Larval Accumulation in the Lee of a Small Headland: Implications for Marine Reserves in an Upwelling Region

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Larval accumulation in the lee of a small headland: Implications for marine reserves in an upwelling region

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ABSTRACT

Identifying where and how larvae accumulate in space and time is key to understanding the dynamics of benthic marine populations and communities and for locating marine reserves, particularly in recruitment-limited upwelling regions. The interaction of alongshore coastal currents with large headlands has been shown to increase the accumulation of planktonic organisms through the formation of headland eddies. Larval settlement of benthic invertebrates and circulation around Bodega Head, a small headland in an upwelling region, was investigated to determine if similar processes are at work around both large and small headlands. During the upwelling seasons of 2000 through 2004, invertebrate settlement rates and physical variables, including wind, current, and water properties, were monitored to identify spatial and temporal settlement patterns, circulation features, and larval transport mechanisms. A larval accumulation zone was identified in the lee of the headland where crabs, mussels, and barnacles settled in greater abundance than along the exposed coast. Oceanographic sampling revealed a sub-surface recirculation feature in the lee of Bodega Head. This recirculation feature strengthened as upwelling increased providing a mechanism for larvae to accumulate in an area thought to have extensive offshore transport. During relaxation this recirculation feature weakened allowing the potential export of larvae to adjacent habitats. High frequency sampling revealed interspecific differences in larval transport mechanisms. Strongest correlations with physical variables that are indicative of upwelling and relaxation conditions were observed for *Cancer magister*, which settled primarily during relaxation-favorable conditions, and for *Cancer antennarius/productus*, which settled primarily during upwelling-favorable conditions. Further, *C. magister* and *C.*

antennarius/productus settled at different depths and exhibited different spatial distributions, suggesting that these two congeners employ different strategies for returning to adult habitat. Non-cancrid crab settlement was correlated with tidal periodicity, indicating the importance of multiple taxon-specific delivery mechanisms. We suggest that both small and large headlands predictably accumulate larvae and are particularly effective during periods of strong upwelling. Thus larval accumulation zones should be included in networks of marine reserves in upwelling regions where advection of larvae may limit recruitment to adult populations.

Sub-surface recirculation and larval retention in the lee of a small headland: A variation on the upwelling shadow theme

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Abstract

The interaction of alongshore coastal currents with large headlands has been shown to increase the retention of planktonic organisms through the formation of headland eddies or upwelling shadows in their lee. This study investigates the circulation within Bodega Bay, an upwelling region in the lee of a small headland, and the potential for retention of plankton. During the upwelling season of 2004, time series of temperature and velocity were recorded throughout Bodega Bay; CTD surveys were conducted and surface drifters were released during upwelling, downwelling, and relaxation conditions. Postlarval settlement was monitored daily over two periods coinciding with CTD surveys. Under strong upwelling favorable conditions, wind-driven surface currents were equatorward both offshore and throughout the bay. However, there was significant current shear along the eastern shore of the bay where cold bottom waters move poleward, counter to the direction of the wind-driven surface flow. During downwelling and relaxation conditions, flow was poleward throughout the water column along the eastern shore of the bay. Postlarvae settled during all wind conditions, but greatest settlement was observed at the onset of upwelling-favorable conditions. While no ‘typical’ upwelling shadow is evident in the lee of the Bodega headland, sub-surface recirculation driven by the alongshore flow past Bodega Head may facilitate the retention of plankton in the bay. Previous studies have generally focused on large headlands; however, it is likely that other small embayments in the lee of small headlands may also provide retention opportunities for planktonic organisms in upwelling regions.

INTRODUCTION

In recent years, substantial progress has been made in understanding wind-driven dynamical processes in coastal upwelling systems. Specifically, observations from the Coastal Ocean Dynamics Experiment (CODE) (Kosro and Huyer 1986, Huyer and Kosro 1987, Kosro 1987, Winant et al. 1987), the Northern California Coastal Circulation Study (NCCCS) (Largier et al. 1993), and the Surface Mixed Layer Experiment (SMILE) (Dever 1997) highlight the spatial and temporal variability of wind forcing in the northern California region and the associated upwelling response. This work has been continued by Wing et al. (1995a, 1995b, 1998) and the Wind Exchange Shelf Transport (WEST) program (Largier et al. In review) which aimed to link physical oceanographic processes with the response of plankton communities in the region between Pt Reyes (38°N) and Pt Arena (39°N) on the west coast of the USA (Figure 1.1). Still poorly known, however, is the influence of coastal topographic form on physical and biological processes (e.g. meroplanktonic dispersal), in particular the effect of headlands and associated bays on the structure of coastal flows.

Headlands and capes can play a dominant role in causing alongshore variability of upwelling-driven coastal flow (Gan and Allen 2002a, Gan and Allen 2002b), but the in-bay processes are poorly understood. Furthermore, the physical mechanisms responsible for biological patterns are often deduced with little direct observation of transport and forcing. For example, it has been suggested that the interaction of alongshore coastal currents with headlands would increase offshore transport and thus negatively affect the recruitment of meroplanktonic populations (Ebert and Russell 1988). However, several studies have observed increased zooplankton abundance in headland-generated oceanographic features such as fronts and eddies (Caffey 1985, Murdoch 1989, Rankin et al. 1994, Graham and Largier 1997, Wing et al. 1998). Additionally, some studies have reported higher larval settlement patterns in headland associated embayments compared to surrounding areas, suggesting that bays can act as retention zones (Gaines and Bertness 1992, Wing et al. 1995a, Archambault and Bourget 1999, Lagos et al. 2002), however, few of these studies (Wing et al. 1995a, Lagos et al. 2002) were conducted in upwelling systems. For example, Wing et al. (1995a) found evidence of limited larval dispersal even in areas of intense upwelling, despite extensive offshore transport of water, suggesting local retention mechanisms on a scale of approximately 100 km. Thus, marine populations in wind-driven upwelling regions may not be as open as once thought (Sponaugle et al. 2002, Strathmann et al. 2002, Swearer et al. 2002). A better understanding of flow around headlands and in bays, particularly on a small scale, may resolve the apparent contradiction between Ebert and Russell's (1988) view of weaker settlement and Wing et al.'s (1995a) view of stronger settlement associated with headlands.

In this study 'retention' is used to describe a region where plankton are subject to reduced dispersion. In particular, for the propagules of coastal benthic populations this may be important in two ways: 1) reduced offshore dispersion may increase the probability of being nearshore when competent to settle; and 2) reduced alongshore dispersion may increase local recruitment. Multiple mechanisms may be responsible for the retention of zooplankton in embayments associated with headlands. In particular, residence in bays may be promoted by frontal zones at the mouth of bays (Graham et al. 1992, O'Donnell

1993, Wing et al. 1998, McCulloch and Shanks 2003, Shanks et al. 2003, Miller and Shanks 2004), recirculation features (Murdoch 1989, Chen et al. 1997, Graham and Largier 1997), and through vertical migratory behavior in the presence of vertical shear (Peterson et al. 1979). Furthermore, warmer water and elevated concentrations of food in embayments may speed development, thereby reducing the pelagic larval duration and exposure to pelagic predators (Castilla et al. 2002, Lagos et al. 2002, Largier 2004). Physical evidence for increased residence time of water in an embayment may consist of warmer water in the bay than along the adjacent exposed coast; a lag between change of water temperature inside and outside the bay; increased water column stratification in the bay; or a reversal of current direction from the predominant flow. These circulation features may be due to tides, wind, offshore currents, and buoyancy. Because tidal and wind influences are variable, circulation features and zooplankton retention are likely to be spatially and temporally transient.

