles and Sinclair, 1982; O'Boyle *et al.*, 1984).

As yet, no one has attempted to relate geographical and year-to-year variation in recruitment of a nearshore species to ocean current variations on the same scales. Hence, the purpose of this study is to describe the pattern of recruitment of a temperate wrasse, the California sheephead (*Semicossyphus pulcher*), throughout a major portion of its range and to relate this pattern to both spatial and year to year variations in the current regime within the region. By examining fluctuations in recruitment on such large scales, insight may be gained into the role recruitment plays in community structure, the cause of geographical distributions, and how individual longevity may act to modulate the influence of variable recruitment.

2. Study area

This study covers the major portion of the geographic range of sheephead: Point Conception, California in the north to Isla Santa Margarita, Baja California, Mexico in the south (a straight line distance of approximately 1400 km; Fig. 1). Point Conception is the northern range limit of sheephead (and many other species, see below) except for a few occasional occurrences north of this point. To the south, sheephead extend to Cabo San Lucas and into the Gulf of California. However, except for a small population at Isla Santa Margarita, near Bahia Magdalena, they are relatively rare south of Punta Abreojos. Near Cabo San Lucas, the species occurs only in rather deep water (60–100 m, R. Rosenblatt, pers. comm.).

Most field work was done at San Nicolas Island, Isla Guadalupe, Islas San Benitos and Cabo Thurloe, though observations have been drawn from several additional sites within the above area (Fig. 1). Most of these sites are fairly remote and have not been subjected to an extensive sports fishery for sheephead. Densities of sheephead are highest at the sites located within the southern and central portion of the range, intermediate at San Clemente and Santa Catalina Islands, and lowest at the most northwest islands (Table 1).

3. Methods

a. Yearly recruitment success. Yearly recruitment success (defined here as the proportion of the population represented by the year class in question) was determined from a combination of field counts and age-structure data. For year classes 1980–1983, counts were made of sheephead populations along 5 × 50 m transects and categorized as follows: young-of-the year, 1-year-olds, 2-year-olds, and >2 years. In the field, young-of-the-year, first year, and second year age classes could be identified by a combination of color pattern and size. A minimum of ten transects were counted

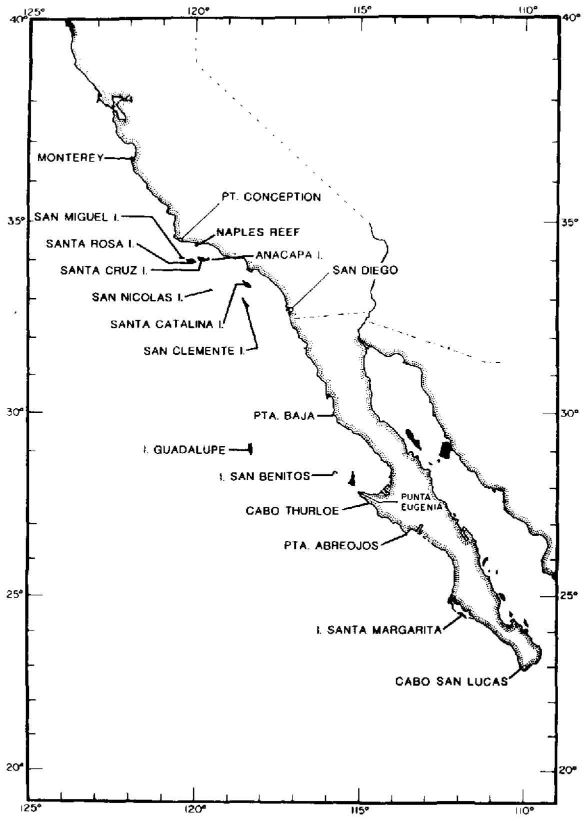

Figure 1. Map of all sites mentioned in this study.

at each site, (May, 1982 and June, 1984 at Islas San Benitos and Cabo Thurloe, May, 1982 at Isla Guadalupe, and April and September/October, 1981, 1982, 1983, 1984 at San Nicolas Island).

Ages greater than 2 years could not be determined by field observations. Therefore, the estimate of annual recruitment prior to 1980 was based on age-structure of the population. Collections were made by spearing and ages were determined by counting annual rings in dorsal spines (Warner, 1975). An attempt was made to minimize bias toward a particular size class while spearing by collecting the first fish seen after each previous fish was collected. The total number of fish collected at each site was: 220 at San Nicolas Island, 92 fish at Isla Guadalupe, 82 at Islas San Benitos, and 108 at Cabo Thurloe. The estimation of recruitment success from age-structure data does not consider mortality, hence only a minimum estimate is possible (Ricker, 1975). In addition, biases inherent in aging fishes increase with older fish (Chilton and Beamish, 1982). To minimize both of these problems, recruitment success determined from age-structure was not estimated beyond the fifth year class. Finally, I assumed that

Table 1. Sheephead densities at main and secondary sites. Main sites are: SNI—San Nicolas Island, ISB—Islas San Benitos, IG—Isla Guadalupe, CT—Cabo Thurloe. Secondary sites are: SMI—San Miguel Island, SRI—Santa Rosa Island, SCrI—Santa Cruz Island, AI—Anacapa Island, NR—Naples Reef, SClI—San Clemente Island, SCaI—Santa Catalina Island, PtB—Punta Baja.

