

# Spatial structure of relaxation events and crab settlement in the northern California upwelling system

Stephen R. Wing<sup>1,2,\*</sup>, Louis W. Botsford<sup>1,2</sup>, John L. Largier<sup>3</sup>, Lance E. Morgan<sup>1,2</sup>

<sup>1</sup>Wildlife, Fish and Conservation Biology, University of California, Davis, California 95616, USA

<sup>2</sup>Bodega Marine Laboratory, PO Box 247, Bodega Bay, California 94923, USA

<sup>3</sup>Center for Coastal Studies, Scripps Institution of Oceanography, La Jolla, California 92093-0209, USA

**ABSTRACT:** During spring and summer 1993, we monitored settlement of crabs (primarily *Cancer* spp.) and sea urchins *Strongylocentrotus* spp. in conjunction with physical variables associated with coastal circulation to investigate how physical conditions influence the spatial distribution of recruitment along the coast. Observations were made along a 100 km stretch of the northern California coast (USA), from the Gulf of the Farallones north to Point Arena. Temperature, salinity and wind stress data indicated fluctuations in upwelling and provided evidence for the alongshore, northward flow of warm, low salinity water during upwelling relaxation events which typically lasted several days. On a weekly time scale, crab settlement was positively correlated with temperature, and negatively correlated with salinity, indicating that settlement occurred during relaxation events. Correlations were higher north of Point Reyes, where high settlement occurred only during relaxation, than south of Point Reyes, where settlement occurred both during relaxation events and to a lesser degree during upwelling. Overall crab settlement was higher south of Point Reyes. On a daily time scale, crab settlement north of Point Reyes was associated with the sharp increase in temperature observed as the relaxation current reached that point on the coast. This association suggested that crabs were transported northward alongshore in the thermal front which propagated northward during each relaxation event. This along-shore transport mechanism may be responsible for the predictable pattern of settlement variability within this system: with continuous, event-modulated settlement south of Point Reyes and episodic, event-dependent settlement to the north. Similar physical/biological interactions may occur at other points along this coast and along the midlatitude boundaries of other oceans.

**KEY WORDS:** Settlement · Upwelling · Space

## INTRODUCTION

One of the obstacles to understanding the population dynamics of meroplanktonic, benthic marine invertebrates such as crabs and sea urchins is a lack of understanding of the causes of spatial variability in settlement and recruitment. While the recruitment dynamics of individual subpopulations of benthic invertebrates with dispersing larvae has been studied extensively (Underwood & Denley 1984, Connell 1985, Gaines & Roughgarden 1985, Roughgarden et al. 1985, 1988, Holm 1990), they are usually treated as separate, 'open' populations receiving a constant supply of

propagules from an exogenous source. There is little understanding of the alongshore, spatial component of recruitment variability over the range of the complete, closed metapopulation formed by a number of subpopulations connected by larval dispersal. This variability is a consequence not only of differing habitat along the coast, but also of temporal and spatial variability in dispersal patterns within the metapopulation. Recent studies have shown that the latter may be as important to regional metapopulation dynamics as life history characteristics such as mortality rates and reproductive rates are to local subpopulation dynamics (e.g. Pulliam 1988, Possingham & Roughgarden 1990, Botsford et al. 1994, Hastings & Higgins 1994). In spite of this importance, the mechanisms controlling variability in along-

\*E-mail: wing@megalonga.ucdavis.edu

shore dispersal between subpopulations have not been well studied (cf. Gaines & Bertness 1993a, b).

Dispersal patterns of marine meroplanktonic larvae can be studied in a number of ways. Physical models of circulation in the coastal ocean can be used to infer movement of zooplankton with specific physical and behavioral characteristics (Hofmann et al. 1991, Botsford et al. 1994). Direct observation has been limited to species with relatively large larvae that disperse over relatively short distances (e.g. Olson 1985, Davis & Butler 1989, Carlon & Olson 1993). Another approach is to compare temporal variability in settlement at different locations on a variety of scales from meters to many kilometers (e.g. Caffey 1985, Judge et al. 1988, Rumrill 1988, Raimondi 1990, Sewell & Watson 1993). A fourth approach, the one taken here, seeks to identify the physical mechanisms underlying larval dispersal by observing larval distributions and settlement over space and time concurrently with physical oceanographic conditions (e.g. Pedrotti & Fenaux 1992).

In the California Current, mesoscale oceanographic features associated with wind forced currents and coastal topography may be important sources of settlement variability for some benthic invertebrates. The dynamics of wind driven coastal upwelling in the California Current have been linked to settlement and recruitment in several ways. For example, Ebert & Russell (1988) argued, based on adult size distributions, that recruitment of purple sea urchins is strongly affected by the mesoscale variability in upwelling associated with headlands in northern California, USA. Graham et al. (1992) identified differences in zooplankton distribution between an 'upwelling shadow' in Monterey Bay, south of Point Año Nuevo, California, and adjacent waters. Investigators concerned specifically with recruitment of Dungeness crab have observed correlations between recruitment and upwelling (Peterson 1973, Botsford & Wickham 1975), alongshore winds (Johnson et al. 1986) and alongshore geostrophic flow (McConnaughey et al. 1992). Recent studies monitoring barnacle recruitment have shown that larvae only return to settle in the intertidal zone during periods of upwelling relaxation, when the upwelling 'front' moves cross-shelf and 'collides' with the shore (Farrell et al. 1991, Roughgarden et al. 1991).

To explain the temporal variability in crab settlement north of Point Reyes off northern California during 1992, Wing et al. (1995) proposed that settlement was associated with alongshore as well as cross-shelf transport during upwelling relaxation. During the upwelling season on the northern California coast there are periods when cessation or slight reversal of upwelling winds results in an alongshore flow of

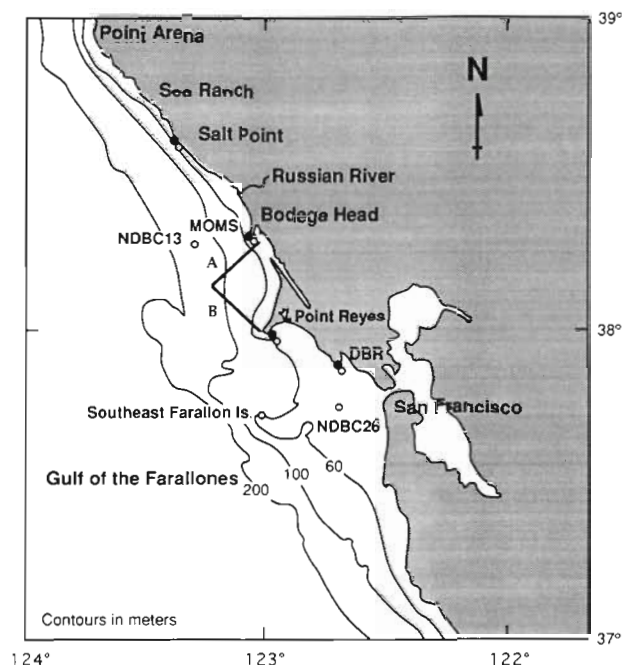


Fig. 1. Location of settlement sites (●) and oceanographic sampling sites, meteorological buoys (○), and 2 transects for CTD and plankton samples (A and B)

warm, low salinity water from the Gulf of the Farallones, poleward along the coast north of Point Reyes (Send et al. 1987, Largier et al. 1993, Wing et al. 1995) (Fig. 1). These relaxation currents are partially buoyancy forced and, by virtue of Coriolis effects, they remain coastally trapped as they flow poleward. They move alongshore over the inner shelf and midshelf from Point Reyes as far north as Point Arena. From the observation that crab settlement at Bodega Head, California, was associated with increasing temperature, Wing et al. (1995) proposed that planktonic crab larvae that had either accumulated in the Gulf of the Farallones or had moved onshore there were transported northward in such an alongshore coastal flow during upwelling relaxation. However, this study lacked information on the spatial variability of settlement across the region needed in order to compare the Gulf of the Farallones with points to the north.