Previous studies of headland dynamics have typically been conducted on scales ranging from 10-100 km (Murdoch 1989, Rankin et al. 1994, Graham and Largier 1997, Wing et al. 1998), although a more recent study has reported on circulation at a smaller scale (<10 km) in the lee of Pt Loma, California (Roughan et al. in press). Addressing whether similar mechanisms operate at smaller scales is important for understanding local marine community dynamics and for siting marine reserves, which typically have alongshore scales less than 10 km. Thus the goals of this study are 1) to describe and explain flow patterns within Bodega Bay; 2) to relate these flow patterns to the concept of an 'upwelling shadow' and the potential for larval retention in Bodega Bay; and 3) to interpret postlarval crab settlement in terms of these flow patterns.

METHODS

The Study Area

This study was conducted during the 2004 upwelling season in the region of Bodega Bay, California (Figure 1.1). Typically, the spring and summer months (May–July), are characterized by persistent equatorward (upwelling favorable) winds in this region. A previous review of Bodega Bay circulation (Shenker 1989) suggested the dynamics are complex and highly variable over short temporal and spatial scales and are influenced by winds, tides, and local and regional topography. Bodega Bay is a shallow broad southwest facing embayment located in the lee of Bodega Head (38°18' N 123°04' W). The mouth of the bay is approximately 11 km from the northern tip (Bodega Head) to the southern tip (Tomales Point), expanding to 15 km wide landward of the mouth, and is approximately 3.5 km from mouth to shore. The rocky outcrops of Bodega Head and Tomales Point continue as a shallow (<15 m) submarine ridge across the mouth of the bay. At the northern end of the bay, this ridge rises to the surface to form Bodega Rocks and offshore of the ridge, depths increase quickly to 40 m or more. Onshore of the ridge, depths of 20–25 m are observed creating a deeper, more enclosed bay. Deep, narrow passages lead through the ridge immediately south of Bodega Rocks (~½ km wide and 20 m deep) and at the southern end of the bay (2 ½ km wide, 25 m deep). The semi-enclosed waters of Bodega Harbor and Tomales Bay (to the north and south respectively) connect directly to Bodega Bay, more than doubling the surface area. Tides in the bay are mixed semi-diurnal with a tidal range of 1.2–2.9 m. Strong tidal currents at the mouth of Bodega Harbor extend as a tidal jet up to 2 km into Bodega Bay (Rasmussen et al. 2004). Bodega Bay is also influenced by the tidal outflow from Tomales Bay, mixing with offshore waters, and winter freshwater influx from Tomales Bay and two small creeks that enter Bodega Bay.

Data

The field data collected during this study include 1) time series observations of wind speed and direction, current velocity profiles, and temperature throughout the water column; 2) spatial hydrographic surveys from a small boat; 3) measurements of surface velocities with Lagrangian drifters inside Bodega Bay; and 4) settlement of postlarval crabs.

Wind

Offshore wind speed and direction were obtained from an automatic weather station at the offshore site NDBC 46013 (38°13' N 123°19' W; http://www.ndbc.noaa.gov/) and local wind velocities were obtained from a land-based site at the Bodega Marine Laboratory (http://bml.ucdavis.edu/boon/). The 10 minute averaged data were adjusted to a height of 10 m above sea level using a neutral stability wind profile, decimated to hourly data, and rotated to a principal axis of 320°T and 305°T (NDBC 46013 and BML respectively).

Current Profiles

Time series of current velocity and direction were obtained using bottom-mounted RDI 1200 kHz acoustic Doppler current profilers (ADCPs) at three nearshore locations: off Bodega Marine Laboratory (BML) on the open coast west of Bodega Head and north of Bodega Bay; on the inshore southeastern flank of Bodega Rock (BR) in the lee of Bodega Head; and off Pinnacle Rock (PR) along the eastern shore of northern Bodega Bay (Figure 1.1). The BML site was located so as to represent alongshore flow upstream of the mouth of the bay while the BR and PR sites were selected to be at each side of the entrance to the northern sub-embayment formed by Bodega Rocks. The ADCPs were deployed at a depth of 11.5 m, 13 m, and 12 m (BML, BR, and PR respectively) for periods of 33 (BML and BR) and 49 days (PR) (Table 1.1). Magnetic compass directions were corrected to true north and the principal axis of each time series was calculated from the sub-tidal depth averaged velocity (BML, BR, and PR were found to be -30°, -3°, and -8° respectively). Velocity records were then rotated through the principal axis to minimize the variance in the across-shore direction such that positive alongshore flow (v) is in the y direction (poleward) and positive across-shore flow (u) is in the x direction (onshore). Because the tidal range is 25% of the maximum instrument depth, all current velocities are reported in 1 m bins at a depth above the bottom rather than depth below the surface.

Temperature

Ten thermistor moorings were deployed throughout the bay for the period 20 May to 1 August 2004 (Figure 1.1). Most of the moorings were in approximately 15 m of water

(Table 1.1). Three Optic StowAway TidbiT® thermistors (which recorded temperature (T ± 0.2 °C) every 2 min) were placed on each mooring: (1 m off the bottom, (~14 m); mid water column (~8 m); and 1 m below the surface).

Hydrography

Spatial patterns in the hydrography and stratification of Bodega Bay were characterized using data from boat-based conductivity-temperature-depth (CTD) surveys. On each survey, vertical CTD casts were taken at 30 locations throughout the bay (Figure 1.1), using a Sea-bird SBE19-plus profiling CTD with a submersible pump (SBE 5T), an irradiance meter (Li-Cor PAR Sensor, model Li-193SA), a WET-Labs WETStar fluorometer, and a WETLabs transmissometer. Four surveys were conducted during June and July 2004, each under a different wind regime (Table 1.2): 3 June (well-developed upwelling); 19 June (active downwelling); 8 July (relaxation from upwelling) and 11 July (incipient upwelling).

Lagrangian Drifters

Pacific Gyre Lagrangian drifters were used to characterize the surface velocity field during different wind regimes. The drifters have a tristar drogue that tracks near-surface waters (<2 m). Positions were fixed every 10 min by GPS, and transmitted via a cellular phone network, allowing data to be downloaded in near real-time. As many as 10 drifters were deployed for periods of up to 8 hrs under the four wind regimes outlined in Table 1.2.

Postlarvae

Postlarvae were collected during periods of two different oceanographic conditions coincident with CTD surveys: May 31–June 5 (upwelling) and 14–21 June (downwelling). Three moorings were placed 50 m apart along the 10 m isobath adjacent to the ADCP mooring off Pinnacle Rock (PR). A mesh collector bag (10 x 30 cm), containing three Tuffy® kitchen scrub pads was attached to each mooring both at the surface and 1 m above the bottom. Collectors were retrieved and replaced at 24 hr intervals. Postlarvae were counted and identified to the lowest possible taxa. A two-factor analysis of variance was used to determine the effect of oceanographic condition (upwelling and downwelling winds) and taxa on postlarval density (surface and bottom settlement were combined for the analysis).