	Sheephead densities by site	
Main sites	No. of areas sampled	Density (no./hectare)
SNI	3	35–185
SBI	1	210
IG	1	355
CT	1	510
Secondary sites		
SMI	2	0–16
SRI	1	32
SCrI	2	120–290
AI	2	72–200
*NR	1	78
SClI	2	148–250
SCaI	2	136–275
PtB	1	288

*Data from Ebeling *et al.*, 1980.

immigration and emigration were minimal, based on the observation that sheephead appear to be rather parochial fish (Cowen, 1983; unpublished data).

b. Larval distribution. To determine the spawning season and availability of larvae to dispersal, data were drawn from the California Cooperative Fisheries Investigation (CalCOFI) data base as well as from monthly cruises of the Ichthyoplankton Coastal and Harbor Studies (ICHS) during 1978–1980. The CalCOFI data base encompasses over 30 years of extensive sampling effort from the tip of Baja California (and the Gulf of California) to northern California. Although designed primarily to investigate the biology of clupeoid stocks of the California current, data are collected on a wide variety of species. Samples from the years 1956–1960 will be used here, because most of the sheephead's range was sampled monthly during this period.

The standard sampling techniques and laboratory procedures used in the CalCOFI program are detailed in Ahlstrom (1948). During the sampling program used in this study, a regular pattern of stations was sampled with a 1 m zooplankton net (.505 mm mesh) to 140 m. Stations were placed every 10–16 n.m. (nautical miles) along transects that ran from 2–4 n.m. offshore to 40–160 n.m. offshore. The sampling program of the ICHS program was intended to be compatible with the present CalCOFI sampling techniques (details in Brewer and Smith, 1982), but inshore of the CalCOFI stations and hence provide comparable data on the immediate nearshore distribution of larvae (within 1–2 nautical miles of the shore). In addition to the use of an oblique 70 mm bongo tow (which is currently used in the CalCOFI programs, thereby replacing the 1 m zooplankton net, Kramer *et al.*, 1972), the ICHS program also sampled larvae very close to the bottom (epibenthic) with an Aurora net and the near surface water layer (neuston) with a Manta net. By comparing the results of these three kinds of nets, the vertical position within the water column occupied by the sheephead larvae could be determined.

To establish the length of time spent in the plankton, recently settled sheephead were collected at San Nicolas Island and increments on their otoliths (presumed to be daily, see below) were counted (Pannella, 1971; Brothers *et al.*, 1976). The otoliths were also examined for settlement marks (i.e. conspicuous transition in the increments formed at the time of settlement by the larvae). By counting inward from the settlement mark (or the edge of the otolith from newly settled fish), the length of the pelagic stage can be determined (Brothers and McFarland, 1981; Victor, 1982; Brothers *et al.*, 1983). The initial collections included individuals that had recruited 3–4 days earlier. To check whether the increments were daily, subsequent collections were made exactly 30 days later. Recruitment occurred as one major event with relatively few individuals occasionally settling thereafter, therefore it is probable that these two samples were from the same settlement event. Lapilli and sagittae were removed from the young recruits and glued to glass slides with finger-nail hardener. In general, the lapilli were most easily read. The otoliths were too thick to read in some of the older fish (i.e. ≥30 days on the reef); these were then gently ground on 300 and 600 grit paper to about one-half of their original thickness, thus enabling the increments to be seen. Viewing and counting were done with a video-equipped compound microscope and a polarized light source.

4. Results

a. Pattern of recruitment. At San Nicolas Island, the percentage of the sheephead population composed of recruits varied markedly from one year to the next (Fig. 2). From 1975–1978, there was some recruitment with a minor peak in 1977. In the following three years (1979–1981) no recruitment was observed. In 1982 there was a small recruitment and then a very successful recruitment in 1983, with over 100 recruits seen in the study area (approximately one hectare). This pattern of recruitment was observed to be an island-wide event.

In comparison to San Nicolas Island, the remaining three sites had a different pattern of recruitment (Fig 2). In all three areas, recruitment occurred annually from 1977 to 1981 (Isla Guadalupe) and 1982 (Islas San Benitos and Cabo Thurloe). These sites did not show any major fluctuations in year class strengths compared with San Nicolas Island. When no recruitment occurred on San Nicolas Island there was consistent recruitment at the other three sites. This situation contrasts sharply from the 1983 season. During this year, no sheephead recruited at Islas San Benitos and Cabo Thurloe.

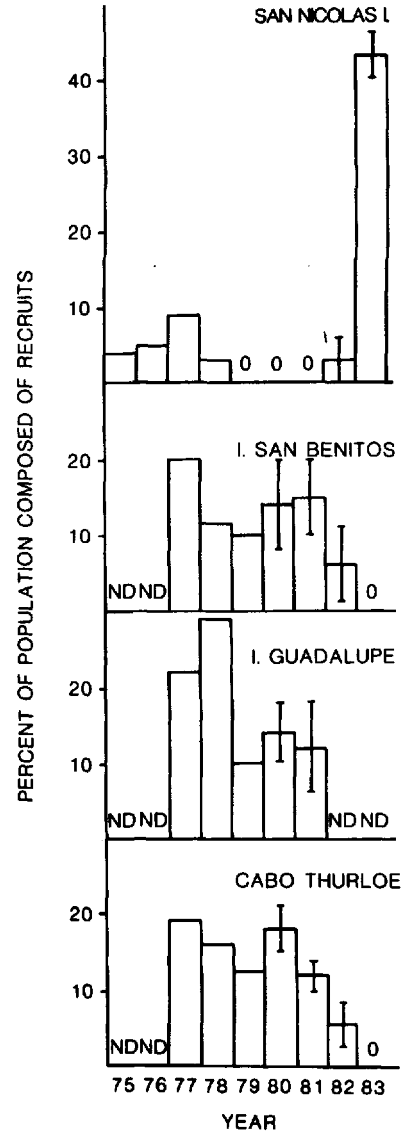

Figure 2. Relative annual recruitment success at main study sites. ND = no data; 0 = site visited but no recruits were observed. Data prior to 1980 based on age structure of population. Data from 1980–1983 based on field counts and given as $\overline{X} \pm$ S.E.