The study described here is an attempt to improve our understanding of this potential mechanism by monitoring settlement and temperature at 4 points along the coast and investigating the spatial pattern of the observed association between settlement and temperature. Here we measured spatio-temporal patterns of larval settlement rates for several species of crabs (particularly *Cancer* spp.) and 2 species of sea urchins (*Strongylocentrotus* spp.) nearshore at Duxbury Reef (37° 53' N, 122° 42' W) within the Gulf of the Farallones; Point Reyes (37° 59' N, 122° 58' W) at the north-

ern limit of the Gulf of the Farallones; Bodega Head (38° 18' N, 123° 04' W) and Salt Point (38° 33' N, 123° 19' W) along the California coast north of Point Reyes but south of Point Arena (Fig. 1). We also measured cross-shelf distributions of planktonic crab larvae at Bodega Head during a relaxation feature. The resultant patterns of settlement were compared with time series of temperature collected at each site as well as temperature (including satellite images), salinity, wind velocity and sea level height from offshore and on-shore sites. Results from this study elucidate a mechanism that may influence the spatial scale and magnitude of settlement variability across a large part of the northern California coast.

### LARVAL LIFE HISTORIES

Because prevailing winds and currents vary seasonally along this coast, the way in which local circulation will influence settlement during the late larval period depends in part on the date of release and length of the larval period. During winter and early spring, near-shore flow near the surface is predominantly poleward and onshore. During spring (typically March–April), the winds shift from southerly to northerly, an event referred to as the spring transition (cf. Strub et al. 1987). Nearsurface water moves offshore and upwelling begins, leading to a strong equatorward jet over the shelf (cf. Largier et al. 1993, Wing et al. 1995). Larvae released nearshore earlier in the year, before upwelling begins, are likely to be found offshore of the coastal zone of upwelled water because they would have been transported offshore with these surface waters. Larvae released later, on the other hand, may be found within the cool upwelled water and are likely to be transported southward rapidly (cf. Richardson & Pearcy 1977, Richardson et al. 1980).

Although the timing of larval release and development periods is not well known for all of the species of interest here, some generalities can be drawn. *Cancer* crabs are ovigerous early in the year and have relatively long larval periods, 80 to 160 d (Strathmann 1987). Dungeness crab *Cancer magister* larvae are released nearshore (<50 m) between December and March (Waldron 1958, Wild 1983), and may settle nearshore in May and June (Poole 1966, Carrasco et al. 1985, McConnaughey et al. 1992). *C. productus* is ovigerous between October and January and generally settles between February and September with peak settlement 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. 1995). The porcellanid

group (*Pachycheles* spp. and *Petrolistes* spp.) can be ovigerous in February through April; however, a second brood may be produced as late as August. This group has short larval periods, generally 34 to 40 d (cf. MacMillan 1972). Settlement of *Pugettia* spp. and *Loxorhynchus* spp. occurred in May–June at Bodega Head during the 1992 season; however, we lack information regarding the local reproductive timing and larval period (Wing et al. 1995). Spawning of red sea urchins *Strongylocentrotus franciscanus* may occur from March through July (Strathmann 1978, Kato & Schroeter 1985), and purple sea urchins from December through June (Pearse et al. 1982, Strathmann 1987). Larval periods estimated from laboratory studies are 7 to 19 wk for *S. franciscanus* and 4 to 12 wk for *S. purpuratus* (Strathmann 1978, Cameron & Schroeter 1980). In 1992, spawning of *S. franciscanus* occurred in April, and settlement of both species peaked in July in northern California (Wing et al. 1995).

To summarize, we studied several taxonomic groups within which species share similar characteristics. *Cancer* spp. crabs are released primarily before the spring transition and have a larval period that extends beyond the spring transition. Porcellanid crabs and purple sea urchins can be released both before and after upwelling starts, and have shorter larval periods. Red sea urchin larvae are released near the time of the spring transition or later, and they have a relatively short larval period.

### MATERIALS AND METHODS

**Oceanographic data.** Oceanographic data used in this study were collected from a variety of sources. We obtained satellite AVHRR (advanced very high resolution radiometer) images of the region from the U.S. National Oceanic and Atmospheric Administration (NOAA), and time series of temperature from the Bodega Marine Laboratory (BML) at Bodega Head, NOAA buoys NDBC 46013 (38° 14' N, 123° 20' W), NDBC 46026, (37° 45' N, 122° 42' W) and the Southeast Farallon Island field station (37° 42' N, 123° 00' W) (Fig. 1). We also collected temperature time series at the 10 m isobath for each of our settlement collection sites at Duxbury Reef, Point Reyes, Bodega Head and Salt Point with small *in situ* temperature sensors sampling temperature at 24 min intervals. Salinity time series were collected at BML and Southeast Farallon Island; wind velocity and subsurface pressure were also collected at BML. BML data were collected as 20 min averages. Daily subsurface pressure data were obtained from a piezoelectric transducer mounted at 10 m depth off of Bodega Head. We filtered the 20 min data to remove tidal and diurnal signals using the WHOI PL64 filter (Limeburner 1985).

Cross-correlations between daily alongshore (317°) wind stress at NB 46013 for April 1 through September 18, 1993 (Days 91 to 261) and daily temperature at each site were calculated for lags from 0 to 10 d following the methods of Kope & Botsford (1988). 95 % confidence intervals were calculated from the time series sample size ( $n = 160$ ).

In addition, we collected information on temperature and salinity structure of the inner shelf during several upwelling and relaxation events. CTD (conductivity, temperature, depth) casts were made at 1.5 km intervals running out 15 km at 240° from BML (line A in Fig. 1), returning alongshore to the northern tip of Point Reyes (line B, Fig. 1). On these transects we also collected plankton from the surface layers (1 to 3 m) using a 1 m<sup>2</sup> Bongo net (115 µm mesh). Plankton samples were preserved in ethanol and sorted for presence of crab and sea urchin larvae.

**Settlement.** Settlement of crabs and sea urchins was determined roughly weekly from April 1 until September 4, 1993 (Days 91 to 247) at 4 sites along the coast: Duxbury Reef, Point Reyes, Bodega Head, and Salt Point (Fig. 1). At each site, we deployed 6 collectors over a 100 m length of the 10 to 12 m isobath. These arrays of collectors were exposed to the dominant ocean swell and on a rocky substratum. Retrieval of settlement collectors occurred on a 7 to 10 d interval and collectors at all sites were retrieved within a 24 to 48 h period when possible. During the period from July 18 until August 8, 1993 (Days 199 to 220), which overlapped an alongshore relaxation event, we sampled settlement at Bodega Head on a 2 to 4 d retrieval schedule separate from our regular weekly regime.

Each settlement collector consisted of four 7 inch (ca 18 cm), wood-backed scrub brushes with polypropylene bristles, attached to a polypropylene line with net floats for buoyancy, anchored to the bottom with a 25 kg cement anchor so that when deployed they floated 0.5 to 1 m above the bottom. Upon retrieval, the collectors were washed in fresh water, and the resulting material was sorted for newly settled crabs and sea urchins which were fixed in ethanol for later identification.

Species identifications for crabs was accomplished using guidelines from Lough (1975) and Smith & Carlton (1975). We identified 9 species of juvenile crabs: *Cancer antennarius*, *C. productus*, *C. magister*, *Pachycheles* spp., *Petrolistes* spp., *Loxorhynchus* spp., *Pugettia* spp., *Pagurus* spp., *Hemigrapsus* spp.; several species of megalopal stage larvae were also found. Sea urchins were identified using the methods of Rowley (1990) and R. Emlet (pers. comm.). We identified 2 species of sea urchins: *Strongylocentrotus franciscanus* and *S. purpuratus*. For this analysis we separated the crabs into 2 groups: *Cancer* spp., consisting of *C.*

*antennarius*, *C. productus* and *C. magister*; and total crabs, including all crab species.

Correlations between settlement of *Cancer* spp. and total crabs with site temperature were calculated by averaging site temperature over each settlement sampling period and calculating the correlation for the time series using a standard linear correlation statistic (Sokal & Rohlf 1981). 95 % confidence levels were calculated based on sample size for each site ( $n = 15$  to 18). Correlations between settlement and salinity at Bodega Head were calculated by the same method. These correlations were calculated for the whole study period first; due to concern that the correlations were dominated by a single event in the early part of the season, we then calculated the correlations for the later part of the season separately (Days 163 to 247).

Intersite correlations for settlement of total crabs and *Cancer* spp. were calculated by obtaining averages of the settlement time series of all 4 sites over synchronous sampling periods ( $n = 13$ ). Sample periods that were collected within 24 h were considered synchronous in this analysis. These correlations were also scrutinized with a 95 % confidence limit (i.e.  $R > 0.541$ ).