RESULTS AND DISCUSSION

During spring and summer, the Bodega Bay region is characterized by upwelling winds with brief periods of weaker wind. Largier, et al. (In review) used 36-hour low-pass filtered wind strength at NDBC 46013 as an index of wind conditions in the region, identifying upwelling periods as times when equatorward winds exceed 5 ms^{-1} and relaxation events as times when winds are less than 3 ms^{-1}. Downwelling can similarly be identified as periods when poleward winds exceed 5 ms^{-1}. All three stages of wind forcing were observed during the study period (marked in Figure 1.2). While wind events were coherent between offshore (NDBC 46013) and nearshore (BML) on all occasions (95% confidence, correlation coefficient = 0.8849), offshore winds were notably stronger during upwelling events (Figure 1.2), suggesting that the bay and nearshore waters are sheltered from the full strength of the equatorward winds. Generally alongshore winds at BML precede those at NDBC 46013 (lag of 2 hrs) primarily due to wind relaxations occurring earlier at BML (Figure 1.2). This difference in speed reflects the complex spatial patterns of wind forcing in this region (Koracin et al. 2004, Dorman et al. In review).

Water temperatures throughout the bay fluctuate in response to synoptic scale wind forcing. Periods of cold water were observed 29 May–16 June, 22–28 June, 3–4 July, and 13–21 July, corresponding to periods of wind-driven upwelling on the open coast (e.g. T02 in Figure 1.3). Warm-water periods were observed during relaxation and downwelling conditions between upwelling events. Warmest waters were found following prolonged relaxation of upwelling conditions (e.g. 9–12 July and 26–31 July). Maximum surface temperatures were about 15 °C at these times, while minimum temperatures were about 8.5 °C during strong upwelling (Figure 1.3 and Figure 1.4). The temperature time series show there was a distinct and coherent spatial pattern in stratification and water temperatures in the bay. Stronger stratification and warmer surface waters were observed in the southern bay (T06, T07, and T08) and at stations immediately outside the southern bay (T09). The northern bay (T01 and T04) and the open coastal waters (T02, T11) were characterized by cooler waters and weaker stratification.

Temperature also exhibits high-frequency variability associated with tides and diurnal forcing (Figure 1.3 and Figure 1.4), resulting in high-frequency changes in thermal stratification. At sites near the mouth of Tomales Bay (notably T07), strong tidal (semi-diurnal) temperature variability is observed at depth (e.g. T07 Figure 1.5, 13–14 July, 4 °C change at depth), consistent with tidal outflow of warm water from Tomales Bay (Largier et al. 1997). Whereas in the surface waters at other sites, diurnal variability is more distinct (e.g. T01 Figure 1.5, 13–14 July, 3.5 °C change at the surface). During periods of increased stratification, this diurnal variability is most notable at sites along the eastern shore (T01, T05, and T06) and it is likely due to diurnal surface warming.

Wind forcing may be important not only in offshore transport of warm surface waters and upwelling of cold deeper waters, but also in vertical mixing. For example, at T06 and nearby thermistor strings on 12–13 June it appears that the cooling of surface waters were accompanied by the warming of bottom waters, suggesting vertical mixing at these sites. Weak diurnal variability is also observed when the water column is mixed, which is likely due to diurnal tidal effects and diurnal surface warming.

Currents in Bodega Bay also exhibit a strong response to both wind and tidal forcing. The time series of current velocities are shown in the alongshore and across-shore directions at each of the three moorings (Figures 1.6 and 1.7). Wind is also plotted to delineate periods of upwelling, downwelling, and relaxation. Currents were predominantly alongshore, equatorward during upwelling periods and poleward during relaxation or downwelling periods. High frequency fluctuations in velocity, resulting from tidal forcing, are evident in the ADCP time series shown as banding in Figure 1.6 and Figure 1.7 (unfiltered data) consistent with tidal fluctuations in sea level elevation (pressure).

Circulation during Upwelling

During upwelling conditions, Bodega Bay is subject to at least four co-occurring forcing phenomena: 1) strong equatorward flow past the mouth of the bay; 2) alongshore pressure gradients due to alongshore variations in wind forcing; 3) wind stress on the surface of the bay; and 4) the presence of dense upwelled waters at the mouth of the bay. These forcing mechanisms interact with coastal topography, bottom stress, and tidal forcing to determine both the circulation within the bay and exchange between the bay and the shelf.

During the main upwelling event (28 May to 15 June), current velocities at the BML site were strongly equatorward and slightly onshore with a near-surface maximum of 0.25 ms^{-1} decreasing to less than 0.05 ms^{-1} near-bottom (Figure 1.6). Currents at the BR site were remarkably coherent with currents along the open coast (BML), with only a slight weakening (Figure 1.6). Currents at the PR site were also correlated with wind forcing, but strong vertical shear was evident. While near-surface velocities (9–11 m above bottom) were up to 0.1 ms^{-1} equatorward, near-bottom velocities (2–5 m above bottom) were up to 0.1 ms^{-1} poleward (Figure 1.6). The depth of zero velocity fluctuates from 7–9 m above the bottom, which coincided with the approximate depth of the thermocline at the base of the surface mixed layer. A similar pattern of sheared alongshore flow was seen at PR during the second upwelling event in late June evident in Figure 1.8.

Under upwelling conditions temperature was well mixed offshore and in the outer bay (<10 °C). However warmer water (11-12 °C) and stratification was observed along the eastern shore (Figure 1.9, column 1). Salinity was high (33.8 psu) and homogeneous indicating that the bay was filled with upwelled waters, some of which had warmed while in the bay (density 26-26.2 kg m^{-3}). Turbidity increased slightly near the entrances to Bodega Harbor and Tomales Bay. The cool isothermal waters were also evident at northern thermistor sites (Figure 1.3 and Figure 1.4); and during strongest winds 12–15 June, the entire bay was cold and isothermal at all sites except those subject to Tomales Bay outflow.

Strong equatorward flow past Bodega Head was recorded by the ADCP moored at BML. This site is within a coastal boundary shear zone and flow further offshore is significantly stronger (Kaplan and Largier In review). The bulk of this equatorward flow can be expected to separate from the coast at the southern end of Bodega Head, and run along the west side of Bodega Rock and the submarine ridge at the mouth of the bay. This free shear zone can entrain waters from Bodega Bay and may induce a cyclonic (anti-clockwise) circulation in the bay. In the absence of surface wind stress, this recirculation can be expected throughout the water column. However, the surface of the bay is not typically sheltered from the winds that blow along the open coast, because Bodega Head is joined to the mainland by a low-lying sand spit. These equatorward winds blow surface waters south and, through Ekman response, away from the eastern shore of the bay, precluding the development of a resident warm surface layer in the northern bay (in contrast to Monterey Bay, (Graham and Largier 1997)). This direct wind forcing is suggested by the strong correlation of equatorward surface flow with wind at the PR site (correlation coefficient = 0.77 at 9 m above bottom).

From the observation of vertically sheared flow at the PR site, it appears that this wind forcing only dominates near-surface waters and that the separation-driven cyclonic recirculation continues at depth in the bay. The argument that this nearshore undercurrent is forced by flow past the mouth of the bay is supported by a strong negative correlation of flow along the open coast (BML site) with near-bottom flow at the PR site (correlation coefficient = -0.80 at 2 m above bottom). In other words, the poleward flow at PR is not in spite of the upwelling, but rather it is due to the upwelling: the poleward flow along the eastern shore of the bay strengthens as the equatorward flow past Bodega Head strengthens. While a large-scale poleward pressure gradient may be present (Largier et al. 1993), this correlation indicates that it is the separation process that controls the strength of this poleward undercurrent nearshore in Bodega Bay. However, this may be enhanced by a local alongshore pressure gradient between BML and PR due to a depression of the sea level during active upwelling along the open coast, although the resolution of the ADCP pressure sensor was inadequate to determine whether this occurred.

