Limnol. Oceanogr., 43(7), 1998, 1710–1721

Meroplanktonic distribution and circulation in a coastal retention zone of the northern California upwelling system

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Abstract

Previous studies have shown that settlement of several crab species along the coast north of Point Reyes (38°00′N, 123°00′W) occurs primarily during relaxation from upwelling, when warm water flows poleward from the Gulf of the Farallones. During 1994 and 1995 we sampled planktonic larval distributions and hydrography both south and north of Point Reyes during upwelling to test whether high concentrations of crab and rockfish larvae were concentrated in the source of the relaxation flow to the south of Point Reyes. An upwelling plume off Point Reyes and an "upwelling shadow," indicated by warmer, less saline water in the northern Gulf, were evident in both years, as were frontal regions that marked the boundaries between water types of three different types: (1) newly upwelled, (2) oceanic, and (3) San Francisco Bay outflow. In addition, there was a fourth type, termed Gulf water, that was a mixture of these three types. Concentrations of larvae of cancrid, pinnotherid, and "coastal" crabs and rockfishes were high south of Point Reyes but were low or absent in the newly upwelled water north of the point. Within the upwelling shadow, these meroplankton taxa were associated with different water masses. Several intertidal crab species and early-stage cancrid crabs were concentrated in San Francisco Bay outflow water, and coastal Gulf water late-stage cancrid crabs, early- and late-stage pinnotherid crabs, and rockfishes were concentrated at the frontal region between newly upwelled and Gulf water. Of the taxa examined, only rockfishes were found offshore in oceanic water. The high concentrations of meroplankton observed suggest that the Gulf of the Farallones is an important retention area for larvae that settle into coastal populations in the Gulf and to the north via poleward transport during upwelling relaxation.

In the California Current System (CCS), the presence from March through July of offshore transport and an equatorward coastal jet due to upwelling (e.g., Huyer 1983), offshore jets near promontories (e.g., Davis 1985), and eddies and meanders offshore from the U.S.–Canada border to Mexico (Strub et al. 1991) has led researchers to question how larvae of meroplanktonic coastal species avoid being transported offshore or equatorward, beyond areas where they can successfully settle and develop to reproduce (e.g., Parrish et al. 1981; Simpson 1987; Roughgarden et al. 1991; McConnaughey et al. 1994). This question indicates a general issue in marine population ecology related to this region, that being the manner in which physical/biological interactions provide the larval transport and survival needed for successful closure of the life cycles of fishes and invertebrates (Simpson 1987; Sinclair 1988; Frank 1992).

Stratification of mero- and holoplanktonic larvae along the shore suggests the existence of physical mechanisms (e.g., fronts) that might serve to limit cross-shelf loss of larvae off the coast of Oregon (Richardson and Pearcy 1977; Peterson et al. 1979; Richardson et al. 1980; Wroblewski 1980). In central California, Roughgarden et al. (1991) proposed that concentration of barnacle larvae in an offshore upwelling front during active upwelling and subsequent onshore transport during upwelling relaxation explained the occurrence of settlement pulses during relaxation (e.g., Farrell et al. 1991). There is evidence that some types of larvae can be washed far offshore by the eddy structures and filaments in the CCS (Haury et al. 1986; Kosro and Huyer 1986; Washburn et al.

Acknowledgments
We thank the following, who made this work possible: National Marine Fisheries Service, Scripps Institution of Oceanography, National Marine Sanctuary Program, Pacific Fisheries Environmental Group, Bodega Marine Laboratory, Point Reyes Bird Observatory, David Woodbury, Keith Sakuma, Dale Roberts, Jennifer Diehl, James Leichter, Lance Morgan, Carolyn Lundquist, John LaFargue, Ken Baltz, Heather Parker, Todd Switzer, Kimball Milikan, Ron George, Elizabeth McClaren, Allison Roup, Dan Howard, and Susan Sandretto. This work benefitted from discussions with Jack Barth, Mike Kosro, and Leslie Rosenfeld. This article was funded in part by a grant from National Sea Grant College Program, under grant NA89AA-D-5G138, project numbers R/F-136 and R/F-150, through the California Sea Grant College, and in part by the California State Resources agency.

1993). For example, offshore transport of larval hake was the mechanism proposed to underlie the negative correlation between year class strength and offshore transport (Bailey 1981).

During the upwelling season in the CCS, both the nearshore jet (Huyer 1983) and the general, meandering equatorward flow tend to transport larvae southward, and therefore must be overcome to maintain populations at latitude. Although it is possible that transport during the upwelling period is compensated for by northward transport during the Davidson Current period (e.g., Johnson et al. 1986), we focus here on the possibility that larvae are retained at latitude by retention in recirculating flows and/or migrate deep enough to be transported in the northward and onshore flowing near-bottom flows over the upper slope (Kosro 1987; Graham et al. 1992). Persistent eddies are believed to provide retention of larvae nearshore in other locations (e.g., Emery 1972; Lobel and Robinson 1986; Wolanski and Hamner 1988; Murdoch 1989; Crawford et al. 1990; Boehlert et al. 1992). The tendency for eddies to be associated with capes in upwelling regions suggests that this mechanism may account for the observed differences in recruitment variability across capes (e.g., Ebert and Russell 1988; Wing et al. 1995*b*).

In a previous study of settlement of crabs and sea urchins north of Point Reyes, we observed settlement of both groups only during upwelling relaxation. We proposed (Wing et al. 1995*a*) that the larvae were retained to the south of Point Reyes during upwelling and were then transported northward during relaxation in the alongshore current described by Send et al. (1987). A test of this hypothesis, conducted by monitoring settlement at four points along the coast from south of Point Reyes to north of Point Reyes, revealed that settlement to the south occurred at a constant low rate, while settlement to the north occurred only during episodic lulls in the wind or during wind reversals, when a warm, coastally trapped current extended from south of Point Reyes poleward (Wing et al. 1995*b*). The effects of this mechanism on annual time scales were greater settlement south of Point Reyes and lesser settlement to the north of Point Reyes.

These results lead naturally to the hypothesis that meroplanktonic larvae are retained in the cyclonic flow in the Gulf of the Farallones, which is formed during active upwelling. Here we present the results from 2 yr of shipboard surveys across this region, that show both persistent hydrographic features associated with Point Reyes and the San Francisco Bay outflow and predictable distributions of meroplankton relative to these features. We show that larvae are found in higher concentrations immediately to the south of Point Reyes, we describe associations between different types of larvae and specific hydrographic features, and we propose the existence of physical/biological interactions that may explain these associations.

Although the Gulf of the Farallones shares a common macroscale oceanographic and meteorological regime with the well-studied (e.g., Brink 1983; Lentz 1987; Strub et al. 1987), open coast north of Point Reyes (i.e., it is dominated by seasonal upwelling dynamics), there are clear differences at this cape-and-bay mesoscale. The upwelling season winds in the Gulf are generally weaker than those to the north or south (Dorman and Winant 1995) and tend to curve east toward the mouth of San Francisco Bay. Circulation in the vicinity of Point Reyes differs from that off the straighter coast between headlands. There are indications of cyclonic circulation in the Gulf from advanced very high resolution radiometer (AVHRR) imagery that are consistent with the separation of an equatorward jet from the shore boundary at Point Reyes (Wing et al. 1995*b*). Currents measured by shipboard acoustic Doppler current profiler (ADCP) during National Marine Fisheries Service (NMFS) surveys in May through June of 1993–1995 show weak currents in the northern part of the Gulf, while the flow offshore and to the north of Point Reyes is strongly equatorward and seaward during favorable upwelling winds. This strong southward flow exhibits vertical shear, with bottom currents being weaker and in an opposite direction from the surface currents. In the northern Gulf of the Farallones, because wind forcing is ineffective and upwelling absent, the water warms up and becomes less dense than water upwelling at the apex of the cape. When wind forcing weakens, this surface layer of warm water propagates poleward as a rotating buoyancy current (Send et al. 1987; Wing et al. 1995*a*,*b*). In AVHRR images, this buoyant feature propagates as far north as Point Arena during 5- to 6-d periods of quiescent winds (e.g., Wing et al. 1995*a*).