## RESULTS

### Upwelling and relaxation features during 1993

The 1993 upwelling season was marked by one major and several other relaxation events (Fig. 2). As in 1992 (Wing et al. 1995), temperature and salinity showed the expected response to periods of upwelling and relaxation in most instances. Periods of high equatorward alongshore wind stress (Fig. 2a) typically resulted in decreases in temperature (Fig. 2b) and sea level (Fig. 2d) and increases in salinity (Fig. 2c). Relaxation in equatorward wind stress resulted in lagged increases in temperature and sea level and decreases in salinity (Fig. 2). There were significant negative correlations between wind stress at NB 46013 and temperature for each of the study sites for lags from 0 to 10 d, typical of upwelling dynamics (cf. Brink 1983, Lentz 1987) (Fig. 3).

The extent to which temperature changes are due to surface heating can be estimated from calculation of the amount of solar warming to be expected based on the bulk equations of Gill (1982; meteorological data including solar irradiance are available from BML). This indicated that, as in 1981–1982 (Send et al. 1987) and 1992 (Wing et al. 1995), the water warmed faster than could be explained solely by solar heating (Fig. 2). Advection of warm water into the region is necessary to explain the rapid increase in water temperature. Similarly, advection is necessary to explain the con-

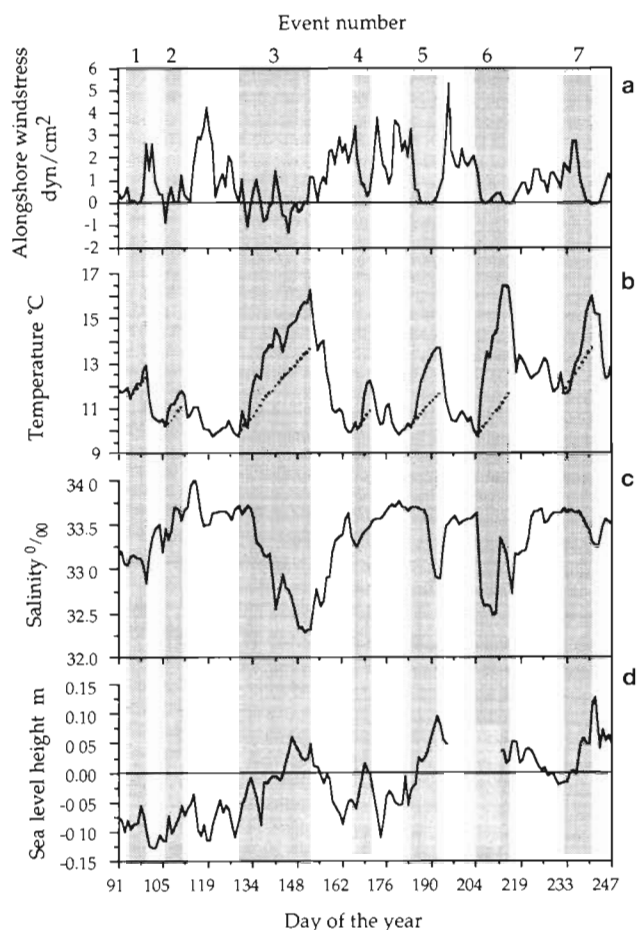


Fig. 2. Oceanographic and meteorological variables from Bodega Marine Laboratory and NB 46013: (a) daily average wind stress from  $317^\circ$  at NB 46013 (i.e. positive values are alongshore equatorward), (b) daily average temperature at 10 m (dotted lines are the calculated surface warming for each relaxation period), (c) daily average salinity and (d) deviations from daily average sea level height. Shaded areas: relaxation events on the basis of temperature increases greater than those predicted by solar warming of the surface (cf. Send et al. 1987). Blank area in sea level height record is a group of missing data.

comitant decrease in salinity during the longer relaxations in upwelling wind.

It is this correlated temperature-salinity signal, in response to relaxation in local upwelling winds, that we used as an indication of an advective inflow of non-upwelled water. Warm poleward flows over the shelf were observed directly in current-meter data from relaxation events during the Coastal Ocean Dynamics Experiment (CODE) and the Northern California Coastal Circulation Study (NCCCS) which showed that during relaxations there is a poleward flowing warm water current along the inner shelf that may extend from the Gulf of the Farallones as far north as Point Arena. These features can be seen clearly in ear-

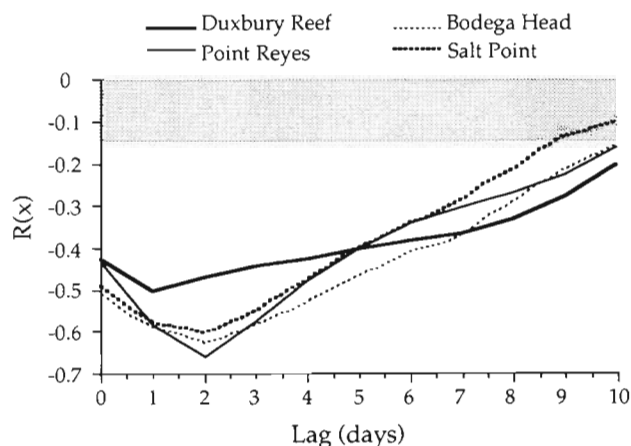


Fig. 3. Correlations between alongshore wind stress (at NB 46013) and temperature at each of the 4 settlement sites calculated for April 1 through September 18, 1993 (Days 91 to 261). Sample size for the time series with lags calculated from 0 to 10 d is 160,  $p < 0.05$  at  $R > 0.154$ . Shaded region: 95% confidence limit. Note the lag in cooling at all sites typical of coastal upwelling.

lier AVHRR images of the region [e.g. Send et al. (1987, Plate 1), Largier et al. (1993, Fig. 7b) and Wing et al. (1995, Fig. 6)]. Similar warming events during 1993 are marked as shaded bars in Fig. 2. These are periods when the rate of warming is greater than that due to calculated surface heating, and temperature rises by more than  $1^\circ\text{C}$ . Calculated surface heating is marked as a dashed line for each of these warming periods. Note that Events 1, 2 and 4 were very weak warming periods and probably do not reflect significant along-shore flow. In contrast, Events 3, 5, 6 and 7 were longer lasting, exhibiting large increases in temperature and concomitant decreases in salinity.

Patterns of near-coastal circulation during upwelling and relaxation are well represented by AVHRR images from 1993. A typical pattern of surface temperature during upwelling shows a center of cooler water next to the coast just south of Point Arena, extending in a jet equatorward and offshore near Point Reyes (Fig. 4a). Note the anticyclonic flow immediately to the south of Point Reyes in Drakes Bay, suggesting entrainment of newly upwelled and offshore water into the region. Also note larger-scale eddy features centered offshore of Point Arena and in the Gulf of the Farallones. An image from later in the season illustrates a relaxation event involving a coastally trapped warm feature propagating poleward on the inner shelf (Fig. 4b). Between Days 212 (July 31) and 214 (August 2) during relaxation Event 6 this feature moved from just north of Bodega Head to just south of Point Arena (image not shown) in the 49 h between the 2 images. AVHRR images from other relaxation periods in the 1993 season show similar patterns.

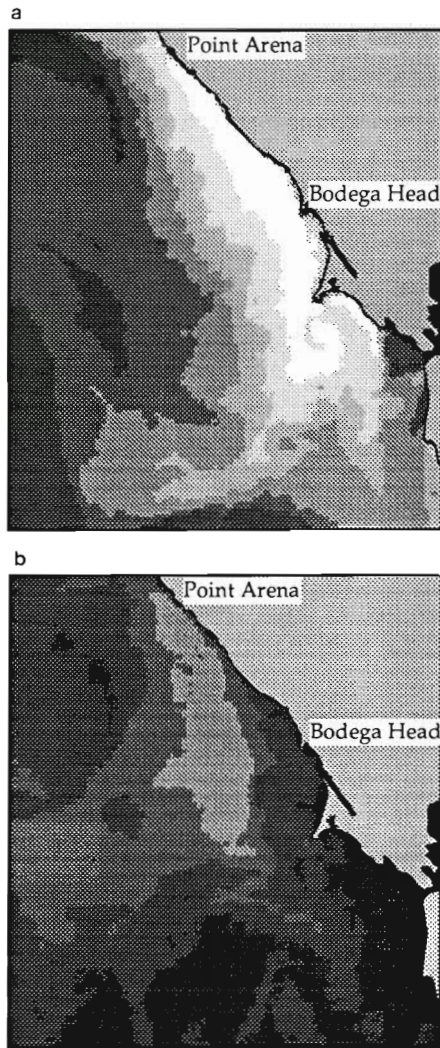


Fig. 4. AVHRR images of surface temperature on Days (a) 163 (June 12, 23:00 h GMT), (b) 212 (July 31, 15:00 h GMT). The temperature scale ranges from approximately 9°C light grey to approximately 16°C for the darkest grey

The spatio-temporal patterns of flow during upwelling and relaxation are reflected in the temperatures recorded at the array of coastal thermistors. Warm water events vary in duration and alongshore extent, being more frequent and lasting longer at the Gulf of the Farallones sites, while more episodic and ephemeral on the coast north of Point Reyes (Fig. 5). Temperature increases occur sequentially from south to north, especially during the later part of the season, whereas temperature decreases occur more synchronously alongshore (cf. Fig. 6).