In addition to forcing by ambient shelf currents and surface wind stress, upwelling may also impose forcing by the gravity-driven intrusion of cold bottom waters (e.g. Saldanha Bay, (Monteiro and Largier 1999)). Cold waters, at depths below 15 m, may only intrude into the southern bay (at the deep entrance, south of the submarine ridge) and then propagate along the east side of the bay. While the bay is small relative to the baroclinic Rossby radius, the effect of rotation would result in density-driven propagation along the eastern boundary. Southern intrusion and northward propagation of cold bottom water was observed on three occasions during incipient upwelling: 28–29 May, 21–22 June, and 10–14 July. The July event provides the clearest example (Figure 1.5), with sub-10°C water observed first at T10 (bottom depth ~24 m), followed closely at T02 (open coast, bottom depth ~13 m). In the bay, bottom temperatures only decreased later at T06 and T07 about a day after T10 and T02. The decrease in bottom temperature due to this event was 4–5 °C and took more than three days to propagate throughout the bay. While this cold-water intrusion has a speed consistent with density-driven intrusion, and while the propagation up the east shoreline is consistent with a rotating density current, these data do not allow one to distinguish density-driven intrusion from advection of cold water by the separation-driven cyclonic flow at depth in the bay. However, the burst of near-bottom poleward flow at the PR site on 29 May (Figure 1.8), suggests that the separation-driven cyclonic circulation is briefly enhanced by the transient density-driven intrusion of cold bottom water. Also of interest during onset of upwelling conditions (e.g. 28 May) was a burst of equatorward flow throughout the water column at PR. At the start of this upwelling event, nearshore winds increased quickly to 7 ms^{-1}, concurrent with winds offshore (Figure 1.8), so that direct wind forcing on the shallow nearshore waters at PR would have had an immediate effect, whereas the forcing of the cyclonic circulation in the bay would have only evolved a day later following development of a strong equatorward flow over the shelf. A schematic diagram of the circulation within Bodega Bay during upwelling conditions is shown in Figure 1.10.

Circulation during Relaxation and Downwelling

Despite the Bodega Bay region having the strongest and most persistent upwelling winds along the west coast of the USA (Dorman and Winant 1995), relaxation periods are common and five events were observed in May–July 2004 in addition to the downwelling event in June (Figure 1.2). On a large scale, relaxation periods are characterized by strong poleward flow over the inner shelf, i.e., past the mouth of Bodega Bay (Send et al. 1987). While the dynamics have yet to be fully resolved, it is expected that a large-scale seasonal poleward pressure gradient is important in this relaxation (Largier et al. 1993, Gan and Allen 2002a, Gan and Allen 2002b) and that this may be enhanced by local and more transient barotropic and baroclinic pressure gradients set up during upwelling.

Observations in May–July 2004 describe poleward flow at the PR site in the bay and at the BML site along the open coast (Figure 1.6) and warming at all depths in the bay. Surface and bottom temperatures increased (Figure 1.3 and 1.4) and salinities decreased (~33 psu) (Figure 1.9), indicating a different water type from offshore or the Gulf of the Farallones. A surface layer of warm water 10–20 m thick forms offshore and contains high levels of phytoplankton. Warm waters may appear suddenly in the bay (e.g. 25 May and 28 June), first in the south and later in the north, consistent with northward propagation of a thermal front at the leading edge of this new water type. The only relaxation event captured by data from all three moored ADCPs occurred in late May. At the open coast site (BML), equatorward flow began to weaken with the weakening of winds at the offshore buoy (24 May). The subtidal alongshore flow at BML did not reverse during this event, perhaps due to the brief upwelling wind on 26–27 May. At BR, the near-surface equatorward flow dissipated quickly following the weakening of winds at the shoreline (23 May), and turned onshore and eventually northeastward into the northern bay (Figure 1.6 and 1.7). At depth, however, equatorward flow continued for the first few days of relaxation, in concert with BML flows, although this flow also veered more into the bay. At PR, surface flows reversed and diurnal pulses of strong poleward flow (>0.1 ms^{-1}) were observed throughout the water column, both during this event and again during events in early July. This vertical shear is consistent with the appearance of warm waters only at the surface initially (e.g. 25–26 May at T11, Figure 1.3).

Downwelling events are unusual in this season and only one substantial event was observed in the May–July period. For 2 days in June, poleward winds of about 5 ms^{-1} were observed both offshore and at the coast (Figure 1.2). This downwelling period was preceded by a burst of equatorward flow at BR, concurrent with a burst of poleward flow at PR (Figure 1.6) i.e. enhanced anticlockwise circulation in the northern bay. This occurred on 15 June, when the upwelling winds had already dissipated over the bay but while strong winds persisted offshore. With the onset of the downwelling winds, flow turned poleward at all ADCP sites (16 June), although this only lasted a day at BR. On 17–18 June, flow was again southeastward out of the northern bay alongside Bodega Rock. By 19 June, a well-developed downwelling structure was observed with isotherms down-turned nearshore (Figure 1.9). Low salinities were also observed, indicating intrusion of a new surface water type.

So, in contrast to the onset of upwelling on 28 May (when local wind forcing was active, but the alongshore flow forcing had not yet developed), on 15 June it appears that the separation of the alongshore flow at the headland in the absence of local wind forcing may have led to a burst of strong cyclonic circulation in the northern bay. Other periods of enhanced cyclonic circulation (stronger BR equatorward flow matched by stronger poleward flow at PR) were observed around 1 June and 7 June.

Once relaxation or downwelling conditions are established, one generally observes an intrusion of new warmer and lower salinity water in the bay; either as a surface layer or throughout the water column. While there may be localized equatorward flow out of the northern sub-bay in the vicinity of Bodega Rock during active downwelling (presumably due to constrictions on poleward flow out of the bay between Bodega Rock and Bodega Head), there is a general poleward flow of waters through the bay under relaxation and downwelling conditions.

Transitional Phases

Transitions to and from upwelling conditions were brief and temperature changes occurred rapidly, often in the form of frontal structures that were tidally advected past the moorings. Sudden changes in temperature are most notable with the transition from upwelling to downwelling winds on 16 June (note that winds reversed at BML a day before NDBC 46013, Figure 1.2). Both surface and bottom temperatures increased suddenly at northern sites (Figure 1.3), indicating an advection of warm water into the bay (Send et al. 1987, Wing et al. 1995b). In contrast, transitions to upwelling resulted in sudden decreases in bottom temperatures, indicating the stratified intrusion of newly upwelled waters into the bay. During these transitional conditions, buoyancy forcing appears to be important.

Observations during transition phases allow improved understanding of the interaction of forcing due to wind stress on the surface of the bay and forcing due to separation of the alongshore current at the mouth of the bay. During transition to upwelling, wind forcing starts immediately while alongshore flow across the mouth of the bay develops later, following sea level set-down along the open coast. During this transition phase, with local wind forcing dominant, equatorward flow is observed at all ADCP sites, including all depths at the PR site (e.g. 28 May, 30 June). Rapid hydrographic changes occur throughout the bay during the transition from relaxation to upwelling and are apparent in the CTD surveys on 7 and 11 July (Figure 1.9). In contrast, during transition to relaxation (or downwelling), winds over the bay weaken immediately while alongshore currents continue across the mouth of the bay for a day (or often longer, owing to the persistence of winds offshore). During this transition phase, with offshore forcing dominant, enhanced lateral shear is observed between PR and BR in the northern sub-bay. Poleward flow was observed at all depths at PR, equatorward at all depths at BR (e.g. 24 May, 15 June, 28 June, 4 July) and a burst of anti-clockwise flow in the northern sub-bay on 15 June and again on 1 and 7 July.