Given this circulation scenario, we expect a combination of different water types from the various sources as well as mixtures of them in the region. Upwelled water originates offshore at depth, and it surfaces along the coast. This water type is cold (8–10°C) and has salinities in the range of 33.5–34.0 psu (e.g., Schwing et al. 1991). Offshore of the coastal upwelling band, the near-surface oceanic water is warmer (12–16°C) and has salinities of 33.0–33.5 psu (e.g., Schwing et al. 1991). This water type is characteristic of surface waters of the mid-latitude eastern Pacific that have moved eastward and have equilibrated with atmospheric conditions en route. Schwing et al. (1991) describe frontal water that is intermediate in temperature and salinity compared with upwelled and oceanic waters. A third type of water originates from the outflow of low salinity, warm bay water from the San Francisco Bay. In the Gulf of the Farallones, old upwelled water mixed with oceanic and Bay water is retained near the coast and heated. Because it is warmer than upwelled water and saltier than oceanic water but has no specific thermohaline definition (Schwing et al. 1991), it is referred to here as Gulf water.

To determine the physical/biological nature of this potential retention zone, we sampled the distribution of larvae from four taxonomic groupings, chosen on the basis of frequency of occurrence in past samples and grouped together because of past occurrence together (Lough 1974; Wing et al. 1995*b*). The cancrid crabs included *Cancer magister, Cancer antennarius, Cancer productus,* and *Cancer gracilis.* We considered megalopal and zoeal stages separately. The rockfishes, *Sebastes* spp., included nearshore species (e.g., *Sebastes auriculatus*), but the majority were of the offshore species, *Sebastes jordani.* Coastal crabs included the two species of grapsid crabs, *Hemigrapsus nudus* and *Pachygrapsus crassipes,* a porcellanid crab, *Petrolisthes* spp., and others, *Pugettia productus* and *Pagarus* spp. For this group, we considered distribution of megalopal and zoeal stage larvae separately. The pinnotherids, a common group of commensal crabs, consisted of *Fabia subquadrata, Pinnixa littoralis,* and *Pinnixa* sp. We considered the distributions of their megalopae and zoeae separately.

These taxonomic groups of larvae can be expected to differ in distribution because of relative differences in season of spawning, location of larval release, hydrodynamic characteristics, and behavior. Larvae released nearshore earlier in the year, before upwelling begins, are likely to be found offshore of the nearshore zone of upwelled water because they would have been transported offshore with these surface waters. On the other hand, larvae released later may be found within the cool upwelled water and are likely to be transported southward rapidly (cf. Richardson and Pearcy 1977; Richardson et al. 1980).

Although the timing of the larval release and development period is not well known for all of the species of interest here, some generalizations can be made. Cancrid crabs are ovigerous early in the year and have relatively long larval periods (80–160 d; Strathmann 1987). Dungeness crab (*C. magister*) larvae are released nearshore (<50 m) between December and March (Waldron 1958) and may settle nearshore in May and June (e.g., McConnaughey et al. 1992). *C. productus* is found to be ovigerous between October and January and generally settles between February and September, with peak settling in May (Trask 1970; Strathmann 1987). Similarly, *C. antennarius* is found to be ovigerous between November and January and may be found settling at Bodega Bay in June through August (Morris et al. 1980; Wing et al. 1995a). The Porcellanid group (*Petrolistes* spp.) can be found ovigerous in February through April; however, a second brood may be produced as late as August. This group has short larval periods of generally 34 to 40 d (cf. MacMillan 1972). Settlement of *Pugettia* spp. occurred in May through June at Bodega Head during the 1992 season; however, we lack information regarding the local reproductive timing, or larval period (Wing et al. 1995a). Rockfish parturition in the central and northern regions of California occurs in late fall to early spring, with a peak in January to March, and may occur across the shelf, seaward of the coastal jet (Wyllie Echeverria 1987; Moser and Boehlert 1991). Larvae are distributed offshore in the upper mixed layer for 3 to 6 months until they reach sizes large enough that they may safely move into a juvenile habitat (30–90 mm SL), at which time they move deeper in the water column and onshore from May to July via unknown pathways (Lenarz et al. 1991; Love et al. 1991; Larson et al. 1994; Ralston and Howard 1995).

Treating groups of larval species provides two advantages. First, sampling and analysis of several similar species (e.g., cancrid crabs) with different larval timing provides a longer sampling period and therefore enables us to sample the distribution of the species complex relative to a physical oceanographic feature over a larger period than sampling a single species (e.g., *C. magister*) would. Second, sampling and analysis of a variety of different taxa that are hydrodynamically (e.g., size and shape) and behaviorally (e.g., vertical migration, swimming) dissimilar allows us to use a comparative approach in seeking explanations as to the way in which circulation features shape horizontal distributions and dispersal paths.

Materials and methods

The data for this study were collected during June of 1994 and June of 1995 aboard the National Oceanic and Atmospheric Administration (NOAA) R/V *David Starr Jordan.* Shipboard sampling during 18–22 June 1994 was on a relatively broad scale. Three 110-km alongshore transects were 5.5–9 km, 46 km, and 92 km offshore. We refer to them as the coastal, the shelf, and the oceanic transects. Each station of the transects was sampled with a 0.236-m^2 bongo net, cast to 70 m (505-μm and 333-μm nets) and conductivity-temperature-depth (CTD) cast during the day and with a 0.133-m^2 manta net during the night (Brown and Cheng 1981). Current profiles were collected continuously during the sampling using an RDI acoustic Doppler flow profiler (ADCP). These data were collected using 8-m bins and 8-m pulse length with 4-m blanking and were calibrated using the methods of Kosro (1987); a calibration correction of amplitude 1.009 and angle -1.65 degrees was applied. Flows at 25 m (1994 and 1995) and at 55 m (1995) are reported. Measures of surface temperature and salinity were collected continuously with a SeaBird thermosalinograph, and values were corrected using concurrent values from a factory-calibrated CTD and bucket sample.

During 15–19 June 1995, stations were sampled on a finer scale with three 75-km transects, at distances of 4–7.5 km (transect C), 18.5–22 km (transect B), and 41–46 km (transect A) offshore. Each station of the transects was sampled with a 0.133-m^2 manta net (505-μm, 333-μm cod end), a 1-m^2 Tucker trawl sampled two depth bins (0–30 m and 30–60 m; 1-mm nets, 333-μm cod end), and a SeaBird SBE19 CTD with attached WetStar fluorometer and Seabird PAR sensor was cast through 90% of the water column during both day and night operations. Tucker trawl depths were measured with an inclinometer. As in 1994, ADCP and thermosalinograph data were collected continuously during the sampling. During both cruises, AVHRR images (channel 4) of the region were supplied to the ship from NOAA Coast Watch and were used to orient sampling transects to the oceanographic features. Volumes of each net tow were recorded with calibrated General Oceanic flow meters, and depth and temperature profiles of Tucker trawl samples were double-checked with a temperature/depth recording devise (TDR). All plankton samples were preserved in EtOH, which was replenished after 12 h.

Plankton samples of larval crabs were identified using guidelines from Lough (1974). In addition, some of the collected larvae and metamorphosed juvenile stages were grown out in the laboratory to double-check the identifications. Rockfish identifications were performed at the National Marine Fisheries Service Tiburon Laboratory. Larval abundance is reported in terms of larvae per 1 m^2.