Also pertinent to this study are observations from several additional localities within this range. San Miguel Island, Santa Rosa Island and Naples Reef are very close to the northern range limit of sheephead (Fig. 1). The sheephead that do live there are relatively scarce (Table 1), very large, and presumably, old individuals. Smaller size classes are either not common or completely absent (pers. obs.), indicating very sporadic recruitment to these populations. However, in September 1983, sheephead recruits were seen on the northern point of San Miguel Island (R. McPeak, pers. comm.). Sheephead recruits were also seen at Naples Reef (A. Ebeling, pers. comm.) and Santa Rosa Island (R. Butler, pers. comm.). In addition, sheephead recruits were seen as far north as Monterey, California (R. Lea, pers. comm.), nearly 250 km north of their normal range. In other areas visited within their normal range (Santa Catalina Is., San Clemente Is., Santa Cruz Is., La Jolla, and Punta Baja), sheephead recruitment appears to be a regular event (including 1983), though it may vary in intensity (pers. obs.).

Other fish and invertebrate species characteristic of the California Province fauna (Brusca and Wallerstein, 1979) experienced unusual recruitment success in these northern areas in 1983. For example, the gobies, *Lythrypnus dalli* and *L. zebra* both recruited heavily to San Nicolas Island where only one individual of each had been seen in the previous four years (Cowen, unpubl. data). *Lythrypnus dalli* recruited as far north as Monterey, a range extension of 250 km (R. Lea, pers. comm.). Other species that showed strong recruitment success at San Nicolas Island (after little or no success in the previous four years) include: *Halichoeres semicinctus* (rock wrasse), *Hypsypops rubicunda* (garibaldi), and *Panulirus interruptus* (spiny lobster). A. Ebeling (pers. comm.) also found *H. semicinctus* recruiting to Naples Reef for the first time in 10 years. Within the southern portion of the sheephead's range, several tropical fish species recruited, well north of their normal range (Thomson *et al.*, 1979). For example, I observed 1983 young-of-the-year of both *Halichoeres dispilus* (chamaeleon wrasse) and *Stegastes rectifraenum* (Cortez damselfish) at Isla San Benitos, Cabo Thurloe and Isla Asuncion in June, 1984.

In summary, it appears that 1983 was a particularly important recruitment year for sheephead, as well as several other species in the northern portions of their range. This is an area that does not receive regular recruitment of these species. In addition, 1983 was an unsuccessful recruitment year for sheephead in the southern portion of the range; an area that normally receives regular recruitment by sheephead.

b. Availability of larvae. Sheephead, like all labrids, have pelagic eggs and larvae. In this paper, the ultimate source of larvae (i.e., where the spawning occurs) is considered to be the main part of the sheephead range (i.e. Point Conception, California, U.S.A. to Punta Abreojos, Baja California, Mexico). Within this area, current patterns are quite variable (see below) and hence the larvae from different regions are subjected to different courses of dispersal.

The presence of sheephead larvae in all plankton samples (1956–60 and 1978–80) showed a seasonal peak in middle to late summer (Fig. 3). This agrees with the finding that adult females have ripe eggs from July to September (Warner, 1975). The few occurrences of larvae in January–May were primarily from the warm water years of 1958–59. Hence, the current regime from July to October is going to have greatest effect on larval dispersal.

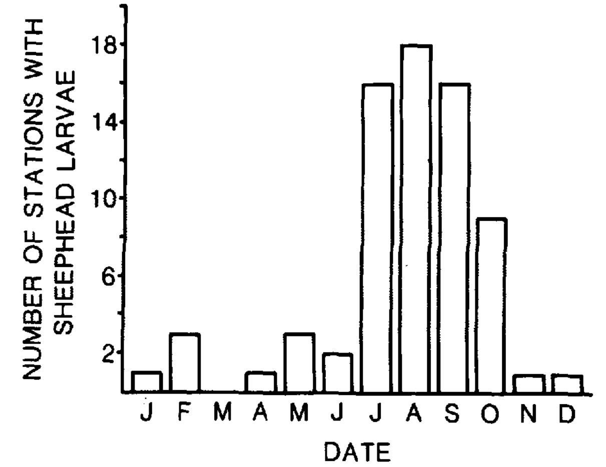

Figure 3. Seasonality of sheephead larval availability. Data from combined CalCOFI samples (1956–1960; N = 1647) and ICHS samples (1978–1980; N = 299). Sampling effort was similar for each month.

Of all the ICHS stations which contained sheephead larvae (N = 25), 88% of the larvae were found in the midwater samples. The midwater presence of sheephead larvae indicates that sheephead larvae are available to transportation by currents and are not displaying any behavioral responses (e.g. staying near the bottom) to avoid offshore transport. Additional support is found in the distribution of sheephead larvae with distance from shore (Fig. 4). There is a definite peak in larval abundance within 20 miles of shore although sheephead larvae were consistently found up to 130 miles

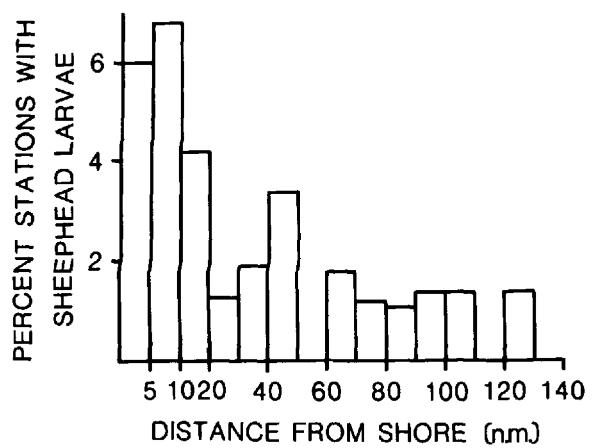

Figure 4. Distribution of the distance from shore (nautical miles) that sheephead larvae were collected. Same data base as in Figure 3. Overall, 71 (3.6%) of all stations had sheephead larvae.

from shore. These findings demonstrate that dispersal of sheephead larvae depends on transport by ocean currents.