Variation on the Upwelling Shadow Theme

The concept of upwelling shadows, as described by Graham and Largier (1997), has received considerable attention due to the potential importance of these retention zones in upwelling regions. Based on the feature observed in northern Monterey Bay, one can identify three key characteristics of an upwelling shadow; reduced local wind forcing, localized reversal of alongshore flow, and warm surface waters. This combination of circulation and stratification is particularly valuable in the retention of both holoplankton and meroplankton, and in enhanced primary production by phytoplankton. Elevated temperatures are not only important in terms of stratification, but also because the presence of high-salinity warm water indicates aged upwelled waters in this region. While similar upwelling shadows are also evident in the northern Gulf of Farallones (Wing et al. 1998), Bahia Mejillones (Marín 2001), and St Helena Bay (Penven et al. 2000), (among others), these are all larger bays (>10 km). This study in Bodega Bay set out to investigate the possibility of upwelling shadows in smaller bays, such as Bodega Bay (<10km).

Winds in Bodega Bay are generally weaker than offshore (Figure 1.2) and relaxation of winds over the bay may occur a day or two prior to offshore. While this suggests that local wind-forced upwelling in the bay is weaker than along the open coast, the small Bodega Head headland does not block nearshore winds, and at times wind forcing along the bay shoreline may be as strong as along the open coast, resulting in active upwelling along the northern and eastern shores of the bay (see surface drifter tracks, Figure 1.11a, and low temperatures at T01 and T04). Similarly, in-bay upwelling is observed at times in the Farallones upwelling shadow and in the St Helena Bay upwelling shadow, both of which are also bounded by low-altitude headlands. As a result of this wind forcing of the surface of the bay, recirculation of surface waters is observed only briefly following relaxation of local winds. The absence of near-surface recirculation is presumably due to the near-surface dominance of equatorward wind stress during active upwelling periods. However, recirculation is observed at depth, providing the opportunity for retention of near-bottom or vertically migrating plankton in this small northern sub-bay. In addition to the vertical shear observed along the eastern shoreline of the bay, near-bottom cyclonic circulation is also reflected in a clear lag in the appearance of upwelled waters from south to east to north. Consistent with the presence of wind forcing in the bay and the absence of inflow and recirculation at the surface, there is seldom a warm surface lens due to retention and warming of upwelled waters in the bay. Thermal stratification is only observed in the northern sub-bay during incipient upwelling or during upwelling periods when the coastal wind is weak (e.g. warm surface waters were observed at T01 for about a week following the start of upwelling winds on 28 May).

Thus, we have observed a variation on the upwelling shadow theme in Bodega Bay that may be common in smaller bays, a variation that does not exhibit near-surface retention, but one that does exhibit recirculation and retention opportunities at depth. This subsurface upwelling shadow will be of value to a different suite of plankton, specifically those that exhibit vertical migration (e.g. crab postlarvae), rather than those that remain near-surface.

Implications for Larval Transport

Postlarvae of 9 taxa (*Cancer antennarius, C. magister, C. productus*; *Hemigrapsus* spp.; *Pugettia* spp.; *Pagurus* spp.; *Petrolisthes cinctipes*, *P. eriomerus*, *P. manimaculus*) were collected during upwelling (when equatorward winds > 5ms^{-1}) and downwelling (when poleward winds >5 ms^{-1}) conditions. Settlement was higher during upwelling (79% of 9,678 crabs) than during downwelling (df=1, p-value <0.001). Although settlement varied among taxa (df=8 p-value <0.001) all taxa, with the possible exception of *Cancer magister* were more abundant during upwelling than downwelling (taxa vs. oceanographic condition df=8, p-value=0.22) (Figure 1.12).

We propose that diel postlarval vertical migration and vertical current shear may account for the observed higher rate of settlement during upwelling in the northern region of the bay. Field studies (Peterson et al. 1979) showed the importance of vertical migration in maintaining populations over shelf regions where winds (and thus shelf export) are strong. In the case of Bodega Bay, during periods of upwelling, crab postlarvae may vertically migrate to take advantage of the surface equatorward flow and deep poleward flow, thus allowing them to remain in the bay for longer periods of time. Surface drifter data (Figure 1.11a) confirm that postlarvae would be exported from the bay during upwelling conditions if they were to remain in surface waters. During periods of downwelling and relaxation, the poleward flow along the eastern shore could act to transport postlarvae poleward, again confirmed by the surface drifter data (Figure 1.11b). During these conditions postlarvae may be exported out of the bay to the north or may return along the eastern edge of Bodega Rock. Cyclonic recirculation in the bay can be present at depth under most conditions, providing a mechanism for postlarval retention. However, during upwelling, the cyclonic recirculation patterns are strongest due to the separation-driven sheared flow along the eastern edge of the bay, which may account for the increased settlement observed during strong upwelling favorable winds.

To investigate the possibility of larval retention in the vicinity of the PR settlement site, depth averaged velocities in near-surface and near-bottom layers (Figure 1.8) were used to advect ‘larvae’ for a 3 day period. One thousand particles were released for each of three conditions; upwelling, downwelling, and relaxation and were advected either in the upper layer, the lower layer, or with a combination of diel vertical migration (Hobbs and Botsford 1992). The vertically migrating particles spent 9 hrs in the surface (night) and 15 hrs at depth (day) based on the average hours of daylight in Bodega Bay during summer. At each time step the velocities were perturbed with a random white noise component (of the same order of magnitude as the standard deviation of the velocity), which represents the shear dispersion a particle would experience in the ocean. By way of comparison the same procedure was undertaken at the BML site on the open coast.

During upwelling conditions any ‘larvae’ in the surface waters at the BML site would be advected alongshore, away from the local region (traveling 18–24 km equatorward, Figure 1.13). By contrast if larvae were in the surface waters at the PR site they would only travel 7–14 km equatorward. At depth, particles/larvae at the PR site would be advected 8–10 km poleward compared with 5–6 km equatorward from BML (Figure

1.13). Clearly the displacement estimates do not indicate the real destination of particles/larvae, but rather the transport effect in the vicinity of the ADCP similar to a ‘progressive vector diagram’.

The retention benefit of the recirculation at depth can be seen for ‘larvae’ that migrate vertically between the upper and lower layers in response to local light conditions. The majority of particles experienced near-zero alongshore advection at PR (with a maximum advection of 3 km poleward). Whereas the same behavior at the BML site on the open coast, (where the current velocity exhibits less vertical shear) does not prevent equatorward transport. Here there was displacement (although reduced) of the order of 12 km, occurring in 3 days (Figure 1.13). Clearly the PR site and northern sub-bay provide a location in which vertically migrating larvae may be retained.

SUMMARY

This comprehensive field study, conducted during the summer of 2004, provided a thorough investigation of the flow patterns within Bodega Bay during upwelling, downwelling, and relaxation conditions and allowed for a generalized description of the circulation within Bodega Bay under each wind-forcing regime. The oceanographic data show evidence of a variation on the upwelling shadow theme, where during upwelling, surface waters are flushed rapidly from the bay by strong equatorward winds, yet water is retained at depth in the northern bay through vertical current shear along the eastern shore. Postlarvae settled in higher numbers in the lee of Bodega Head during upwelling conditions, and we propose that postlarvae accumulate in the northern region of the bay by vertically migrating within the sheared flow. Despite the small scale of the Bodega headland, recirculation features are apparent, and can facilitate the retention of zooplankton. Hence circulation studies of this scale hold an important place in interdisciplinary marine ecology.