Surface temperature differences between the offshore sites (i.e. the 2 offshore buoys and Southeast Farallon Island), and the onshore sites (i.e. Bodega Head, Point Reyes and Duxbury Reef) indicate the cross-shelf thermal differences during upwelling and relaxation

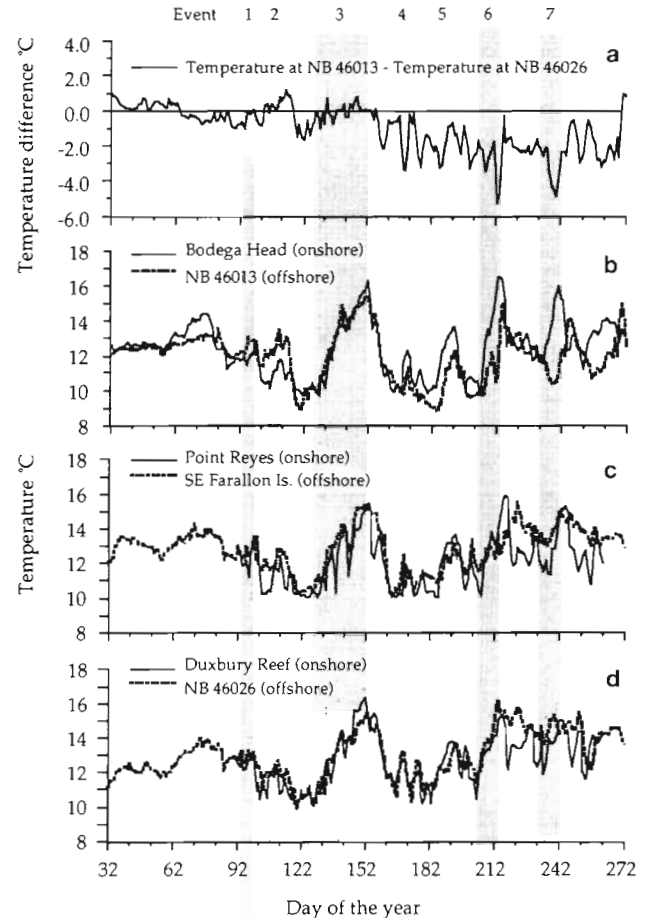


Fig. 5. Spatial differences in average daily temperature: (a) north-south difference in temperature indicated by differences between NOAA buoys NB 46013 and NB 46026; (b to d) temperatures at cross-shelf pairs of stations. Solid lines: onshore sites; dashed lines: offshore sites (as indicated in Fig. 1)

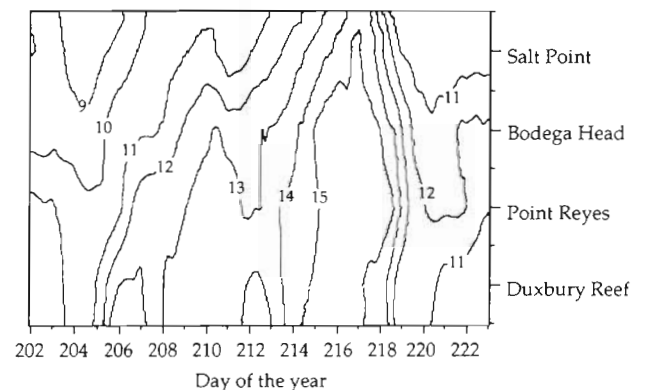


Fig. 6. Spatial variability of temperature during Event 6 shows progression of warming from south to north across the 4 settlement sites as the alongshore current propagates poleward during Days 205 to 216 (July 24 to August 4). Note the rapid and more uniform cooling at all sites marking the beginning of upwelling on Day 218 (August 6). Temperature is collected as daily averages at 10 m at each settlement site

(Fig. 5). During the later part of the season (i.e. after Day 152, June 1), it was generally warmer in the Gulf of the Farallones than north of Point Reyes (Fig. 5a), providing a reservoir of warm low-density water which could propagate northward as a buoyancy current. During relaxation events in this late summer period, warming at NB 46013 occurred later than warming at Bodega Head (Fig. 5b), indicating that the front of this thermal feature was at an angle to the coast (roughly NE-SW), consistent with the wedge shape evident in satellite images (cf. Fig. 4b). Cooling, on the other hand, occurs relatively synchronously at the onshore and offshore sites. This same lag in warming was not seen between the 2 southern comparison sites in the Gulf of the Farallones (Fig. 5c, d), indicating that warming and cooling occurred closer to the same time nearshore than offshore (i.e. onshore advection or broad alongshore advection). During the early part of the season (i.e. before Day 152), there was no persistent temperature difference between north and south (Fig. 5a), and relaxation events involved uniform shelf-wide warming, suggesting onshore relaxation flows. An exception was warming Event 2.

The physical conditions associated with relaxation Event 2 are of special interest because of an unusually large settlement of purple sea urchins and porcellanid crabs, primarily at Point Reyes. During the upwelling period prior to relaxation Event 2, coastal temperatures dropped 3°C to about 10°C while offshore temperatures decreased only slightly, resulting in a cross-shelf temperature difference over the shelf at Bodega Head (Fig. 5b) and at Point Reyes (Fig. 5c), but no substantial difference at the most southern pair of stations (Fig. 5d). When the wind subsided on Day 104, the warmer water returned to shore at Point Reyes, but not at Bodega Head where the cross-shelf temperature difference persisted.

### Settlement results

Weekly settlement data show a large early season peak (Days 91 to 119) for crabs other than *Cancer* spp. (mainly due to porcellanid crabs) at Point Reyes, but low settlement at the other sites (Figs. 7 & 8). This early season event accounted for 45% of the total crab settlement at Point Reyes during the study period. Also during this period there was a large settlement of sea urchins that accounted for 100% of seasonal settlement at Point Reyes. As described above, coastal temperature had increased and the cross-shelf temperature difference had disappeared at Point Reyes, which may indicate the arrival of non-upwelled water during this event (Fig. 5). At the other coastal sites, temperatures did not decrease, indicating that the non-

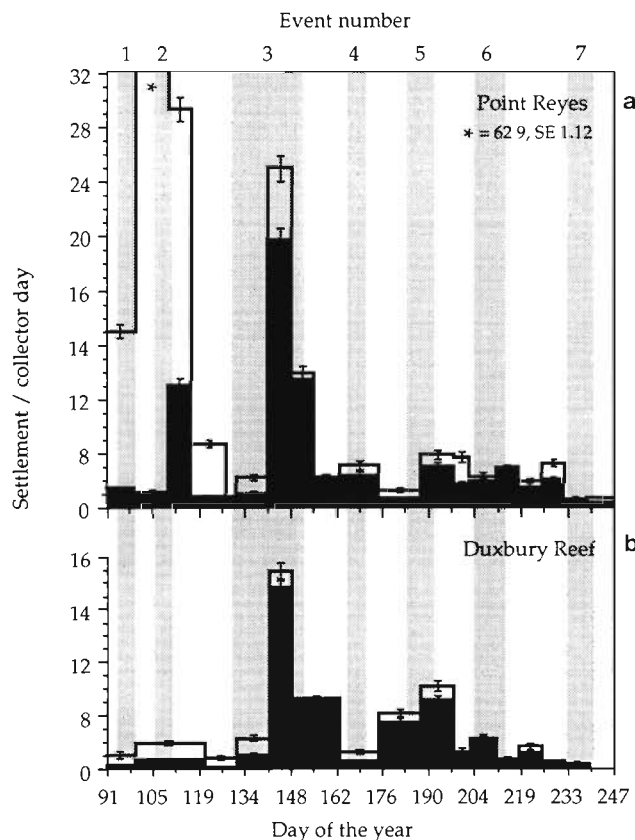


Fig. 7 Settlement per collector day of total crabs (solid line) and *Cancer* spp (dark bars) at the 2 Gulf of the Farallones sites: (a) Point Reyes, (b) Duxbury Reef. Each value in the time series shows the beginning and end of a sample period as width of the bars. SEs are based on an assumed Poisson distribution. Shaded regions: warming events as calculated in Fig. 2

upwelling water did not intersect the coast at the other sites.