Because sheephead larvae are carried by currents, it is also important to know how long the larvae remain in their pelagic phase, and thus, "available" to dispersal by currents. Of 55 sheephead juveniles collected, 20 were used for aging (10 collected on 14 September 1983, 10 on 15 October 1983). The largest settlement event occurred during the week of 12 September 1983. Subsequent settlement occurred through the end of October. The size at settlement was 12–13 mm. Settlement marks were not visible for the very smallest recruits (presumably due to their very recent settlement). In the older fish (i.e. those fish collected 33 days after the initial settlement event), half had distinctive settlement marks 33.4 ± 3.3 ($\bar{X}$ ± S.E.) increments from the edge of the otolith validating the assumption that the increments are laid down daily. Counting inward from the settlement mark or the edge of the otolith in new recruits yielded 64.5 ± 2.0 ($\bar{X}$ ± S.E., $N = 15$, range 55–77) increments. Assuming that the laying down of daily increments starts within 2 days of fertilization in labrids (Fritzche, 1978; Victor, 1982), the pelagic larval stage of sheephead averages 66.5 days or approximately two months.

In summary, the sheephead broadcast their eggs into the water column when mating. These eggs and subsequent larvae live pelagically for approximately two months (sometime between July to October). During this time, the larvae are available to transport by the currents, as evidenced by their presence in the water column and occurrence up to 130 miles from shore.

5. Current patterns

The environments in which the larvae are drifting is a fairly complicated portion of the California Current system. The current tends to flow from the north to the south; however, there are areas of small and large eddies, shoreward flow of the main current, and, importantly, seasonal and year-to-year variations in the overall flow pattern (see review by Hickey, 1979; Owen, 1980). In this section, the general flow pattern of this area will be described. However, caution is warranted here: by examining mean flow (determined by combining many years of data), one may miss events that are transient, but of the greatest importance for understanding variable recruitment patterns. Because of this, year to year differences in the flow will also be examined in detail during the months of July to October.

a. General pattern of flow. From May through July, strong southward flow normally develops from shore to 450 km offshore off Point Conception. This southward flow becomes less pronounced within 150 km of shore in August through October reversing to become a weak northward flow in late November through January (Hickey, 1979). Hence, during July–October (the period pertinent to the dispersal of sheephead larvae), the general pattern is for the California current to flow nearshore south of Pt.

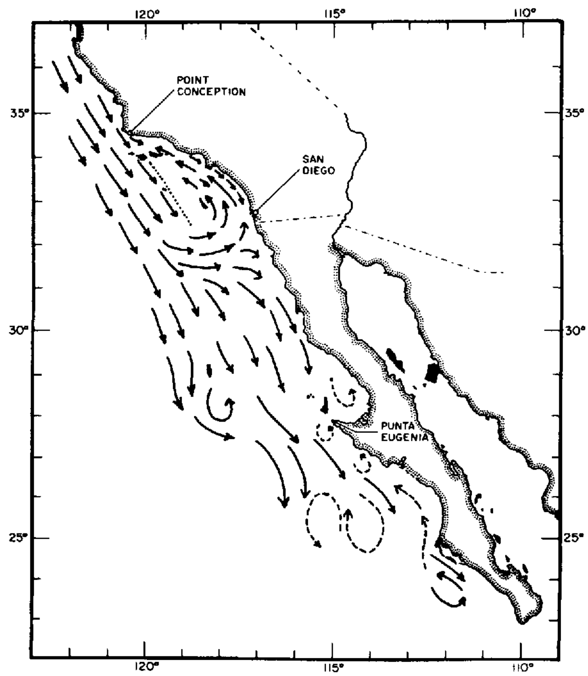

Figure 5. Schematic representation of general flow patterns from Point Conception to Cabo San Lucas, Baja California, based on data from Wyllie (1966) and Hickey (1979). Solid arrows represent consistent flow directions, dashed arrows represent occasional eddy flow, dotted line represents axis of Southern California Eddy. See text for discussion of main features.

Conception (Fig. 5). The current continues south, slightly rounding the point, to flow past San Miguel Island and the western half of Santa Rosa Island. The shoreward portion of the flow also bathes San Nicolas Island. At approximately 30–32N, the eastern portion of the California Current bends shoreward (Reid *et al.*, 1963; Pavlova, 1966). A portion of the onshore flow then bends to the north, bringing warmer water up into the Southern California Bight, thereby forming the Southern California Eddy (Sverdrup and Fleming, 1941).

The Southern California Eddy, like the flow of the California Current near Pt. Conception shows considerable seasonal variation (Sverdrup and Fleming, 1941; Reid, 1965). The axis of the Southern California Eddy is roughly along the Santa Rosa-Cortez Ridge (Sverdrup and Fleming, 1941) with northward flow inshore of this axis being greatest in the southern portion of the eddy (Fig. 6). From July through October, the eddy's inshore flow progressively moves warmer water northward. In July, the warm water intrusion typically reaches San Clemente and Santa Catalina Island, and by September–October has reached as far north as Santa Cruz Island. However, due to the southward flow near San Nicolas Island, the northward flow is typically inshore of San Nicolas Island.

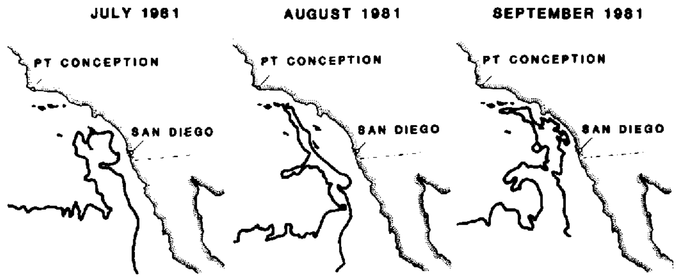

Figure 6. Monthly comparisons of characteristic boundaries between regions with different phytoplankton pigment content (based on satellite images), demonstrating the progressive northward movement of the Southern California Eddy's inshore flow. July 2 and 7 (composite image due to cloud cover), August 26, and September 12, 1981. (Modified from Peláez-Hudlet, 1984.)