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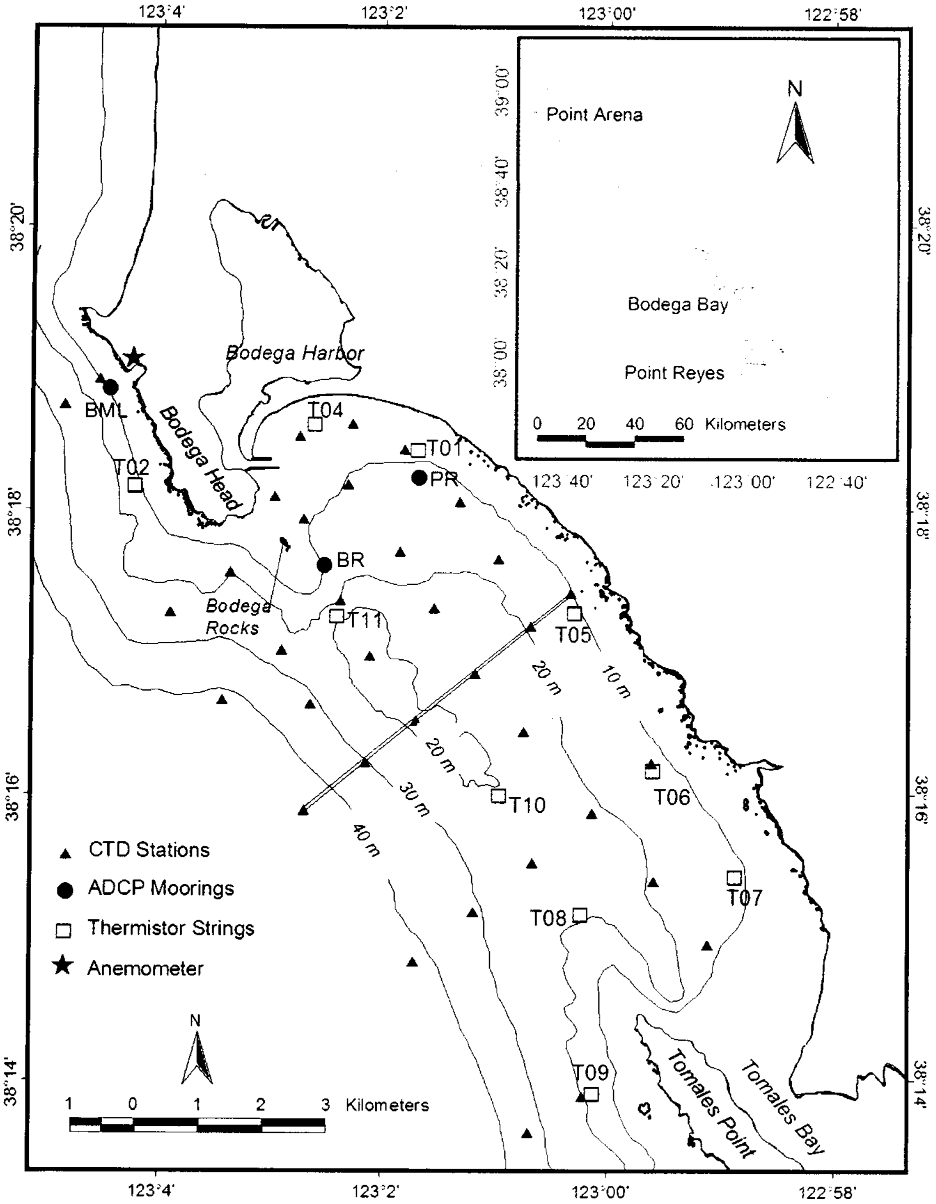

Figure 1.1. Map showing the location of the 30 CTD stations (triangle), 3 ADCP moorings (circle) and 10 thermistor strings (square). The straight black line represents a CTD transect within Bodega Bay and the light black lines are the bathymetric contours. The inset shows the location of Bodega Bay north of Pt Reyes on the west cost of the USA.

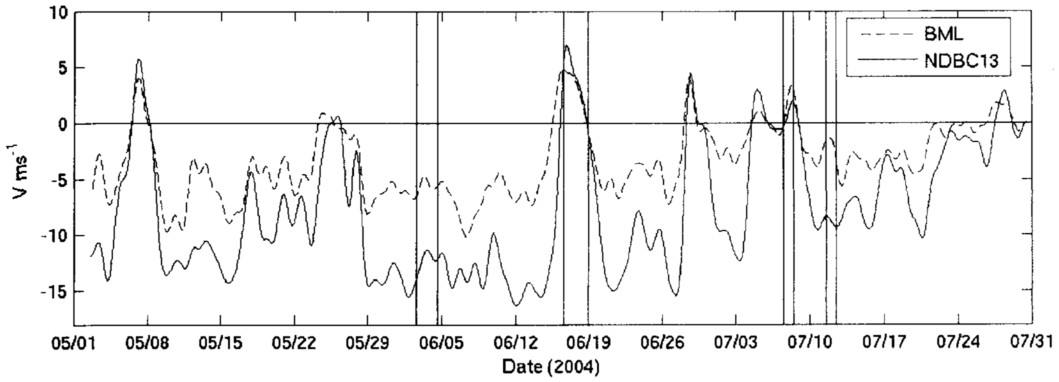

Figure 1.2. Time series of alongshore wind (ms^{-1}) at BML (dashed) and NDBC 46013 (solid). The gray bars represent the 4 survey periods; upwelling, downwelling, relaxation, and incipient upwelling respectively.