We determined water type based on temperature and salinity data collected from the surface at each station, then tested whether species distributions were explained by water type. The continuous surface salinity and temperature values obtained from the thermosalinograph show clear temperature and salinity fronts at Point Reyes between newly upwelled and Gulf (upwelled warm or Bay-influenced) water and near

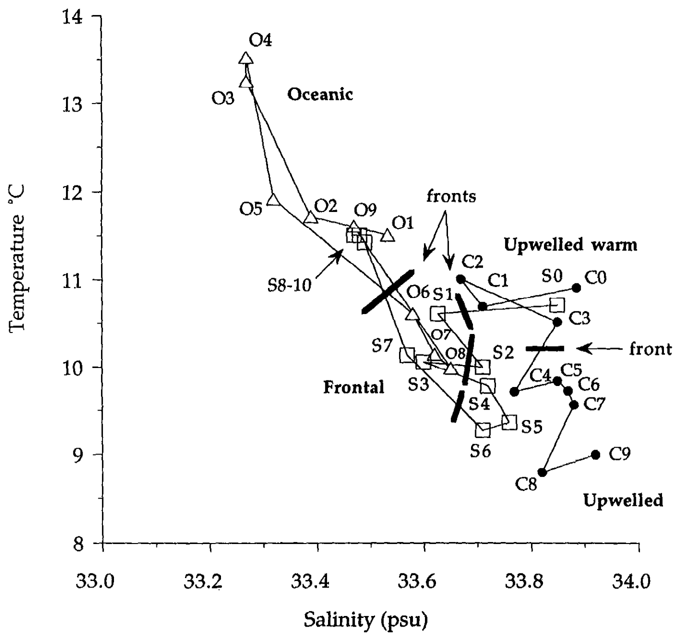

Fig. 1. Temperature and salinity values from the surface at night at each station during the 1994 sampling. Transects and stations are indicated next to each value; coastal (C), shelf (S), oceanic (O). Station numbers increase south to north (e.g., *see* Fig. 5a). Dark bars indicate fronts in temperature and salinity observed on the continuous thermosalinograph (change of >0.5°C and/or >0.1 psu over 2 km).

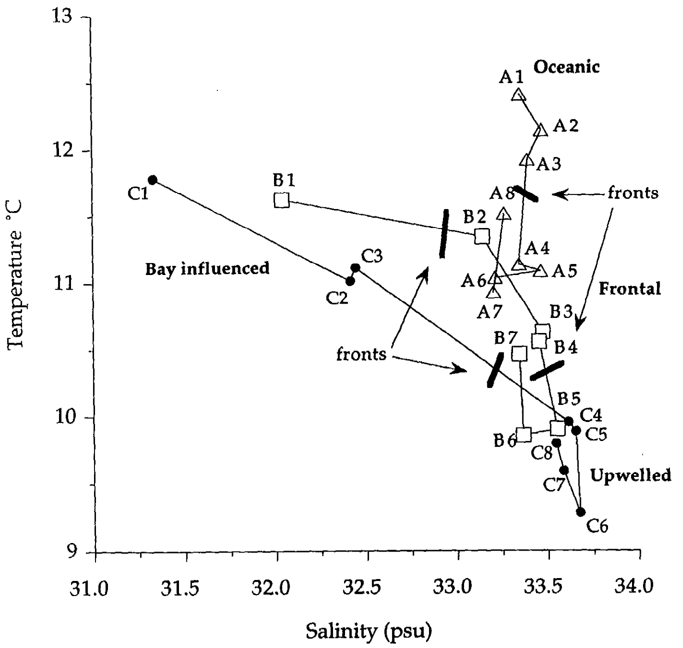

Fig. 2. Temperature and salinity values from the surface at night at each station during the 1995 sampling. Transects and stations are indicated next to each value; C (near shore), B (shelf), A (oceanic). Dark bars indicate fronts in temperature and salinity observed on the continuous thermosalinograph.

the entrance to San Francisco Bay between Bay outflow and Gulf water. Offshore one can see a clear front between oceanic and newly upwelled and Gulf water masses. Fronts were identified by a change in temperature of >0.5°C and/or a change in salinity of >0.1 psu over less than 3 km. We used these fronts as boundaries to help define distinct water types for each year. A one-way analysis of variance using water type as a factor was then applied to log-transformed abundance of each taxon (Sokal and Rohlf 1981). This was followed by a least-squares test to rank effects of water type on abundance of each planktonic taxon.

To test whether ability to vertically migrate might be in part responsible for horizontal distributions, we used abundance data from the inshore transect in 1995 (fine scale) to calculate the mode of the alongshore positions by station. We then compared this position with an index of vertical migration. We calculated the difference in distribution of larvae during day and night sampling between the deep (30–60 m) and shallow (0–30 m) depth bins (including data from neuston sampling) and expressed the index as the fraction of the distribution that changes from the surface layer during the night to the deep layer during the day.

Results

Physical oceanographic conditions—Temperature–salinity characteristics of surface waters from both cruises reflected the presence of waters from the three distinct origins (upwelled, oceanic, and Bay) that mix in the Gulf to form the fourth type, Gulf water. Gulf water differed in temperature and salinity between 1994 and 1995, owing largely to the strong freshwater outflow in 1995. Freshwater outflow from the Golden Gate was 5,620 thousand acre feet in 1994 and 40,828 thousand acre feet in 1995 (data obtained from California Water Resources Board). In 1994, Gulf water registered relatively high salinity (>33.7 psu) but was warmer (>10.5°C) than newly upwelled water (Fig. 1). This water is labeled as "upwelled warmed" in our analysis (Fig. 1). In 1995, Gulf water was strongly mixed with San Francisco Bay outflow waters, was of a lower salinity (<33.0 psu), and was relatively warm (>10.5°C; Fig. 2). This water is labeled as "bay influenced" in our analysis (Fig. 2). Newly upwelled water characterized by low temperature (<10.5°C) and relatively high salinity (>33.7 psu [1994], >33.3 psu [1995]) was found north of Point Reyes, where it formed a coastal jet that separated from the coast at Point Reyes and extended seaward in a cold filament (Figs. 1–2). This water is labeled "upwelled" in our analysis (Figs. 1–2).

During the 1994 survey, flow was strongly southwest in the upper water column offshore and along the seaward edge of the cold plume off of Point Reyes (Fig. 3). Onshore and south of Point Reyes, flow is weak and less coherent (Fig. 3). During the 1995 survey, flow was strongly southwest along the seaward edge of the cold plume in the upper water column but was near zero and slightly onshore and poleward near the bottom (Fig. 4). The filament off of Point Reyes was cold and unstratified; however, on its equatorward edge, weak stratification and upwardly bending isopycnals, slowing, and reversal of flow marked the boundary of the "separation front." This region of intermediate temperature and

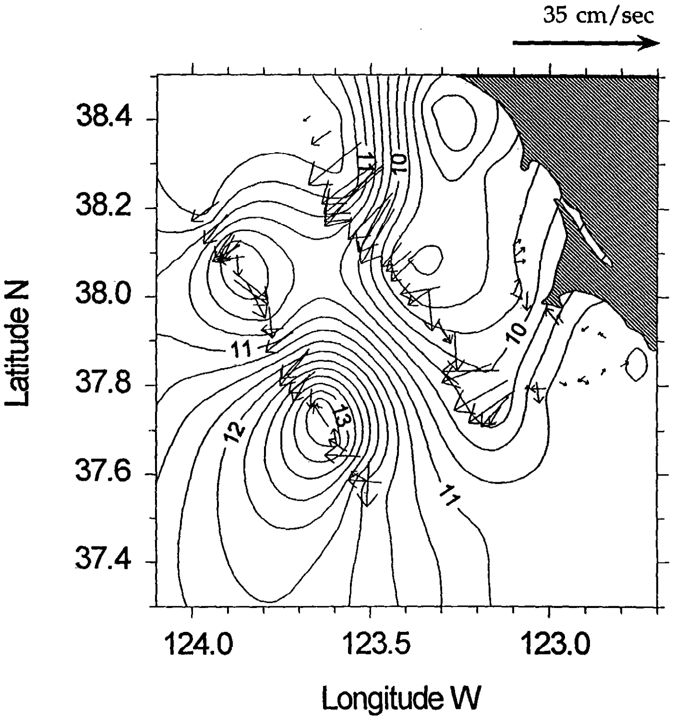

Fig. 3. Flow vectors from the shipboard acoustic Doppler current profiler for the upper 25 m during the 1994 sampling show strong southwesterly flow in the coastal jet as it separated from the coast at Point Reyes: a strong convergence at the offshore extreme of the jet and a strong shear at its southern edge marks the boundary of weak poleward flow in the Gulf. Values are plotted on contours of surface temperature (contoured at 0.25°C).

salinity between newly upwelled waters and oceanic or Gulf waters is labeled "frontal" in our analysis (<11.5°C, <33.7 psu [1994]; >10.5°C, <11.5°C, >33.0 psu [1995]; Figs. 1–2). The Gulf water mass had deeper and more persistent stratification, lower flow rates, warmer temperatures, and a lower range of salinity. Near the mouth of San Francisco Bay, a shallow, low-salinity (33.0–30.0 psu), warm (11–12°C) feature extended as the outflow plume from the Bay/delta. During heavy outflow years, such as we observed in 1995, or during relaxation events, this feature extended northward along the coast from San Francisco Bay. Seaward of the Gulf and frontal water, a shift to warm (>11.5°C), low-salinity (<33.7 psu) conditions marked the boundary of oceanic waters, labeled "oceanic" in our analysis (Figs. 1–2).