South of 31N the flow is southward from nearshore to approximately 500 km offshore (Hickey, 1979). The inshore portion is derived from the eastward bend of the California Current between 30–32N (Pavlova, 1966). The nearshore southward flow appears to be a persistent feature throughout the year as far south as Punta Baja.

In the early summer months, the nearshore flow continues south from Punta Baja toward Punta Eugenia and then continues to flow south parallel to the coast at least to 23N. However, by late summer-early fall, the flow in this region becomes complicated due to the formation of a variety of eddies, which may cause northward flow very near shore between approximately 23 and 28N (from Wyllie, 1966). This results in the region around Punta Eugenia receiving southward flowing (nearshore) water from the north and occasionally northward flowing water from the south.

In the region of Isla Guadalupe, the California current is flowing generally south. However, an eddy (ca. 100 km) is typically present somewhere to the south of the island (Wyllie, 1966). This eddy(ies) may be formed by the influence of the island protruding into the current (a von Karmann vortex street, Choppra, 1973; Owen, 1980).

When one considers the above pattern of flow in relation to the sources of sheephead larvae, a general pattern of recruitment emerges. Since there are few sheephead north of Point Conception, the first major input of sheephead eggs and larvae into the south flowing California Current would be at San Nicolas Island and these would be carried southward. The northward flowing portion of the Southern California Eddy would be expected to carry sheephead larvae from the mainland up through San Clemente and Santa Catalina Islands to as far as Santa Cruz Island. In this general scheme, few if any larvae would be expected to reach San Miguel Island or San Nicolas Island.

With large sheephead populations along the coast of Baja California as far south as Punta Abreojos, the region in the central part of the sheephead's range should be receiving larvae from the north at most times. The region around Punta Eugenia would typically receive water from the north (with sheephead larvae), though the local eddies may retain larvae as well.

The current pattern around Isla Guadalupe may bring larvae from two sources to this island. First, larvae may be carried from the north even as far away as San Nicolas Island as inferred from drift bottle movements (Crowe and Schwartzlose, 1972). Second, possible local entrapment in the persistent eddies off of Isla Guadalupe may return larvae originating from the island.

b. Year to year variation. The general flow pattern described above applies for "normal" years, though variations occur in the timing, size and location of many of the eddies from year to year (Owen, 1980; Davis, 1985). Such year-to-year variation may be important in the transport of larvae to various areas. The extent of variation may be examined by satellite images of sea surface temperature in an area (such as the California Current region) where data demonstrate that the sea surface temperature bears some relationship to the distribution of the main thermocline temperature (Bernstein *et al.*, 1977; Fiedler, 1984).

The area of greatest interest (due to its pattern of variable recruitment success) is around San Nicolas Island and the northern Channel Islands. These islands are typically bathed by the south-flowing California Current during the months of July–October. However, in exceptional years, water from the south can reach these islands (especially San Nicolas Island) in a variety of ways. First, since the axis of the Southern California Eddy lies directly along the Santa Rosa-Cortez Ridge, one would expect mixing to occur along that axis. This would carry any sheephead larvae farther offshore to San Nicolas Island, but at the same time, it would dilute their concentration. Second, as the northward flowing water intrudes into south flowing water, small fingers of water (or jets) may intrude laterally toward the axis of the eddy (see Fig. 7). These fingers, which are transient in time and space, would carry larvae in undiluted concentration farther west. With time, such fingers would be expected to occasionally reach San Nicolas Island. Much stronger (and rarer) events are needed to bring the northward flowing (larvae-carrying) water into contact with San Miguel Island (see below).

Within the central portion of the sheephead's range, circulation is such that larvae are being brought from several directions. Year-to-year variability in eddy formation in one area will not greatly change the overall supply of larvae to this region.

c. Warm water years. In addition to the relatively small, but significant, year-to-year variations in current flow discussed above, much larger scale events occur, but at lower frequency (Chelton, 1981; Chelton *et al.*, 1982). These anomalous events, characterized by northward transport of warm water throughout the range of this study, are typically (but not always) associated with the tropical El Niño events (Chelton, 1981; Simpson, 1984).