Following this event there was a large settlement of *Cancer* spp. at all 4 sites during Event 3, a region-wide relaxation from upwelling conditions that lasted 24 d. In terms of total crab abundance, this event was a large fraction of total settlement for the season, particularly at the 2 northern sites: Salt Point (30%) and Bodega Head (38%) versus 10% at Point Reyes and 25% at Duxbury Reef. For *Cancer* spp. settlement, this event accounted for 56% at Salt Point, 20% at Bodega Head, 28% at Point Reyes, and 28% at Duxbury Reef. Following this large settlement event in late May, there was a series of smaller settlement events at the 2 northern sites that were associated with shorter relaxation events (Fig. 8). However, at the southern sites, settlement of crabs did not appear to be dependent on warming events, and settlement stayed relatively high even during upwelling conditions (Fig. 7).

Intersite correlations indicated different alongshore settlement patterns for different taxa. *Cancer* spp. set-

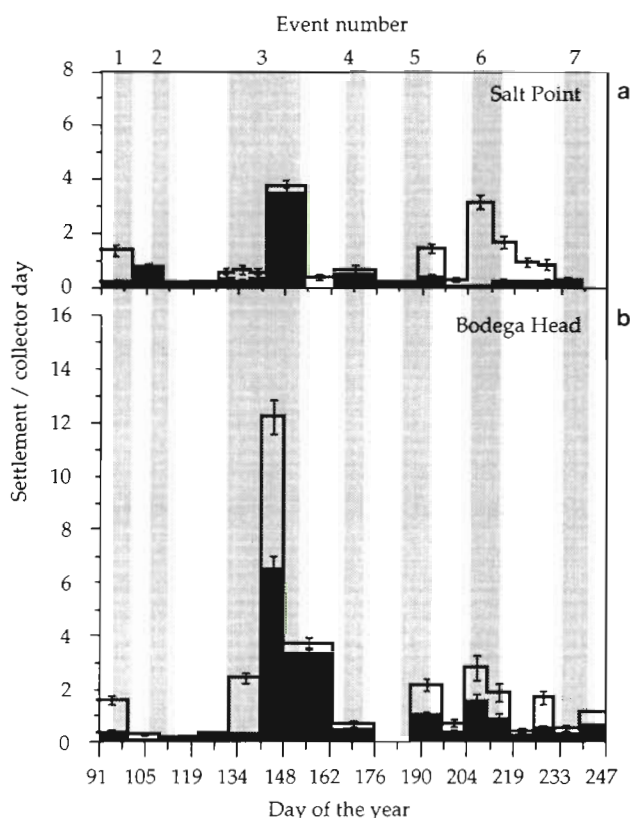


Fig. 8. Settlement per collector day of total crabs (solid line) and *Cancer* spp. (dark bars) at the 2 northern sites; (a) Salt Point, (b) Bodega Head. Each value in the time series shows the beginning and end of a sample period as width of the bars. SEs are based on an assumed Poisson distribution. Shaded regions: warming events as calculated in Fig. 2

tlement was highly correlated between sites (Table 1), reflecting an apparent synchrony of *Cancer* crab settlement across the 4 sites. It should be noted that this correlation is largely due to the high settlement during Event 3. While intersite correlations for total crabs were significant between the 2 northern sites and Duxbury Reef, correlations for total crab settlement between Point Reyes and the other 3 sites were not significant. This result is primarily due to the large early season settlement of crabs other than the *Cancer* species, which occurred only at Point Reyes (Table 1).

Correlations of total crab and *Cancer* spp. settlement during each sample period with average temperature for that sample period at that site indicated a stronger association of settlement with warm events at the northern sites (Bodega Head and Salt Point) than at the 2 southern sites (Table 2). A similar pattern

Table 1. Correlations among total crab and among *Cancer* spp. settlement at different sites. Numbers in bold indicate significant correlations [i.e.  $p > 0.05$  at  $R(x) > 0.541$ ,  $n = 13$ ]

	Salt Point	Bodega Head	Point Reyes	Duxbury Reef
Total crabs				
Salt Point	1	<b>0.693</b>	-0.027	0.329
Bodega Head		1	0.0729	<b>0.682</b>
Point Reyes			1	0.0931
Duxbury Reef				1
<i>Cancer</i> spp.				
Salt Point	1	<b>0.908</b>	<b>0.968</b>	<b>0.733</b>
Bodega Head		1	<b>0.938</b>	<b>0.804</b>
Point Reyes			1	<b>0.777</b>
Duxbury Reef				1

existed for the negative correlation between settlement at each site and average salinity during each sample period at Bodega Head (Table 2). At the Point Reyes site, correlations of total crab settlement with site temperature and with salinity at Bodega Head are near zero because settlement was dominated by the influence of the unique, early season porcellanid settlement event (Table 2). In fact, most of these correlations at Point Reyes are significant, despite a reduced sample size, if the early season event is removed (total crabs vs site temperature,  $R = 0.473$ ; *Cancer* spp. vs site temperature,  $R = 0.528$ ; total crabs vs salinity at Bodega Head,  $R = -0.650$ ; *Cancer* spp. vs salinity at Bodega Head,  $R = -0.714$ ) ( $n = 14$ ; i.e.  $p < 0.05$  at  $R = 0.521$ ).

These patterns indicate that settlement north of Point Reyes occurs during conditions associated with relaxation (i.e. lower salinity and increased temperature), whereas in the Gulf of the Farallones, settlement occurs more persistently, even during upwelling conditions. Although it may appear that this result is dependent on Event 3, correlations between salinity at Bodega Head and total settlement at Bodega Head ( $R = -0.868$ ) and Salt Point ( $R = -0.769$ ) remain significant

Table 2. Correlations of total crab and *Cancer* spp. settlement with average site temperature and salinity at Bodega Head for each sample period. Numbers in bold indicate significant correlations,  $p < 0.05$

	Site temperature versus:		Salinity at Bodega Head versus:		Sample size
	Total crab	<i>Cancer</i> spp.	Total crab	<i>Cancer</i> spp.	
Salt Point	<b>0.655</b>	<b>0.667</b>	<b>-0.788</b>	<b>-0.616</b>	17
Bodega Head	<b>0.650</b>	<b>0.622</b>	<b>-0.742</b>	<b>-0.763</b>	16
Point Reyes	-0.062	0.447	-0.081	<b>-0.549</b>	18
Duxbury Reef	0.349	0.417	<b>-0.588</b>	<b>-0.621</b>	15

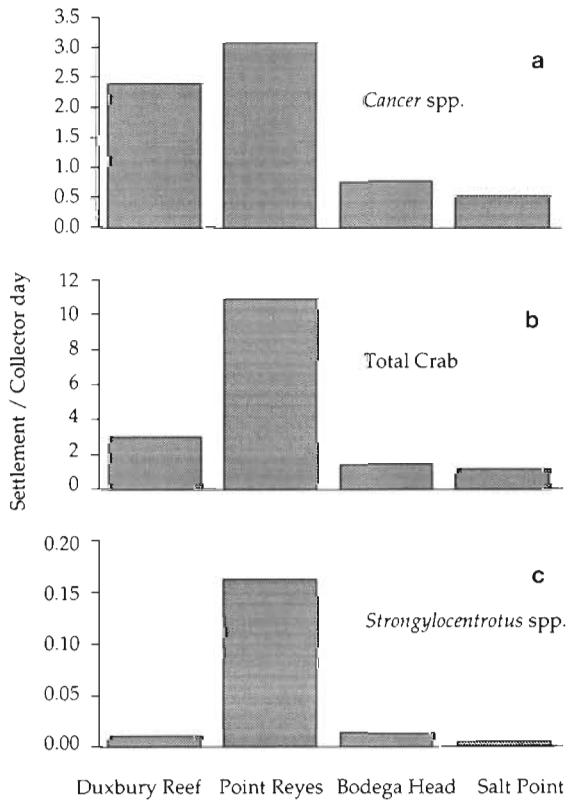


Fig. 9. Distribution of total seasonal settlement rate (per collector day) at each settlement site for the 3 taxonomic groups. Sample sizes for collection periods were: Salt Point 17, Bodega Head 16, Point Reyes 18 and Duxbury Reef 15. Collections were made from April 1 (Day 91) through September 4, 1993 (Day 247)

when the influence of Event 3 is removed by calculating correlations for Days 163 to 247 ( $n = 10$ ,  $p < 0.05$  at  $R = 0.616$ ). These correlations are also significant for *Cancer* spp. and salinity at Bodega Head ( $R = -0.836$ ) using the truncated data series.