Larval distributions—Horizontal distributions of the four larval groups during the 1994 and 1995 surveys are presented as averages of abundance for all day and night sampling at each station throughout the water column. Vertical distributions during day and night sampling are presented as averages of abundance for each depth range over all stations, expressed as the percentage of horizontal density at that location. These distributions are then related to associated water mass types, patterns of circulation, and alongshore position.

During the 1995 vertically stratified sampling, Cancrid crab zoeae were found in large concentrations in the upper 30 m of the water column and neuston at night and in the upper 30 m of the water column and neuston during the day; few were found in the deeper layer (30–60 m) during day

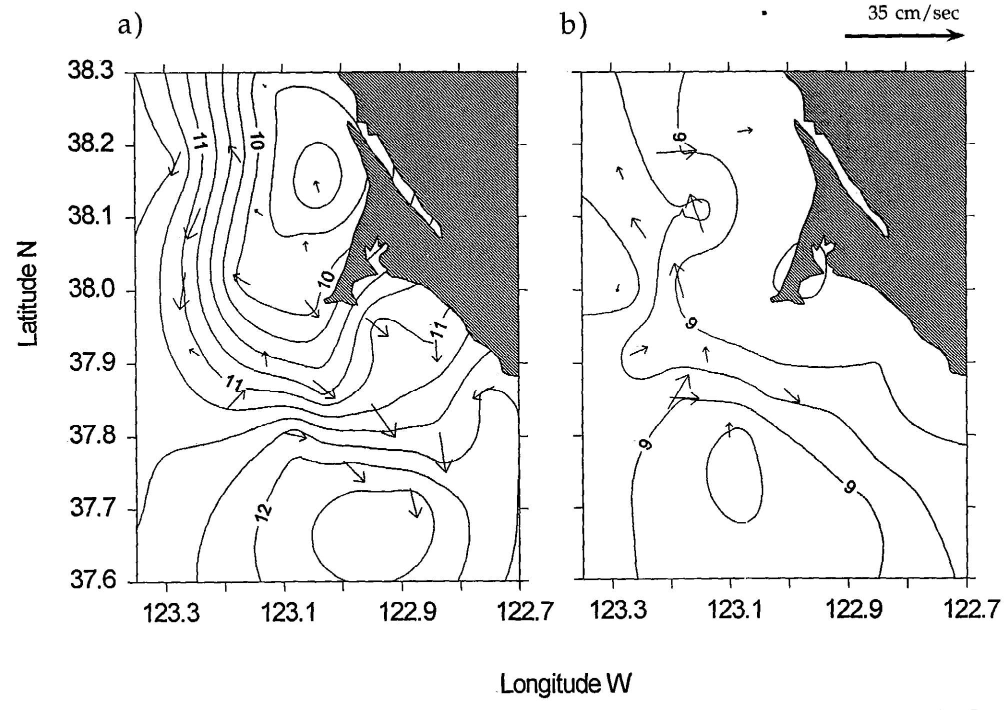

Fig. 4. (a) Flow vectors from ADCP at 25 m and contours of surface temperature and (b) flow vectors from 55 m and contours of temperature at 55 m from 1995 sampling (temperature contours at 0.25°C).

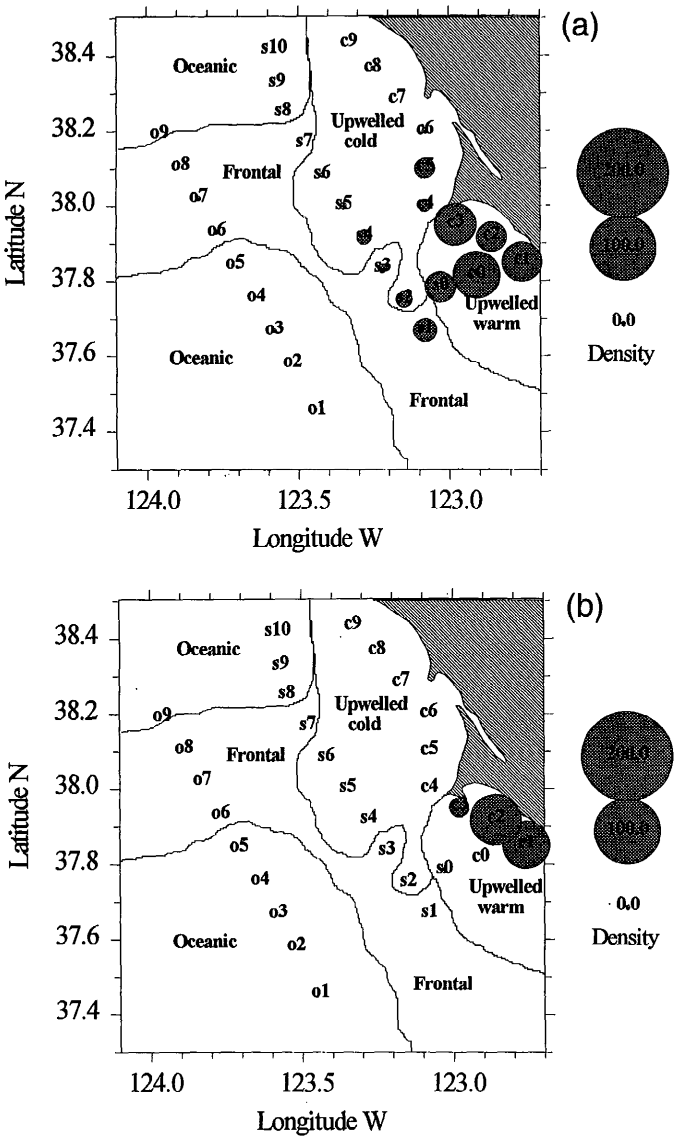

Fig. 5. Horizontal distribution of *Cancer* spp. megalopae (a) and zoeae (b) and contours of water type for 1994 sampling. Abundance is in units of larvae/m^2.

and night (Table 1). Cancrid megalopae were found primarily in the neuston and upper water column (0–30 m) during the night and primarily in the deeper layer (30–60 m) during the day (Table 1). Virtually none were found in the neuston during the day, and the fraction in the upper layer (0–30 m) was greatly reduced.

Horizontal distributions from the 1994, broader scale survey indicate that cancrid megalopae occurred across the shelf, associated most strongly with the warmed upwelled water (Table 2), and were found at high concentrations in the northern Gulf (Fig. 5a). Zoeae were found exclusively on the inner shelf to the south of Point Reyes (Fig. 5b) and were strongly associated with warmed upwelled water (Table 2). During the 1995, finer scale survey, these patterns were similar, with high concentrations of megalopae found across the shelf, especially in the northern Gulf (Fig. 6a). However, there was no statistical relationship between pattern and water type. Cancrid zoeae were found onshore to the south of Point Reyes (Fig. 6b) and were closely associated with the Bay outflow–influenced water (Table 3).