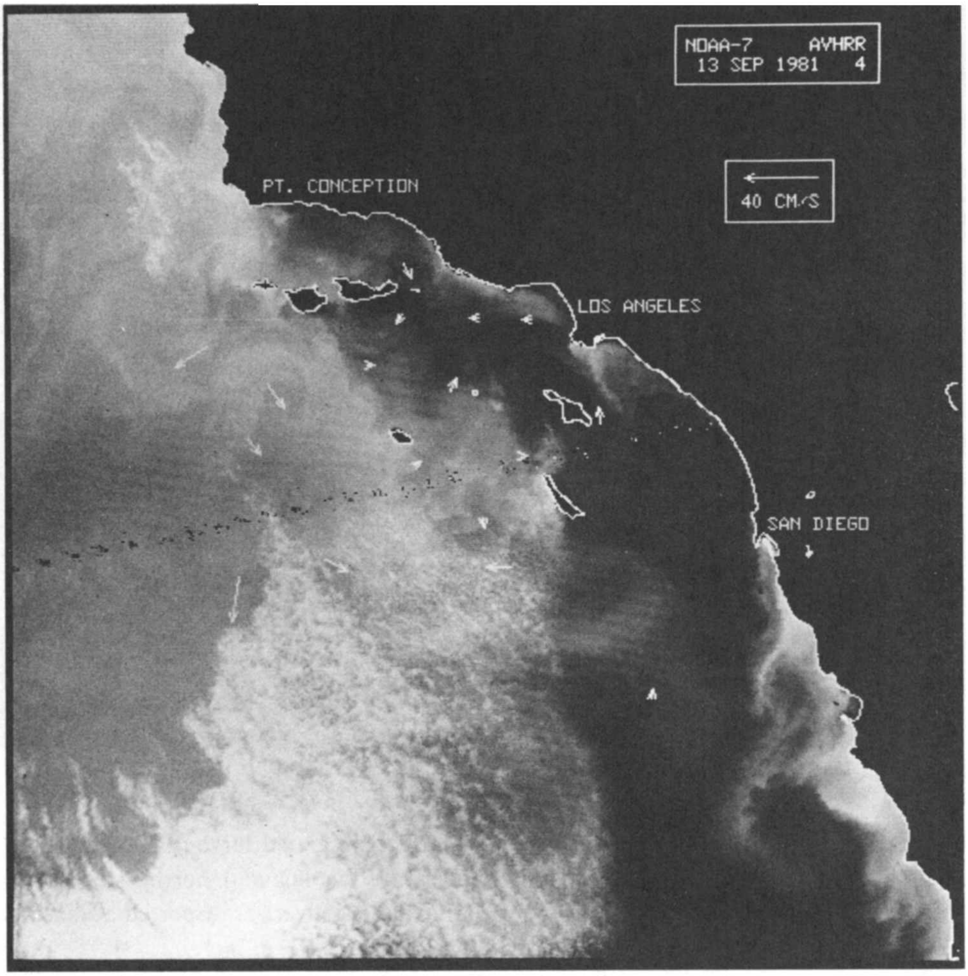

Figure 7. Satellite infrared image of sea surface temperature and apparent flow direction and velocities (vectors) during "normal" years (Sept. 13–14, 1981, and Sept. 21–22, 1982). Flow is estimated by examining images taken one day apart and measuring movement of specifically chosen points between images.

The last three "warm-water" events occurred in 1972, late 1977–78 and 1982–83 (Chelton, 1981; Cane, 1983). The influence on current patterns by these events, in the Southern California Bight is dramatic. In 1983, the normal northward flowing portion of the Southern California Eddy appeared to dominate the flow, encompassing San Nicolas, Santa Rosa and San Miguel islands, and even extending north of Point Conception. The southward flowing California Current was displaced offshore (see Fig. 8). Local areas of upwelling were present along the coast, but they were much smaller than during "normal" years. The northward flowing water (which persisted

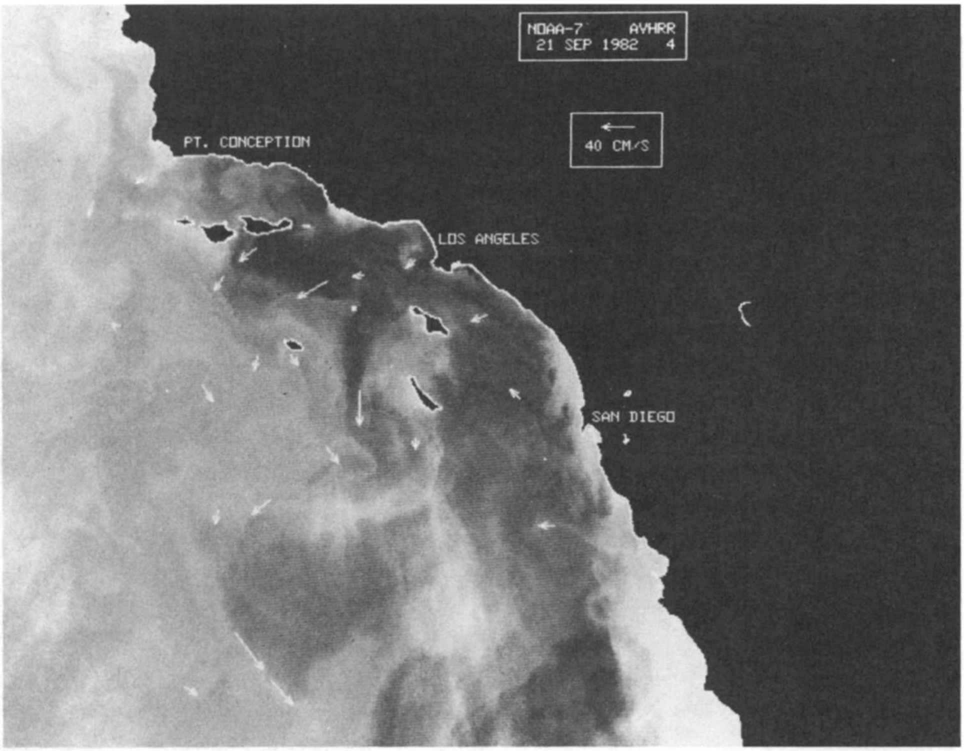

Figure 7. (Continued)

throughout the period of larval availability) probably carried larvae from the south (e.g. the mainland, San Clemente and Santa Catalina Islands) northward to San Nicolas Island and the northern Channel Islands. Larvae were transported at least as far as Monterey Bay, California (R. Lea, pers. comm).

The influence of northward flowing water in the central part of the sheephead's range is less dramatic, for the same reasons stated above for year-to-year variations in the "normal" flow. Since there is a large source of larvae to both the north and south of these central populations, flow from either direction should transport larvae toward those populations. However, in the southern part of their range, northward flowing water will not be carrying sheephead larvae; therefore, during such periods recruitment may be minimal as it was in 1983.