Total seasonal settlement across the 4 sites exhibited a consistent north-south difference and the unusually large settlement of crabs at Point Reyes (Fig. 9). For *Cancer* spp., total settlement at the 2 Gulf of the Farallones sites averaged 5 times greater than settlement north of Point Reyes (Fig. 9a). Total crab and total sea urchin settlement both showed highest settlement at Point Reyes due to the early season settlement event (Fig. 9b, c).

#### High resolution temporal and spatial sampling of settlement

The results from weekly sampling in 1992 (Wing et al. 1995) and 1993 suggest an association between settlement and relaxation events. However, to understand

the physical-biological mechanism underlying this relationship we need finer-scale temporal sampling to determine the timing of settlement within relaxation events. In 1993, we were able to sample more frequently during Event 6.

The northward propagation of warm water in Event 6 is indicated by the lag in warming across the 4 sites (Fig. 6). This is the event depicted in the AVHRR image (Fig. 4b) as a warm, wedge-shaped current trapped over the shelf, similar to the poleward flow events described by Send et al. (1987) and Largier et al. (1993). Direct CTD observations of the cross-shelf thermal structure during relaxation Event 6 (on Day 210) confirmed the thermal structure reflected in the AVHRR image (Fig. 4b). Concurrent plankton samples indicate an association between warmer non-upwelled water and planktonic crab larvae. The 2 sets of CTD casts (transects A and B in Fig. 1) indicated a lens of warm water which is generally thicker along the coast and appears to be separated immediately north of Point Reyes (Figs. 10b & 11b). A clear thermocline was seen at 10 to 20 m. The concurrent larval densities indicate that crab larvae tend to be associated with the warmer water (Figs. 10a & 11a). No urchin larvae were found in these tows. Five days later the feature had moved poleward. A similar survey revealed a deeper

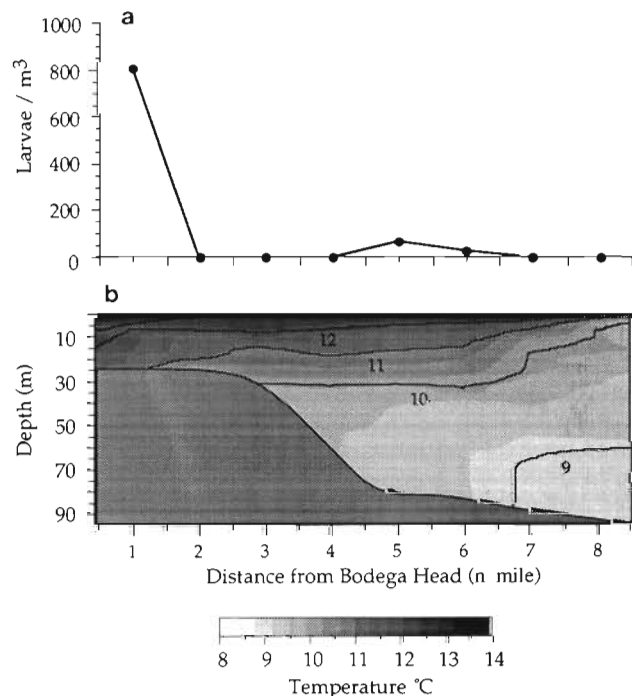


Fig. 10. Total planktonic crab larval density and temperature vs depth along transect A (Fig. 1) on Day 210 (July 29) during passage of warm surface current during relaxation Event 6. Distance along the transect from Bodega Head is given on the abscissa in nautical miles

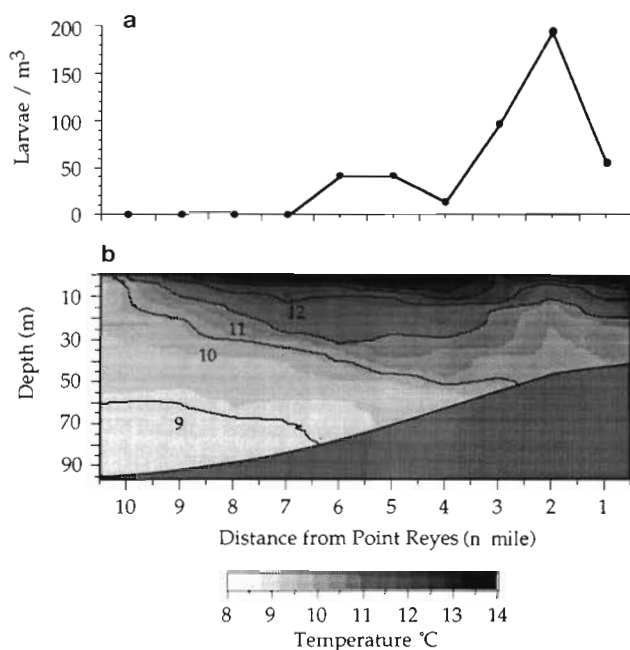


Fig. 11. Total planktonic crab larval density and temperature vs depth along transect B (Fig. 1) on Day 210 (July 29) during passage of warm surface current during relaxation Event 6. Distance along the transect from Point Reyes is given on the abscissa in nautical miles

and sharper thermocline (data not shown), and larval densities were lower.

Comparison of fine-scale settlement with local temperature at Bodega Head during relaxation Event 6 indicates that most crabs settled over a period that overlapped the beginning of the event. Fig. 12 shows the beginning of relaxation Event 6 as a period of rapid warming when a thermal front passed Bodega Head

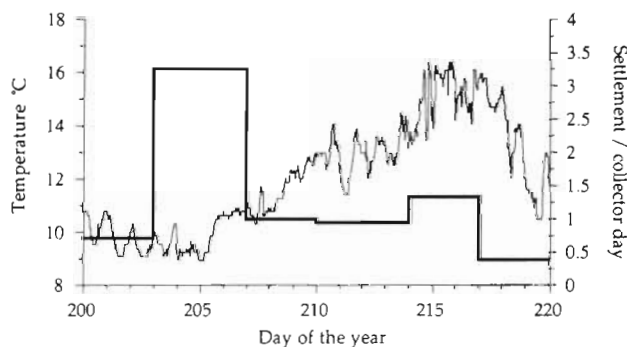


Fig. 12. Total crab settlement sampled at 2 to 4 d intervals during passage of relaxation Event 6. Temperature was collected at 10 m depth off of Bodega Head and is plotted in 24 min intervals. Note that the highest settlement period (Days 203 to 207, July 22 to July 26) overlapped the onset of rapid warming on Day 205 (July 24) signaling the beginning of relaxation Event 6

on Day 205. It should be noted that peak settlement can also occur during the middle of a long warming period (i.e. Event 3).

## DISCUSSION

The important link between upwelling variability and benthic settlement, described for barnacles in Monterey Bay (Farrell et al. 1991, Roughgarden et al. 1991) and for crabs off Bodega Bay (Wing et al. 1995), is central to the understanding of local recruitment. In this work we have expanded this local view to show that settlement is not homogeneous alongshore, but rather may be tied to alongshore structure in hydrodynamic features. In particular, we have described a possible mechanism by which larvae of one taxon, *Cancer* crabs, settle to the north of a coastal promontory (Point Reyes) after being transported there by a flow of warm, low salinity water from south of this promontory during periods of upwelling relaxation. South of Point Reyes some settlement of this taxon occurs during upwelling, and the settlement rate increases during relaxation periods. Identification of a link between physical conditions and settlement over this part of the life history is an important addition to our understanding of the dynamics of recruitment to these and similar populations in the embayment from Point Arena to Point Reyes, and may have implications for other similar embayments to the north in the California Current, and in other eastern boundary currents.