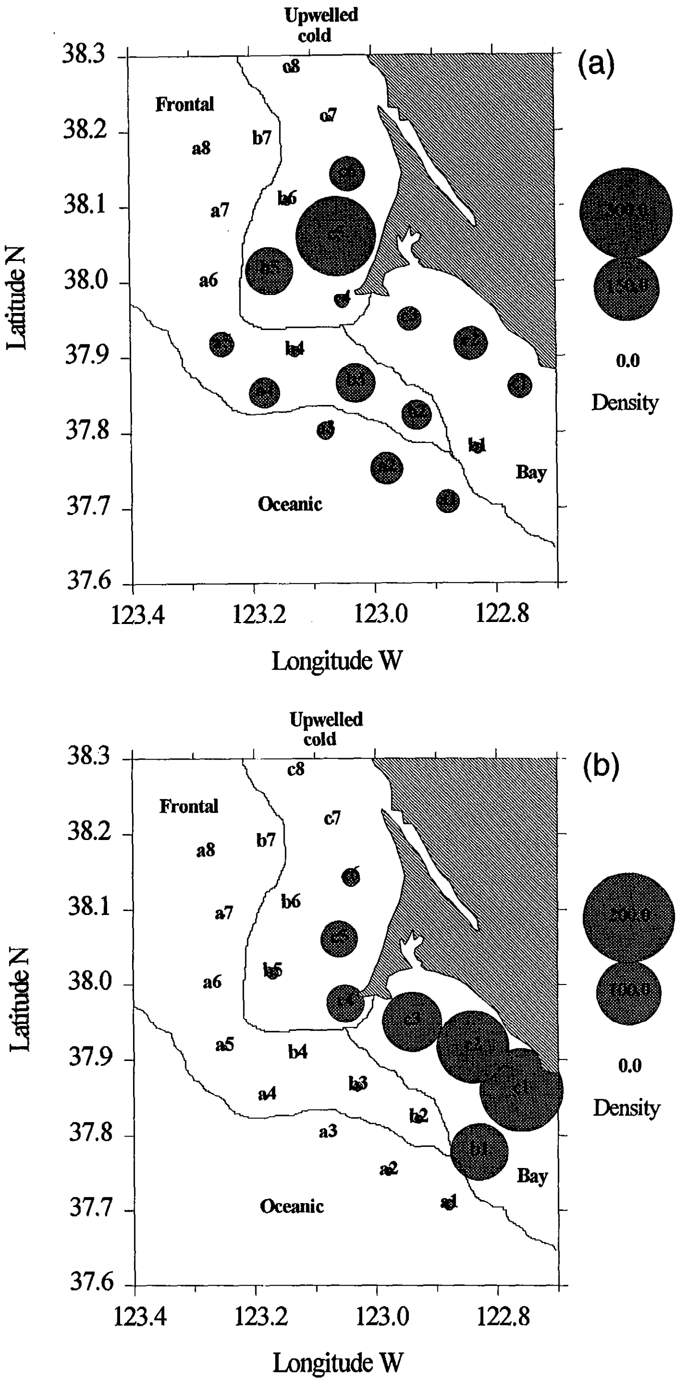

Fig. 6. Horizontal distribution of *Cancer* spp. megalopae (a) and zoeae (b) and contours of water type for 1995 sampling. Abundance is in units of larvae/m^2.

During 1995, Coastal crab zoeae showed little diel change in vertical distribution on the scale by which we measured. High concentrations were found in the neuston and upper water column during both day and night (Table 1). Megal-

Table 1. Percentages of larvae in neuston combined with shallow Tucker trawl (0–30 m) compared with those in deep Tucker trawl (30–60 m) during day and night sampling. Samples were taken during the 1995 fine scale survey ($n = 23$).

Taxon	Day		Night	
	0–30 m	30–60 m	0–30 m	30–60 m
Cancer spp. megalopae	30	70	86	14
Cancer spp. zoeae	83	17	76	24
Coastal crab megalopae	50	50	63	37
Coastal crab zoeae	81	19	74	26
Pinnixa sp. megalopae	24	76	86	14
Pinnixa sp. zoeae	18	82	85	15

opae of this group were skewed more toward the neuston and upper layer at night and were evenly distributed during the day (Table 1). This diel shift in vertical distribution is less strong than that observed in the cancrid group.

Horizontal distribution of coastal crabs during the 1994 survey showed both megalopae and zoeae found on the inner shelf and to the south of Point Reyes (Fig. 7). Zoeae were closely associated with the warmed upwelled water (Table 2), while the distribution of megalopae extended up to the separation front and was equally associated with warmed upwelled and cold upwelled water (Table 2). These trends were again seen in 1995, when the megalopae and zoeae that were found nearshore in the Gulf were skewed strongly equatorward to the south of Point Reyes (Fig. 8). However, their abundance was not explained by association with a single water type (Table 3).

In 1995, Pinnotherid crab megalopae and zoeae were found, primarily in the upper water column (0–30 m), during night sampling (Table 1). Few were found in the neuston at night. During daytime sampling, both megalopae and zoeae were found, primarily in the deep layer and scantily in the upper layer, and they were absent from the neuston (Table 1).

Horizontal distribution of pinnotherid megalopae during the 1994 survey showed that they were confined primarily to the inner shelf, were found in large numbers in the northern Gulf (Fig. 9a), and were associated with warmed upwelled waters. Pinnotherid zoeae were found almost exclusively to the south of Point Reyes (Fig. 9b) and were associated with warmed upwelled water. This pattern was similar to the 1995 distribution, with zoeae and megalopae confined to the inner shelf and found primarily in newly upwelled waters (Table 3) immediately north of Point Reyes (Fig. 10).

Rockfish larvae showed no conclusive pattern of vertical migratory behavior. Presumably this is because of the relatively small sample size of the 1995 depth-stratified sampling.

Horizontal distribution during 1994 indicated the highest abundance of *Sebastes* spp. in the offshore water both north and south of the cold upwelling filament. Concentrations were particularly high in the offshore transect along a region of high flow convergence (Fig. 11a). Larvae were also found across the shelf at the separation zone and onshore in the Gulf waters with the high single concentration observed immediately to the north of Point Reyes at the separation front. Larvae were not found in large numbers in newly upwelled waters. In 1995, larvae were found primarily in the upper Gulf and separation front (Fig. 11b) and on the outer shelf, with concentrations decreasing onshore. Abundance is most closely associated with oceanic and frontal water masses (Table 3).

Alongshore position of the mode of distribution of each taxon of crabs is correlated with the degree to which the larvae move from the surface layer (0–30 m) during the night to the deeper water column (30–60 m) during the day (Fig. 12). This pattern shows that cancrid zoeae and both zoeae and megalopae of the "coastal" crab group, which are poor vertical migrators, are concentrated in the more quiescent Gulf. However, cancrid megalopae and pinnotherids, which are strong vertical migrators, are concentrated near the edge of the separation of the coastal jet in a region of large vertical shear.

Discussion

The data we have presented on observations of large concentrations of crab and rockfish larvae associated with the waters to the south of Point Reyes add support to the idea that regions like the northern Gulf of the Farallones, where coastal waters may be retained onshore during upwelling, are generally important to larval dispersal and the ultimate alongshore distribution of recruitment of meroplankton to coastal populations. This presents a mechanism by which the

Table 2. Results of a one-way ANOVA with water type as a factor, applied to log-transformed abundance data for each taxon from the 1994 samples ($n = 30$). Rank is given from a least-squares test to show effects of water type on abundance of each taxon. Water types are frontal (Fr), oceanic (Oc), upwelled warm (Uw), and upwelled cold (Uc).

Taxon	Log (abundance + 1)					Rank	Number of larvae
	Fr	Oc	Uw	Uc	*P*		
Cancer spp. megalopae	4.94	0.81	10.44	6.49	0.0001	Uw > Uc = Fr > Oc	3,246
Cancer spp. zoeae	0.00	0.00	7.60	0.24	0.0001	Uw > Uc = Fr = Oc	1,582
Coastal crab megalopae	0.00	0.00	3.26	2.49	0.009	Uw = Uc > Fr = Oc	85
Coastal crab zoeae	4.74	5.01	8.98	2.05	0.009	Uw > Oc > Uc = Fr	104
Pinnixa sp. megalopae	2.19	0.00	6.34	2.56	0.0079	Uw > Fr = Oc = Uc	2,397
Pinnixa sp. zoeae	0.31	0.00	3.28	1.86	0.049	Uw > Fr = Oc, Uw = Uc	310
Sebastes spp. larvae	4.97	5.15	4.37	3.39	0.68	Fr = Oc = Uw = Uc	137

Table 3. Results of a one-way ANOVA with water type as a factor applied to log-transformed abundance data for each taxon from the 1995 samples (n = 23). Rank is given from a least-squares test to show effects of water type on abundance of each taxon. Water types are frontal (Fr), oceanic (Oc), Bay-influenced (Ba), and upwelled cold (Uc).