6. Discussion

The significance of large scale studies of larval availability and recruitment depends on which of two approaches is being used. In one approach, the pattern of larval availability in both time (i.e. seasonality) and space is examined in light of the average direction and intensity of current flow. Such studies are important in relation to the

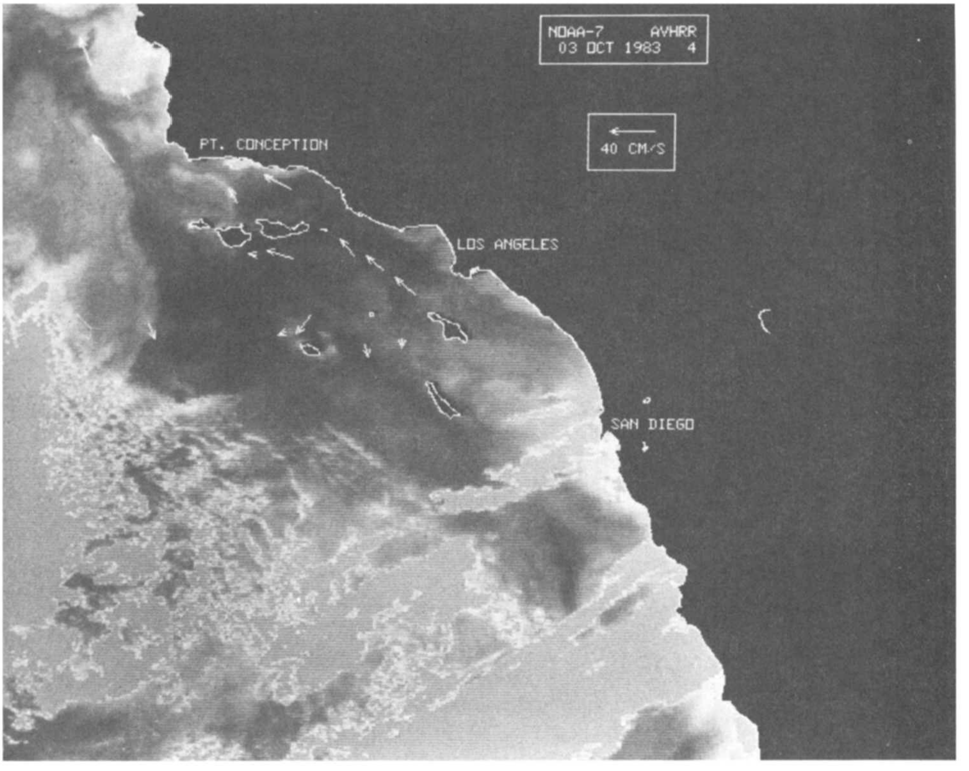

Figure 8. Satellite infrared image of sea surface temperature and apparent flow direction and velocities (vectors) during the 1983 El Niño event (Oct. 3–4, 1983). Flow is estimated as in Figure 7.

evolution of reproductive strategies (Johannes, 1978; Parrish *et al.*, 1981). However, such an approach would explain neither year-to-year variability in recruitment nor recruitment (however sporadic) in areas that have no source of larvae "upstream" (e.g. San Miguel Island). These latter two phenomena can only be explained through the second approach, whereby the variation in the pattern of larval availability and recruitment is examined with respect to variations in the current regime. These variations (or "events," see Yoder, 1983) are integral factors in understanding the causes of varible recruitment success in reef communities throughout the range of a species, but especially at the periphery.

The present study demonstrates that the large scale variations in recruitment are consistent with the variations in current flow. In those areas where currents may approach from either of two directions (both with sources of larval sheephead) recruitment occurs every year. However, in areas where current flow is typically from a direction without a larval source, recruitment is highly variable and dependent upon anomalous events in the current flow.

At San Nicolas Island, these anomalous events can be divided into those events of short duration (days to weeks), here termed low level, and those of long duration (months to years), here termed high level. The low level events occur when flow is mostly from the north (i.e. normal direction) whereby some northward flowing water may reach the island either by mixing along the Southern California Eddy axis or via a small meandering instrusion. Such low level events probably account for the occasional, sparse recruitment of sheephead to San Nicolas Island. High level events, typically associated with El Niño events, bring large amounts of warm southern water (larval rich) into the vicinity of San Nicolas Island, as well as the northern Channel Islands. During these events, recruitment of sheephead is highest at San Nicolas Island (e.g. 1977–78 and 1983). Anomalously high recruitment of *Panulirus interruptus,* lobsters, *Lythrypnus dalli* and *L. zebra,* gobies, *Hypsypops rubicunda,* garibaldi, and *Halichoeres semicinctus,* rock wrasse, also occurred in the northern part of their ranges during the 1983 high level event. Past high level events have affected the distribution and recruitment of a wide variety of organisms (Radovich, 1961; Longhurst, 1968), though in some of these examples, large motile adults may be actively following water masses rather than merely via passive transport by currents.

An important difference between low level and high level events is their timing and duration. High level events usually last from one to two years. Many different species can be affected by such events, since the chance coincidence of their reproductive season is not important, resulting in the successful recruitment of a whole suite of organisms. In contrast, low level events may last only a few days or weeks, thereby benefiting only those species whose larvae are present at the time. Low level events are probably more important than high level events in helping explain the occasional strong year success of particular species while other species show no unusual recruitment. These episodic, strong year class events have long been recognized as important population pulses for many fisheries (Hjort, 1926; Cushing, 1975) but such events may also be important in structuring nearshore communities and the mechanisms contributing to these events must be understood (Dayton and Tegner, 1984).

Jackson and Strathmann (1981) propose that species with longer pelagic stages tend to remain competent (i.e. capable of settling) longer. This would imply that these species would have a better chance of successfully dispersing via low level events than species with short pelagic phases, due to the increased likelihood of their larvae (i.e. species with long competent stages) being present during such an event. Support of this may lie in the relative recruitment success of sheephead (relatively long-lived larvae) versus the gobies (relatively short-lived larvae; Brothers *et al.*, 1983; Wiley, 1976). At San Nicolas Island, the former has sporadic, low level recruitment success in between the high recruitment success associated with high level events, whereas the gobies have only been found to recruit during high level events.