Data presented here and elsewhere provide support for both the physical and biological components of this proposed mechanism. Past observations of temperature-current patterns (Send et al. 1987), drifter tracks (Davis 1985a, b) and movement of an oil spill from the Gulf of the Farallones (Breaker & Bratkovitch 1993) provided evidence that the Gulf of the Farallones is the source of the warm water that reaches the Reyes-Arena coast during relaxation, specifically during the later upwelling season. Our conclusion that this water contains high densities of meroplanktonic larvae that are transported poleward from the Gulf during relaxation, and constitute the main supply of propagules, is based on several lines of evidence. First, *Cancer* crab settlement north of Point Reyes is more tightly correlated with low salinity and high temperatures than is settlement within the Gulf of the Farallones. These are the conditions that indicate alongshore relaxation currents. Correlations between settlement and salinity at the 2 northern sites are still significant even when the largest event of the season (Event 3) is removed by truncating the data, indicating that the spatial result is relatively robust. In addition, total seasonal settlement north of Point Reyes is less than to the south. Fine tem-

poral sampling of settlement at Bodega Head shows settlement of crabs at the beginning of a relaxation feature that propagates poleward along the coast (Figs. 6 & 12). Cross-shelf larval crab distributions during this same relaxation event (Figs. 10 & 11) showed close association of planktonic larvae with the warm poleward moving current, particularly the shoreward edge of this feature.

Despite these lines of evidence, several qualifications must accompany our conclusions. First, we have not shown that larvae are transported in the alongshore flow, only that settlement patterns observed here, in Wing et al. (1995), and in the limited data on larval distribution are consistent with this scenario. Another possible explanation is that larvae are resident at each site and settle in response to warm, low salinity conditions. More data are needed on the alongshore distributions of planktonic larvae to more concretely describe larval supply during relaxation events. Second, it is not clear to what extent the water in the Gulf of the Farallones is entrained from southward shelf flow, supplied by shoreward flow of offshore water into the Gulf, or composed of San Francisco Bay water. Third, there is a need for observation of more events over several years before we can draw conclusions regarding the frequency of the observed pattern on annual time scales. Finally, it must be noted that correlations between variables that indicate physical transport phenomena and settlement rates are often problematical because larval availability may vary between similar transport events.

Whether other species of invertebrates and fish in this or similar embayments are influenced by the alongshore transport mechanism proposed here depends on the specific, underlying, physical-biological interactions. As we have shown, alongshore settlement variability is species specific, possibly depending on timing of larval release, larval life period, duration of the competency phase and a host of other factors in larval development. Our results suggest that the species whose settlement patterns are most consistent with our proposed mechanism are those with the largest, longest lived, and most actively swimming larvae, that probably also have a relatively long competency period (*Cancer* spp.). In contrast, those species with shorter larval duration, smaller larvae and probably shorter competency periods appear more likely to be associated with single events or a small number of relaxation events early in the season (the porcellanid group). For example, sea urchins, with relatively short larval periods and small weakly swimming larvae, fall into this second pattern. We surmise that species with these characteristics may have less reliable settlement in this system and less spatial integrity of settlement.

These results add an alongshore component to interpretation of earlier studies that focused primarily on the effects of cross-shelf transport on successful recruitment. Explanations of reproductive strategies (Parrish et al. 1981) and cross-shelf larval zonation (Peterson 1973, Richardson & Pearcy 1977, Richardson et al. 1980) depended on the cross-shelf effects of upwelling. Observation of the link between barnacle settlement and temporal variability in this cross-shelf effect led to the 'tattered curtain hypothesis' (Farrell et al. 1991, Roughgarden et al. 1991): during periods of upwelling relaxation, the upwelling front moves closer to shore resulting in settlement of barnacles that were concentrated in the upwelling front several km offshore. The mechanism proposed in this paper shifts the focus from one of recruitment success in response to cross-shelf processes to one of recruitment distribution in response to 3-dimensional coastal circulation. It indicates that the same source of temporal variability (i.e. upwelling/relaxation) is responsible for alongshore redistribution of propagules.

This alongshore aspect expands the suite of potential physical-biological influences on recruitment of meroplanktonic species along the northern California coast. Most importantly, it describes the larval interactions between spatially distributed subpopulations, not just local temporal variability in recruitment. For example, our results indicate that there may be retention mechanisms so that larvae released near the coast after the spring transition are not simply swept south. Rather, recirculating regions such as those found in northern Monterey Bay (Graham et al. 1992) and in the northern Gulf of the Farallones (suggested in this paper, in Largier et al. 1993, and in Wing et al. 1995) may provide regions with predictably high settlement relative to neighboring upwelling areas. Our results also indicate that the larvae that settle in this Point Reyes-Point Arena embayment may be derived from a common planktonic pool that collects in the Gulf of the Farallones. The spatio-temporal variability in larval dispersal implied by these characteristics has important implications for metapopulation dynamics and management of these coastal populations (cf. Pulliam 1988, Botsford et al. 1994).

**Acknowledgements.** We gratefully acknowledge the Gulf of the Farallones National Marine Sanctuary for the use of their vessel, and Bodega Marine Laboratory, Ocean Cove Campground, Salt Point State Park, Point Reyes National Seashore, Sea Drift community, and Point Reyes Bird Observatory (California, USA); and Kym Arico, David Wilson, Carolyn Lundquist, Jim Leichter, Jim Quinn, H. V. S. Peeke, and Robert Morgan for other forms of assistance. This article was funded by a grant from the National Sea Grant College Program, National Oceanic and Atmospheric Administration, U.S. Department of Commerce, Washington, DC, under grant number 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. The authors' views expressed herein do not necessarily reflect those of NOAA or any of its sub-agencies. The U.S. Government is authorized to reproduce and distribute this article for governmental purposes.