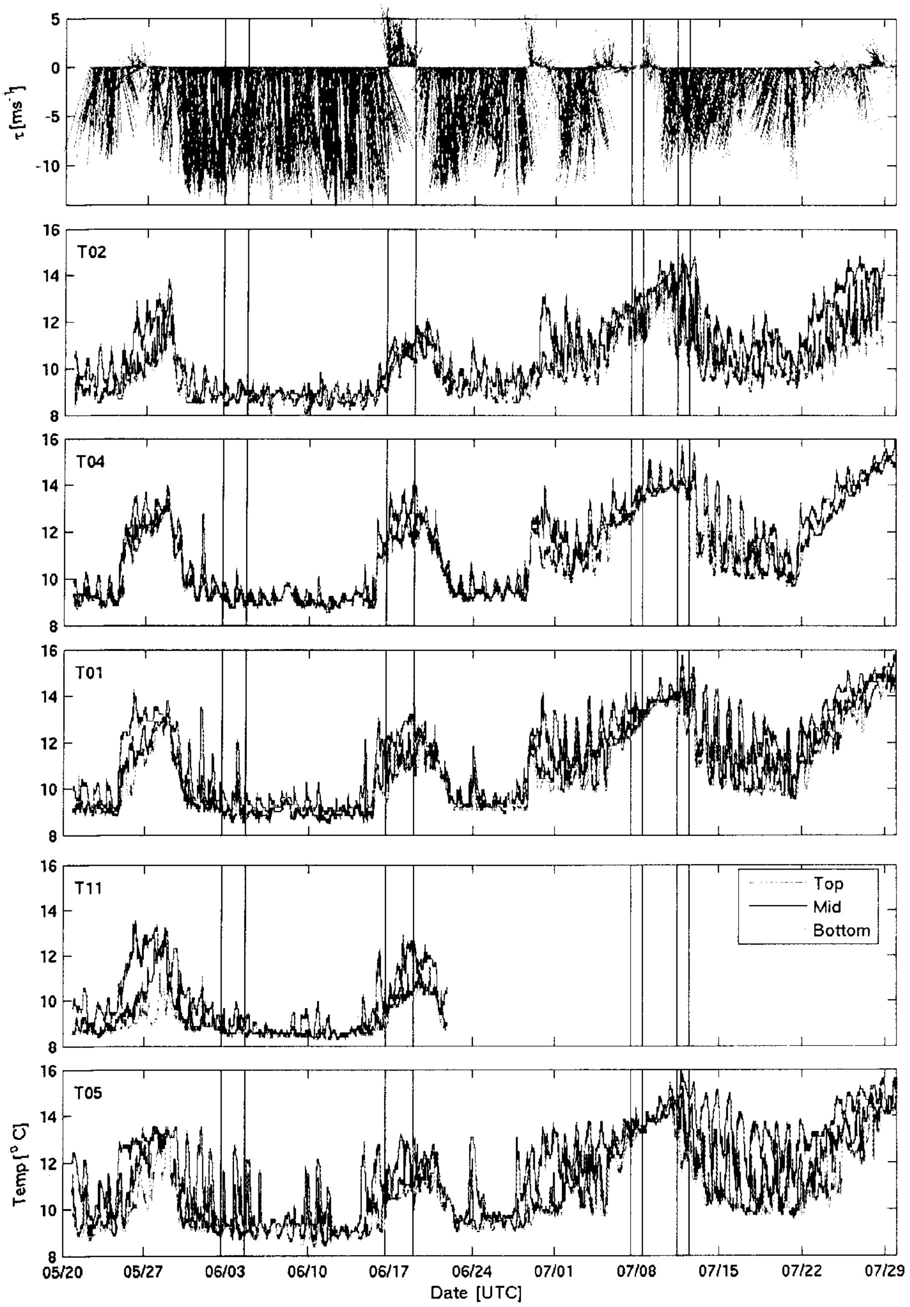

Figure 1.3. Top Panel: Hourly vectors of wind velocity (ms^{-1}) from NDBC 46013 where positive values are alongshore poleward. Lower Panels: time series of temperature ($^{\circ}$C) in the northern half of Bodega Bay at three depths; 1 m off the bottom (approximately 14 m); mid water column (approximately 8 m); and 1 m below the surface. Shaded areas represent the timing of the four hydrographic surveys.

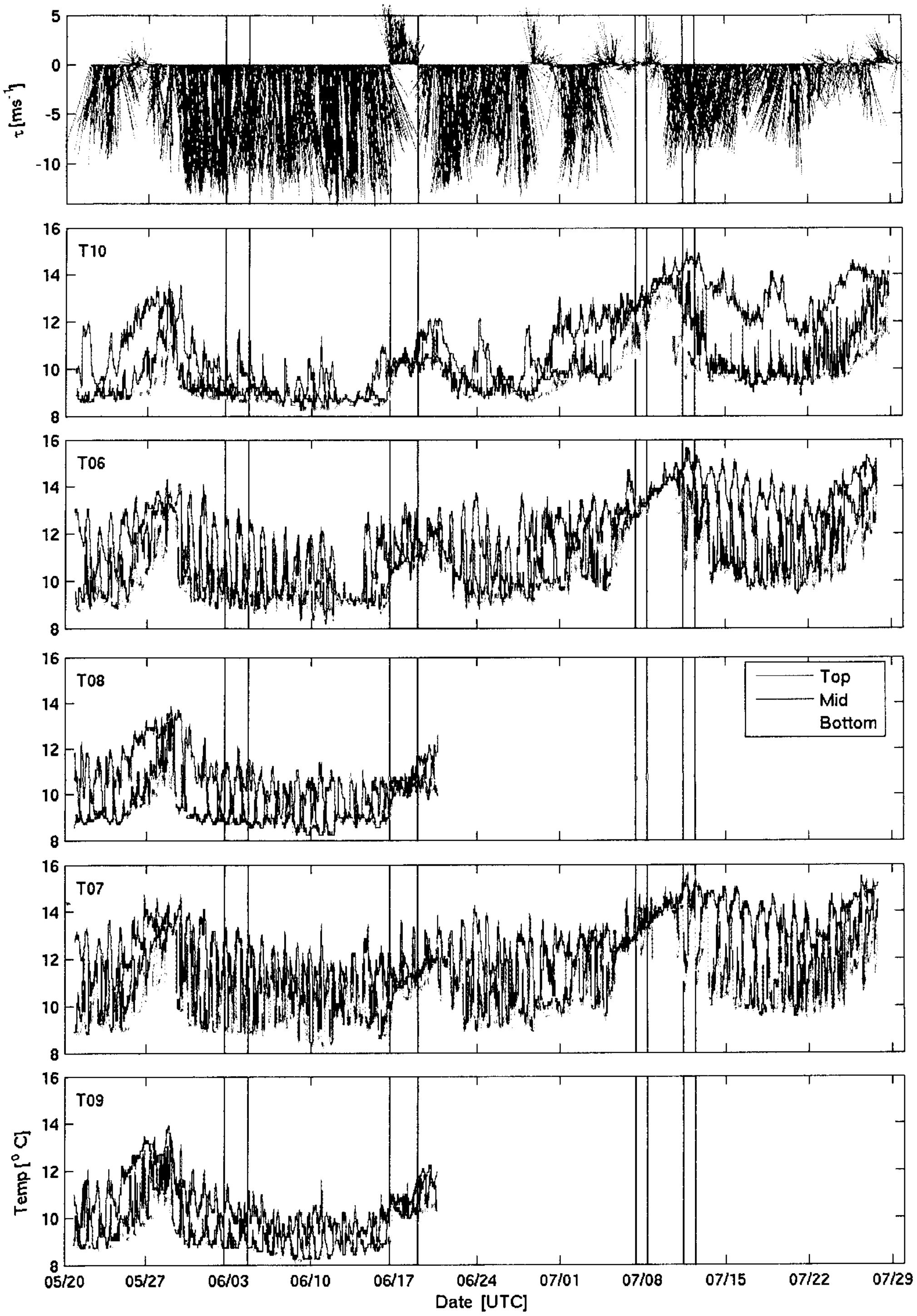

Figure 1.4. As for Figure 1.3 for the thermistors in the southern half of Bodega Bay.