The relative consistency with which a species recruits to its different populations may have important effects on the density of those populations, assuming that once settled there is little or no emigration. Within this study, the sites can be categorized into roughly three levels of recruitment success: (1) recruitment occurs every year, intensity may vary, but is fairly consistent (San Clemente I., Santa Catalina I., I. Guadalupe, I. San Benito, and Cabo Thurloe); (2) recruitment highly variable, typically low or none between rare, high level events (San Nicolas I.); and (3) recruitment only during rare, high level events (San Miguel I. and Santa Rosa I.). The density of adult sheephead populations at these sites reflects the pattern of recruitment (Table 1). The highest densities occur where recruitment is most constant and lowest where it is the most sporadic. This pattern has been noted for other reef fish populations (Williams, 1979, 1980; Doherty, 1983; Jones, 1984). Such a relationship between recruitment rate and density may have profound effects on the influence a given species may impart on its surrounding community as well as its intraspecific interactions.

The persistence of a population is also related to the frequency of recruitment in conjunction with the longevity of individuals. The longer lived individuals are, the less frequent recruitment events need be to sustain a population. Also, there is a relationship between the relative intensity of the recruitment events and the necessary frequency of events. Even though low level events tend to produce relatively low recruitment success during each event, they occur more often than high level events and thereby may sustain the population with a low but more constant influx of individuals (Fig. 9). An example of this was presented by this study. Sheephead are relatively long-lived animals, up to 20–25 years at San Nicolas Island (Cowen, unpubl. data). The population at San Nicolas Island is fairly dense and is apparently being easily sustained between high level events by a few low level events. On San Miguel Island where only high level recruitment events occur, there is a persistent but much less dense population. In contrast, *Lythrypnus* spp. are short-lived (1–2 years, Wiley, 1976). They only appear to recruit to San Nicolas Island during the relatively rare high level events and consequently there is not a sustained population there. However, at Santa Catalina Island, recruitment appears to occur annually thereby sustaining a very dense population of gobies.

Related to the above discussion is the northern distribution of sheephead and other species of the southern fauna. Point Conception is a major faunal break, though it appears to be a more significant barrier for southern species extending north than vice versa (see review by Brusca and Wallerstein, 1979). A change in water temperature has long been invoked as the major cause of this faunal break, from which a physiological barrier has been inferred (Dana, 1853; Hubbs, 1948; Hedgpeth, 1957; Valentine, 1966; Horn and Allen, 1978). However, Brusca and Wallerstein (1979) pointed out that "in a significant number of taxa the confines of a narrow range of thermal tolerance and its associated geographic limitations are non-existent."

The distribution of recruitment success around the various Channel Islands, the resulting fluctuations in adult abundances, and the current regime discussed in this paper all suggest that hydrographic constraints on dispersal may be of importance in

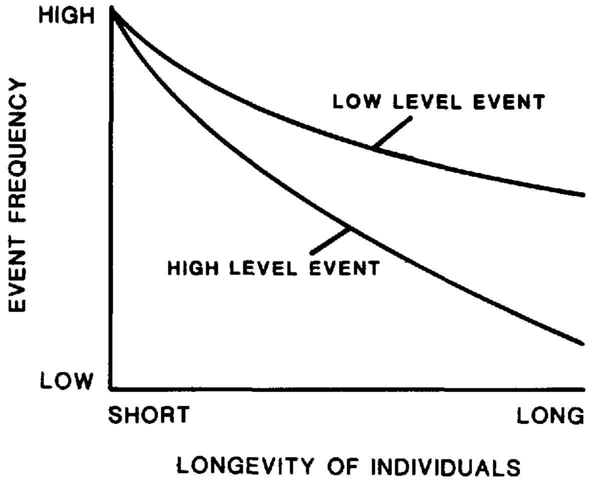

Figure 9. Necessary frequency of event occurrence relative to longevity of the individuals for maintaining a persistent population. Event frequency ranges from low (i.e. less than once per lifetime) to high (i.e., yearly event). Longevity of individuals ranges from short (i.e. annual) to long (i.e. tens of years). In the area below the curves, insufficient recruitment occurs for maintaining a persistent population.

creating a faunal break at Pt. Conception. Depending on the current regime, dispersal of such southern fauna as sheephead will occur in most areas throughout the Southern California Bight with variable frequencies, and on occasion recruitment will occur north of Pt. Conception. However, two factors (discussed above) may play against the persistence of a population north of Pt. Conception. First, for some species, individual life spans may not be sufficient to allow survival until the next successful recruitment event. Second, all of the eggs and larvae will be carried south during normal years (assuming a spring/summer spawning), hence the population will not be able to sustain itself. Evidence against temperature inhibition as the main determining factor in species distribution is provided by the success of southern faunal populations in the many cold water upwelling areas off north-central Baja California (Emerson, 1956; Efford, 1970; Brusca and Wallerstein, 1979).

The distribution and abundance of sheephead around the Channel Islands also reflects the variability of current flow and the resultant recruitment success. The southern fauna is prevalent on the islands most heavily influenced by the northward flowing portion of the Southern California Eddy, e.g. Santa Cruz, Anacapa, San Clemente and Santa Catalina Islands (Ebeling *et al.*, 1980; Cowen, unpubl. data). While the islands influenced primarily by the south flowing California Current (e.g. San Miguel, Santa Rosa and San Nicolas) possess fewer southern species of fishes (Cowen, unpubl. data). This pattern is consistent for intertidal algae (Murray and Littler, 1981; Murray *et al.*, 1980) and invertebrates (Seapy and Littler, 1980).

In conclusion, a thorough understanding of large scale circulation patterns, and their temporal variation, is necessary for explaining large scale patterns of larval availability and subsequent recruitment success on both a spatial and temporal basis. Within this scale, recruitment may be predictable, at least relatively, and thereby provide the opportunity to examine questions of community structure in relation to density and persistence of populations of ecologically important species and the cause of biogeographic patterns of different species.

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