	Log (abundance + 1)						
Taxon	Fr	Oc	Uw	Uc	P	Rank	Number of larvae
Cancer spp. megalopae	9.88	7.23	9.69	9.40	0.23	Fr = Oc = Ba = Uc	11,435
Cancer spp. zoeae	4.16	5.44	11.60	6.33	0.017	Ba > Fr = Oc = Uc	17,826
Coastal crab megalopae	3.36	6.70	7.86	6.72	0.043	Ba = Uc = Oc > Fr	847
Coastal crab zoeae	3.67	7.27	9.51	6.61	0.006	Ba = Uc = Oc > Fr	2,477
Pinnixa sp. megalopae	6.92	9.21	9.52	11.07	0.014	Uc > Fr, Uc = Oc = Ba	13,640
Pinnixa sp. zoeae	4.89	7.75	11.51	10.47	0.003	Ba = Uc > Fr, Oc = Fr	12,276
Sebastes spp. larvae	4.72	6.76	2.83	1.43	0.017	Oc > Ba = Uc, Fr > Uc	163

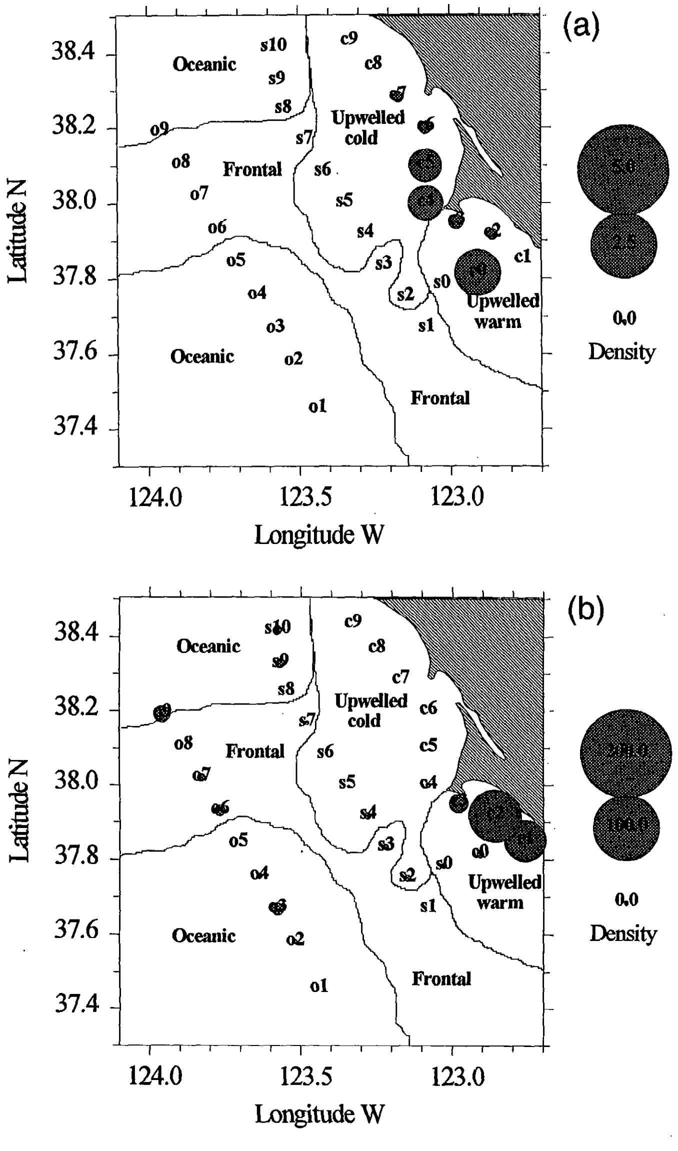

Fig. 7. Horizontal distribution of "coast" megalopae (a) and zoeae (b) and contours of water type for 1994 sampling. Abundance is in units of larvae/m².

larvae of meroplanktonic coastal species are not transported offshore or equatorward during upwelling, but are retained in areas where they can successfully settle and develop to reproduce. While some larval types may be found in the region during all stages of their development, others only enter the region, as late-stage larvae from offshore waters, as a conduit to the nearshore. For example, when comparing broad taxonomic groupings, the peak in the distributions of all stages of crab larvae are nearshore in the upper Gulf, while the rockfishes are distributed offshore, with larvae seemingly only entering the nearshore at the flow reversal along the separation front. This result is consistent with the patterns of dispersal of drifters observed off of the coast of Oregon (Barth pers. comm.); those released on the shoreward side of the coastal jet are retained at coastal retention sites and those released seaward of the jet are retained offshore and are then transported seaward.

Physical features observed in the northern Gulf during both years include the front on the northern edge of the outflow of San Francisco Bay and the separation front at Point Reyes, where the coastal jet formed during upwelling separates from the coast to form a cold offshore filament. Such predictable features form the basis of the physical influence on distribution of meroplankton in this region. The separation front that is found during upwelling off of Point Reyes represents the southern boundary for the coastal jet that dominates flow during upwelling favorable winds on the inner shelf from Point Arena to Point Reyes. Its formation, via interaction with topography, may limit larval dispersal to the south. Other types of features, such as the front formed by the San Francisco Bay outflow, may also limit equatorward transport during upwelling.

South of Point Reyes we observe that total crab larval concentrations are high. This result is consistent with the observation that crab settlement is high and occurs during upwelling favorable winds in this region (Wing et al. 1995*b*). The accumulation of cancrid and "coastal" crab larvae to the south of Point Reyes and relatively low numbers of larvae to the north of the Point were reflected in the relative settlement of crabs at Point Reyes and Bodega Head during the two cruises. In both years, collectors at Point Reyes received a higher rate of settlement (Wing et al. unpubl. data).

Observations of groups of meroplankton that have similar characteristics in terms of size, larval timing, and release areas provide a basis for general conclusions regarding the