#### LITERATURE CITED

- Botsford LW, Moloney CL, Hastings A, Largier JL, Powell TM, Higgins K, Quinn JF (1994) The influence of spatially and temporally varying oceanographic conditions on meroplanktonic metapopulations. *Deep Sea Res II* 41:107–145
- Botsford LW, Wickham DE (1975) Correlation of upwelling index and Dungeness crab catch. *Fish Bull US* 73:901–907
- Breaker LC, Bratkovich A (1993) Coastal-ocean processes and their influence on the oil spilled off San Francisco by the M/V Puerto Rican. *Mar environ Res* 36:153–184
- Brink KH (1983) The near-surface dynamics of coastal upwelling. *Prog Oceanogr* 12:223–257
- Caffey HM (1985) Spatial and temporal variation in settlement and recruitment of intertidal barnacles. *Ecol Monogr* 55:313–332
- Cameron RA, Schroeter SC (1980) Sea urchin recruitment: effect of substrate selection of juvenile distribution. *Mar Ecol Prog Ser* 2:243–247
- Carlson DB, Olson RR (1993) Larval dispersal distance as an explanation for adult spatial pattern in two Caribbean reef corals. *J exp mar Biol Ecol* 173:247–263
- Carrasco KR, Armstrong DA, Gunderson DR, Rogers C (1985) Abundance and growth of *Cancer magister* young-of-the-year in the nearshore environment. In: Melteff BR (ed) *Proceedings of the symposium on Dungeness crab biology and management*. Alaska Sea Grant Prog Rep 85-3, University of Alaska, Anchorage
- Connell JH (1985) The consequences of variation in initial settlement vs post-settlement mortality in rocky intertidal communities. *J exp mar Biol Ecol* 93:11–45
- Davis AR, Butler AJ (1989) Direct observations of larval dispersal in the colonial ascidian *Podoclavella moluccensis* Sluiter: evidence for closed populations. *J exp mar Biol Ecol* 127:189–203
- Davis RE (1985a) Drifter observations of coastal surface currents during CODE: the method and descriptive view. *J geophys Res* 90:4741–4755
- Davis RE (1985b) Drifter observations of coastal surface currents during CODE: the statistical and dynamical views. *J geophys Res* 90:4756–4772
- Ebert TA, Russell MP (1988) Latitudinal variation in size structure of the west coast purple sea urchin: a correlation with headlands. *Limnol Oceanogr* 33:286–294
- Farrell TM, Bracher D, Roughgarden J (1991) Cross-shelf transport causes recruitment to intertidal populations in central California. *Limnol Oceanogr* 36:279–288
- Gaines S, Roughgarden J (1985) Larval settlement rate: a leading determinant of structure in an ecological community of the marine intertidal zone. *Proc Natl Acad Sci USA* 82:3707–3711
- Gaines SD, Bertness MD (1993a) The dynamics of juvenile dispersal — why field ecologists must integrate. *Ecology* 74:2430–2435
- Gaines SD, Bertness MD (1993b) Dispersal of juveniles and variable recruitment in sessile marine species. *Nature* 360:579–580
- Gill AE (1982) *Atmosphere-ocean dynamics*. Academic Press, New York
- Graham WM, Field JG, Potts DC (1992) Persistent 'upwelling shadows' and their influence on zooplankton distributions. *Mar Biol* 114:561–570
- Hastings A, Higgins K (1994) Persistence of transients in spatially structured ecological models. *Science* 263:1133–1136
- Hofmann EE, Hedstrom KS, Moisan JR, Haidvogel DB, Mackas DL (1991) Use of simulated drifter tracks to investigate general transport patterns and residence times in the coastal transition zone. *J geophys Res* 96:15041–15052
- Holm ER (1990) Effects of density-dependent mortality on the relationship between recruitment and larval settlement. *Mar Ecol Prog Ser* 60:141–146
- Johnson DF, Botsford LW, Methot RD Jr, Wainwright TC (1986) Wind stress and cycles in Dungeness crab (*Cancer magister*) catch off California, Oregon and Washington. *Can J Fish Aquat Sci* 43:838–845
- Judge L, Quinn JF, Wolin CL (1988) Variability in recruitment of *Balanus glandula* (Darwin, 1854) along the central California coast. *J exp mar Biol Ecol* 119:235–251
- Kato S, Schroeter SC (1985) Biology of the red sea urchin, *Strongylocentrotus franciscanus*, and its fishery in California. *Mar Fish Rev* 47:1–20
- Kope RG, Botsford LW (1988) Detection of environmental influence on recruitment using abundance data. *Can J Fish Aquat Sci* 45:1448–1458
- Largier JL, Magnell BA, Winant CD (1993) Subtidal circulation over the northern California shelf. *J geophys Res* 98:18147–18179
- Lentz SJ (1987) A heat budget for the northern California shelf during CODE 2. *J geophys Res* 92:1545–1568
- Limeburner R (1985) CODE-2: moored array and large scale data report. WHOI Tech Rep 85-35, WHOI, Woods Hole
- Lough RG (1975) Larval dynamics of the Dungeness crab, *Cancer magister*, off the central Oregon coast, 1970–71. *Fish Bull US* 74:353–375
- MacMillan FE (1972) The larval development of northern California Porcellanidae (Decapoda, Anomura). I. *Pachycheles pubescens* Holmes in comparison to *Pachycheles rudis* Stimpson. *Biol Bull* 142:57–70
- McConnaughey RA, Armstrong DA, Hickey BM, Gunderson DR (1992) Juvenile Dungeness crab (*Cancer magister*) recruitment variability and oceanic transport during the pelagic larval phase. *Can J Fish Aquat Sci* 49:2028–2044
- Morris RH, Abbott DP, Haderlie EC (1980) *Intertidal invertebrates of California*. Stanford University Press, Stanford
- Olson RR (1985) The consequences of short-distance larval dispersal in a sessile marine invertebrate. *Ecology* 66:30–39
- Parrish RH, Nelson CS, Bakun A (1981) Transport mechanisms and reproductive success of fishes in the California current. *Biol Oceanogr* 1:175–203
- Pearse JS, Pearse VB, Davis KK (1982) Photoperiodic regulation of gematogenesis and growth in the sea urchin *Strongylocentrotus purpuratus*. *J exp Zool* 237:107–118
- Pedrotti ML, Fenaux L (1992) Dispersal of echinoderm larvae in a geographical area marked by upwelling (Ligurian Sea, N.W. Mediterranean). *Mar Ecol Prog Ser* 86:217–227
- Peterson WT (1973) Upwelling indices and annual catches of Dungeness crab, *Cancer magister*, along the west coast of the United States. *Fish Bull US* 71:902–910
- Poole RL (1966) A description of laboratory reared zoeae of *Cancer magister* Dana, and megalopae taken under natural conditions (Decapoda, Brachyura). *Crustaceana* 11:83–97
- Possingham HP, Roughgarden J (1990) Spatial population dynamics of a marine organism with a complex life cycle. *Ecology* 71:973–985

- Pulliam HR (1988) Sources, sinks and population regulation. *Am Nat* 132:652–661
- Raimondi PT (1990) Patterns, mechanisms, consequences of variability in settlement and recruitment of an intertidal barnacle. *Ecol Monogr* 60:283–309
- Richardson SL, Laroche JL, Richardson MD (1980) Larval fish assemblages and associations in the north-east Pacific Ocean along the Oregon coast, winter-spring 1972–1975. *Estuar coast mar Sci* 11:671–699
- Richardson SL, Pearcy WG (1977) Coastal and oceanic fish larvae in an area of upwelling off Yaquina Bay, Oregon. *Fish Bull US* 75:125–145
- Roughgarden J, Gaines S, Possingham H (1988) Recruitment dynamics in complex life cycles. *Science* 241:1460–1466
- Roughgarden J, Iwasa Y, Baxter C (1985) Demographic theory for an open marine population with space-limited recruitment. *Ecology* 66:54–67
- Roughgarden J, Pennington JT, Stoner D, Alexander S, Miller K (1991) Collisions of upwelling fronts with the intertidal zone: the cause of recruitment pulses in barnacle populations of central California. *Acta Oecologia* 12:35–51
- Rowley RJ (1990) Newly settled sea urchins in a kelp bed and urchin barren ground: a comparison of growth and mortality. *Mar Ecol Prog Ser* 62:229–240
- Rumrill SS (1988) Temporal and spatial variability in the intensity of recruitment of a sea star: frequent recruitment and demise. *Am Zool* 28:123
- Send U, Beardsley RC, Winant CD (1987) Relaxation from upwelling in the Coastal Ocean Dynamics Experiment. *J geophys Res* 92:1683–1698
- Sewell MA, Watson JC (1993) A 'source' for asteroid larvae?: recruitment of *Pisaster ocraceus*, *Pycnopodia helianthoides* and *Dermasterias imbricata* in Nootka Sound, British Columbia. *Mar Biol* 117:387–398
- Smith RI, Carlton JT (1975) *Light's manual: intertidal invertebrates of the Central California coast*. University of California Press, Berkeley, p 393–412
- Sokal RR, Rohlf FJ (1981) *Biometry*, 2nd edn. WH Freeman and Co, San Francisco
- Strathmann MF (1987) Reproduction and development of marine invertebrates of the northern Pacific coast. University of Washington Press, Seattle
- Strathmann RR (1978) Length of pelagic period in echinoderms with feeding larvae from the northeast Pacific. *J exp mar Biol Ecol* 34:23–27
- Strub PT, Allen JS, Huyer A, Smith RL, Beardsley RC (1987) Seasonal cycles of currents, temperatures, winds, and sea level over the northeast Pacific continental shelf. *J geophys Res* 92:1507–1526
- Trask T (1970) A description of laboratory-reared larvae of *Cancer productus* Randall (Decapoda, Brachyura) and a comparison to larvae of *Cancer magister* Dana. *Crustaceana* 18:133–146
- Underwood AJ, Denley EJ (1984) Paradigms, explanations, and generalizations in models for the structure of intertidal communities on rocky shores. In: Strong DR, Simberloff D, Abele LG, Thistle AB (eds) *Ecological communities: conceptual issues and evidence*. Princeton University Press, Princeton, p 151–180
- Waldron KD (1958) The fishery and biology of the Dungeness crab (*Cancer magister* Dana) in Oregon waters. *Fish Comm Ore Contrib* 24:1–43
- Wild P (1983) Effects of seawater temperature on spawning, egg development, and hatching success of the Dungeness crab (*Cancer magister*). *Fish Bull US* 172:197–213
- Wing SR, Largier JL, Botsford LW, Quinn JF (1995) Settlement and transport of benthic invertebrates in an intermittent upwelling region. *Limnol Oceanogr* 40:316–329

*This article was submitted to the editor*

*Manuscript first received: October 6, 1994*

*Revised version accepted: May 23, 1995*