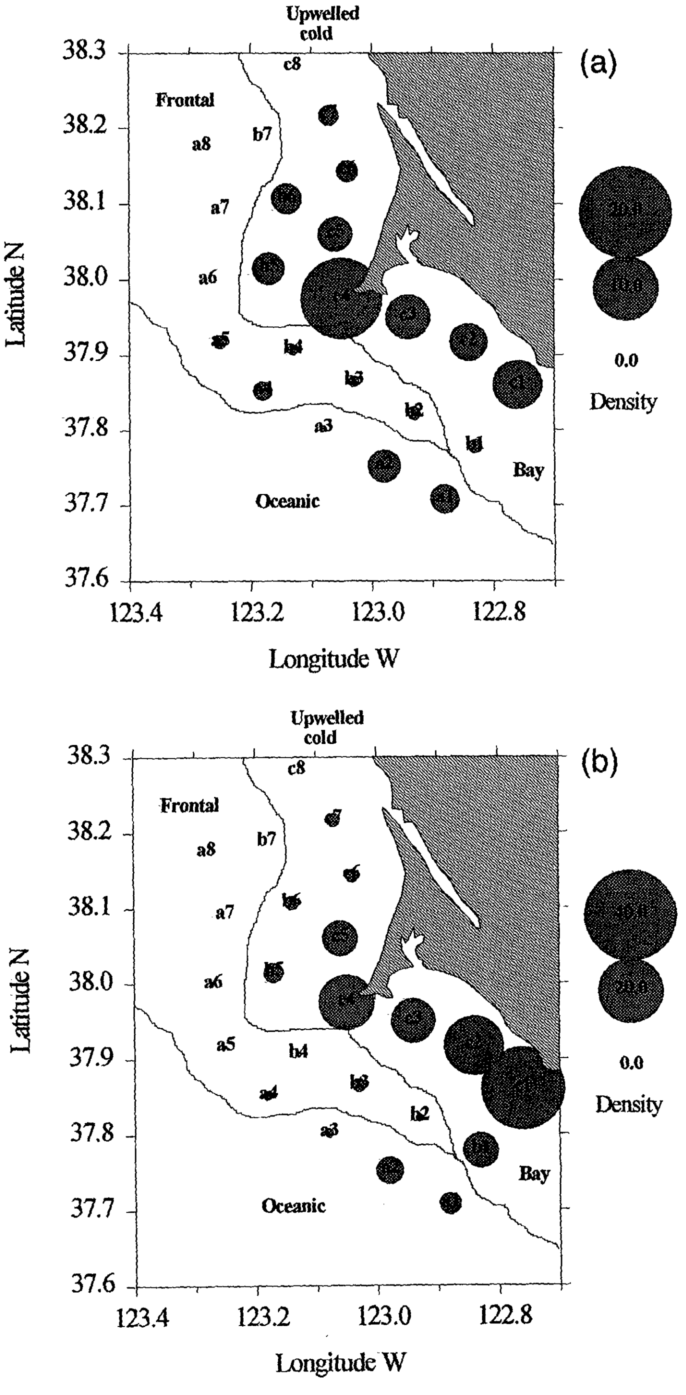

Fig. 8. Horizontal distribution of "coast" megalopae (a) and zoeae (b) and contours of water type for 1995 sampling. Abundance is in units of larvae/m^2.

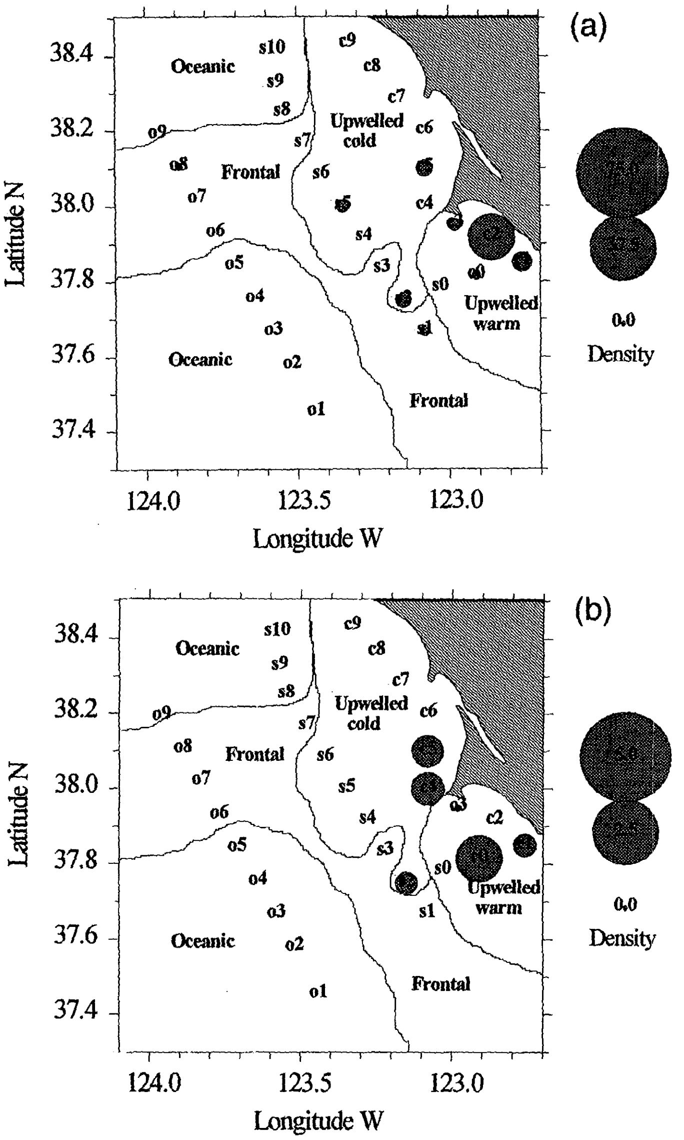

Fig. 9. Horizontal distributions of *Pinnixa* sp. megalopae (a) and zoeae (b) and contours of water type for 1994 sampling. Abundance is in units of larvae/m^2.

biological influence on distribution relative to the physical influences cited above. Differences in diel changes in vertical distribution contribute to the differences seen in horizontal distribution via interaction with flow structures within the retention zone. For example, we observe that larvae that reside in the surface layers are found in association with the Bay outflow and the buoyancy front at its edge. In contrast, larvae that migrate more strongly between surface and deep layers are found poleward of this feature, mainly in association with the separation zone on the edge of the coastal jet. In this region, surface waters are being forced strongly offshore, but flow at depth is onshore and slightly poleward. We propose that the larvae that are retained in this region can remain there because they spend daylight hours at depth out of the rapid offshore surface advection. The third behavior that we observe involves larvae that migrate within the deep layers and that are not found in large numbers on the surface. These larvae have the most polewardly skewed distributions within the retention area. Like the previous group, we propose that they are able to remain close to the edge of the coastal jet by staying out of the rapid offshore surface flow. In contrast to crab larvae, whose larvae are found most concentrated in the retention region, rockfish lar-

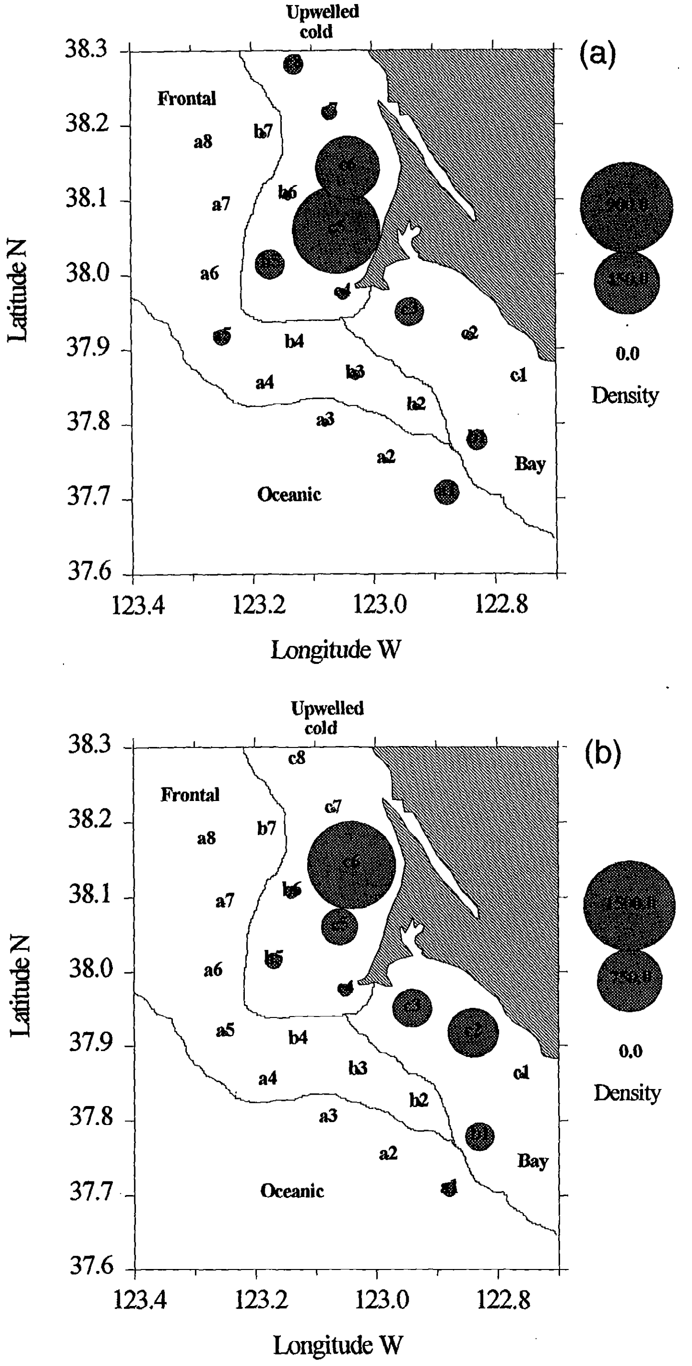

Fig. 10. Horizontal distributions of *Pinnixa* sp. megalopae (a) and zoeae (b) and contours of water type for 1995 sampling. Abundance is in units of larvae/m^2.

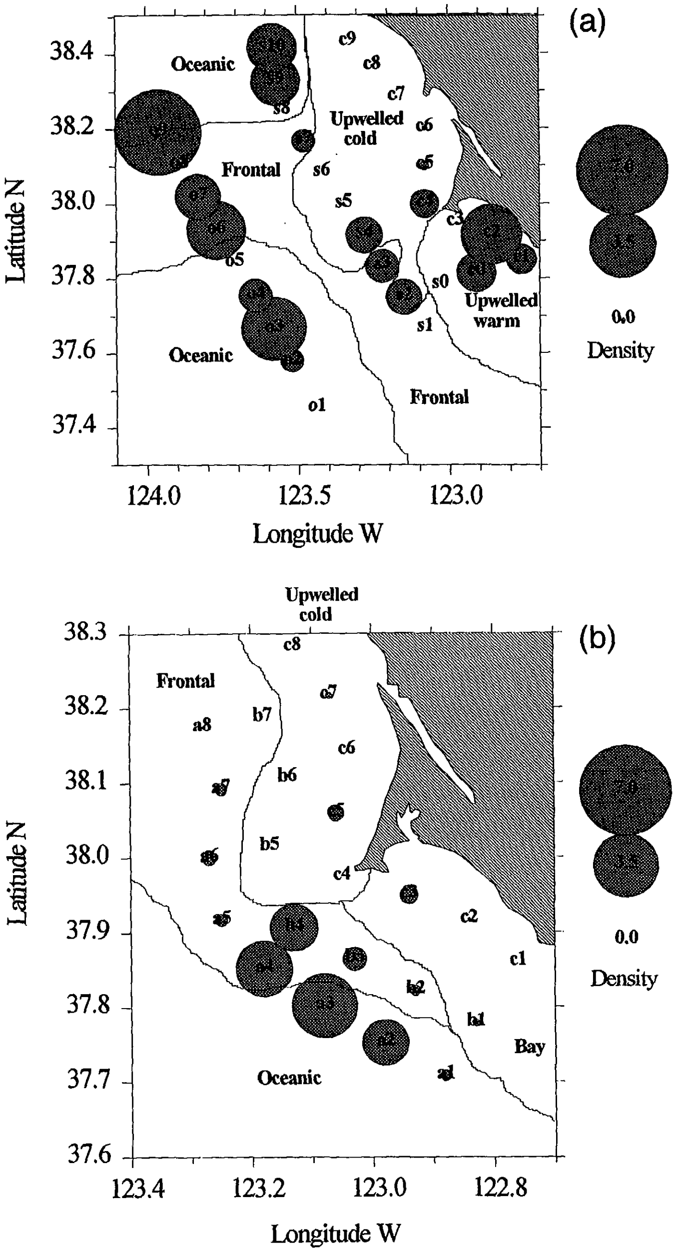

Fig. 11. Horizontal distribution of *Sebastes* spp. and contours of water type from (a) 1994 and (b) 1995 sampling. Abundance is in units of larvae/m^2.

vae appear to enter the nearshore at the separation front and enter the retention region from high offshore concentrations.

While these lines of evidence strongly support the notion that the Gulf is a retention area, several qualifications must accompany our conclusions. The use of surface temperature and salinity data to characterize water type and to identify oceanographic features does not reflect the depth stratification of temperature and salinity. In our analysis, association of larval distribution with water type is based on a surface signature of each oceanographic feature. The horizontal distributions presented represent a single observation during each year and therefore cannot provide information on temporal changes in larval distributions. Treating groups of species restricts conclusions to the broad taxonomic level, and questions regarding the complete life cycle of any one species cannot be answered. We do not describe the exact mechanism for retention in the Gulf and have limited direct observations of the meroplankton dynamics during delivery to the retention zone and poleward; however, we have many indirect observations (i.e., settlement events; Wing et al. 1995*a*,*b*).

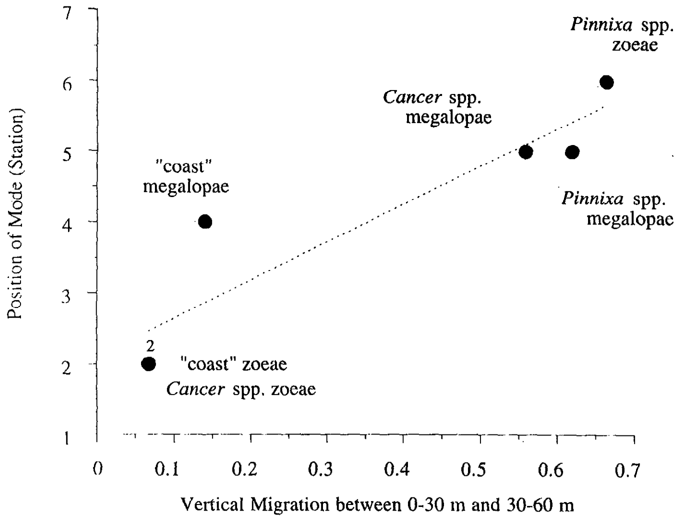

Fig. 12. For 1995 sampling, plot shows fraction of change in larval distribution between surface layer (0–30 m) during the night and deep layer (30–60 m) during the day for each taxon and stage plotted against alongshore position of the mode of distribution, as indicated by station number. Sta. 1 is at the southern end of the transect and Sta. 7 is at the northern end. $y = 2.11 + 5.35x$; $R = 0.924$.

We do not know the origins of larvae that are found in high concentrations in the Gulf. There are four possible sources for larvae retained south of Point Reyes. Larvae could enter the region from the upwelling jet by mixing or entrainment. They could also enter from California Current waters offshore of the upwelled water, when meanders and eddies move shoreward, as during relaxation. A third possible path involves larval transport from the south, with larvae possibly originating in the San Francisco Bay estuary. The fourth possible source of larvae in the retention zone involves reproduction in the Gulf itself.

The observed differences in distribution of larval groups underscore several important points regarding the interaction of meroplankton with the shifting circulation patterns of the coastal ocean in upwelling systems. Alongshore variability in offshore flow during upwelling, such as that seen in the lee of capes, is an important determinant in the dispersal paths of a broad range of larval types, ranging from fairly passive larvae to active swimming types. Each of these larval forms interacts with the flow structure of the coastal ocean in different ways, and none of their paths can be explained by a simple two-dimensional realization of flow. Rather, the complex patterns of distribution are a result of a three-dimensional Lagrangian pathway influenced by behavior and of the timing of shifts from upwelling to relaxation regimes in the flow structure. This complex array of both biotic and abiotic forcing underlies the redistribution of propagules to coastal populations.

Knowledge of the important interaction between alongshore variability in circulation and meroplanktonic distributions is essential for understanding dispersal pathways of species whose larvae move onshore to settle during the upwelling season. Lack of knowledge of the dispersal paths of larvae of meroplanktonic species is a problem that hinders both the understanding of their population dynamics and the prediction of their future responses for the purpose of harvest management. Dispersal has long been known to be a critical aspect of population dynamics; appropriate dispersal was Hjort's (1914) second hypothesis, explaining fluctuations in fish abundance, and it has recently been revived as the member/vagrant hypothesis (Sinclair 1988). Appreciation of the consequences of dispersal patterns for spatial dynamics of metapopulations is increasing (Roughgarden et al. 1988; Possingham and Roughgarden 1990; Botsford et al. 1994). In harvest management, the need for knowledge of dispersal paths is becoming increasingly apparent as managers search for reasons for fisheries collapse and as they employ spatially based management, through the use of marine reserves (e.g., Quinn et al. 1993), and rotating spatial harvest (e.g., Botsford et al. 1994). It is our hope that as population biologists focus more closely on the alongshore spatial dimension in these systems that studies such as this one will be of use in influencing spatial management of marine resources.

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Received: 3 July 1997
Accepted: 16 June 1998