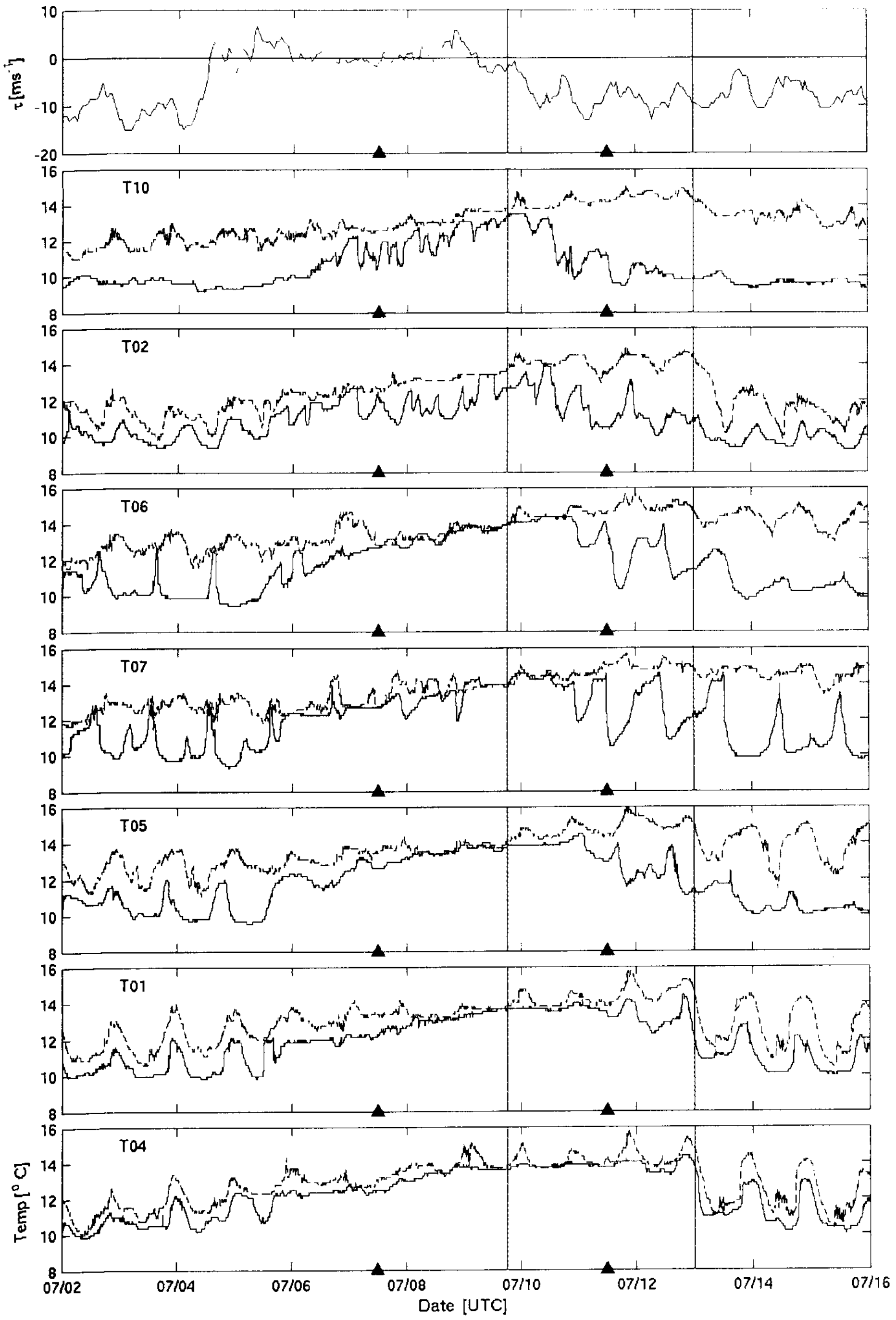

Figure 1.5. Top panel shows alongshore component of wind velocity (ms^{-1}). Lower panels show temperature time series (°C) at each of the thermistor moorings. The vertical lines delineate the timing of an upwelling event and the associated cooling of bottom waters. The triangles represent the timing of the hydrographic surveys.

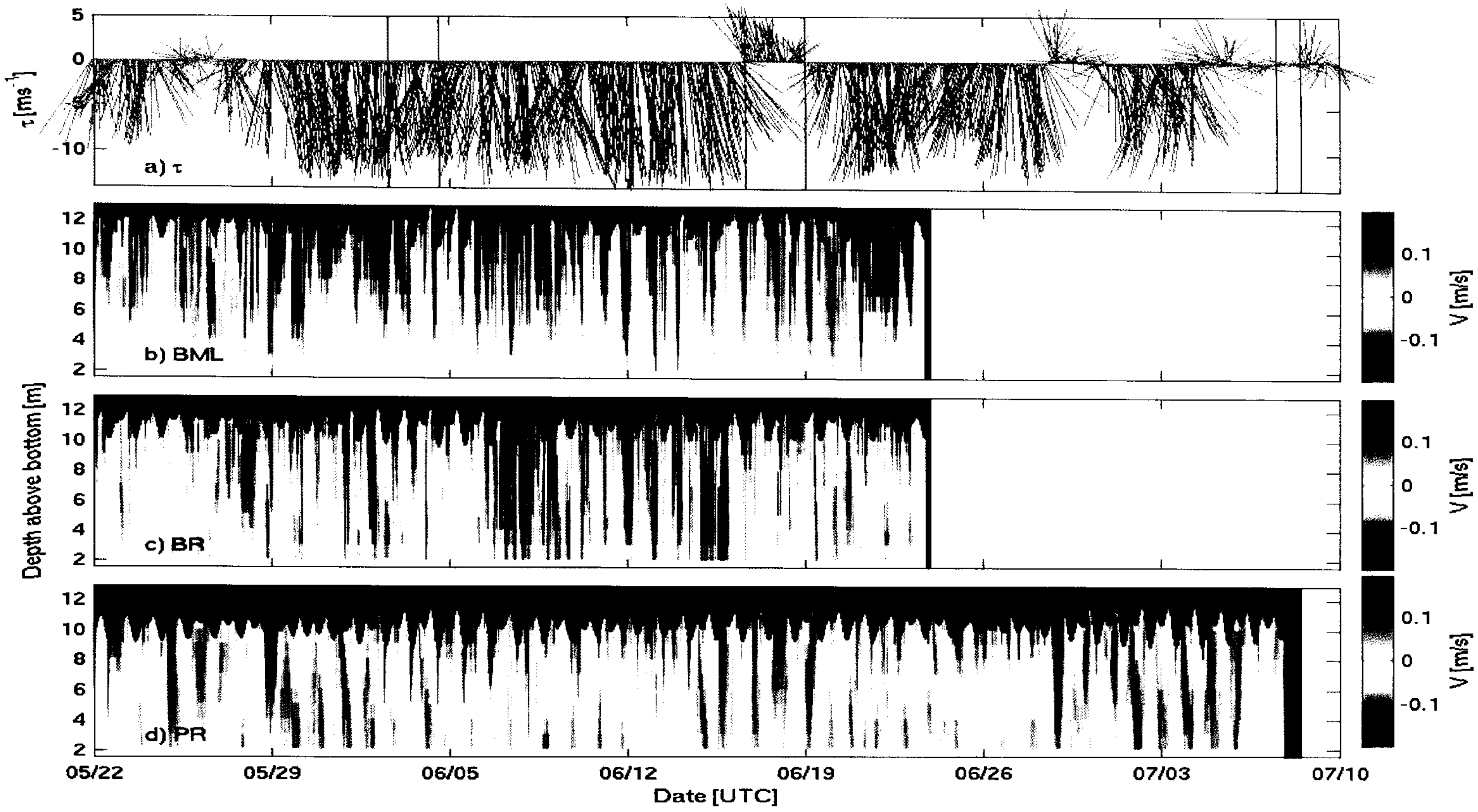

Figure 1.6. Time series of a) wind (ms^{-1}) at NDBC 46013, and alongshore current (ms^{-1}) at b) Bodega Marine Lab (BML), c) Bodega Rock (BR) and d) Pinnacle Rock (PR). For the current plots the y-axis represents distance above the bottom and the black shading in each panel represents the sea surface elevation obtained from the pressure recorded by the bottom-mounted ADCP. As for the wind time series, positive (red) velocities are directed poleward in the alongshore direction.

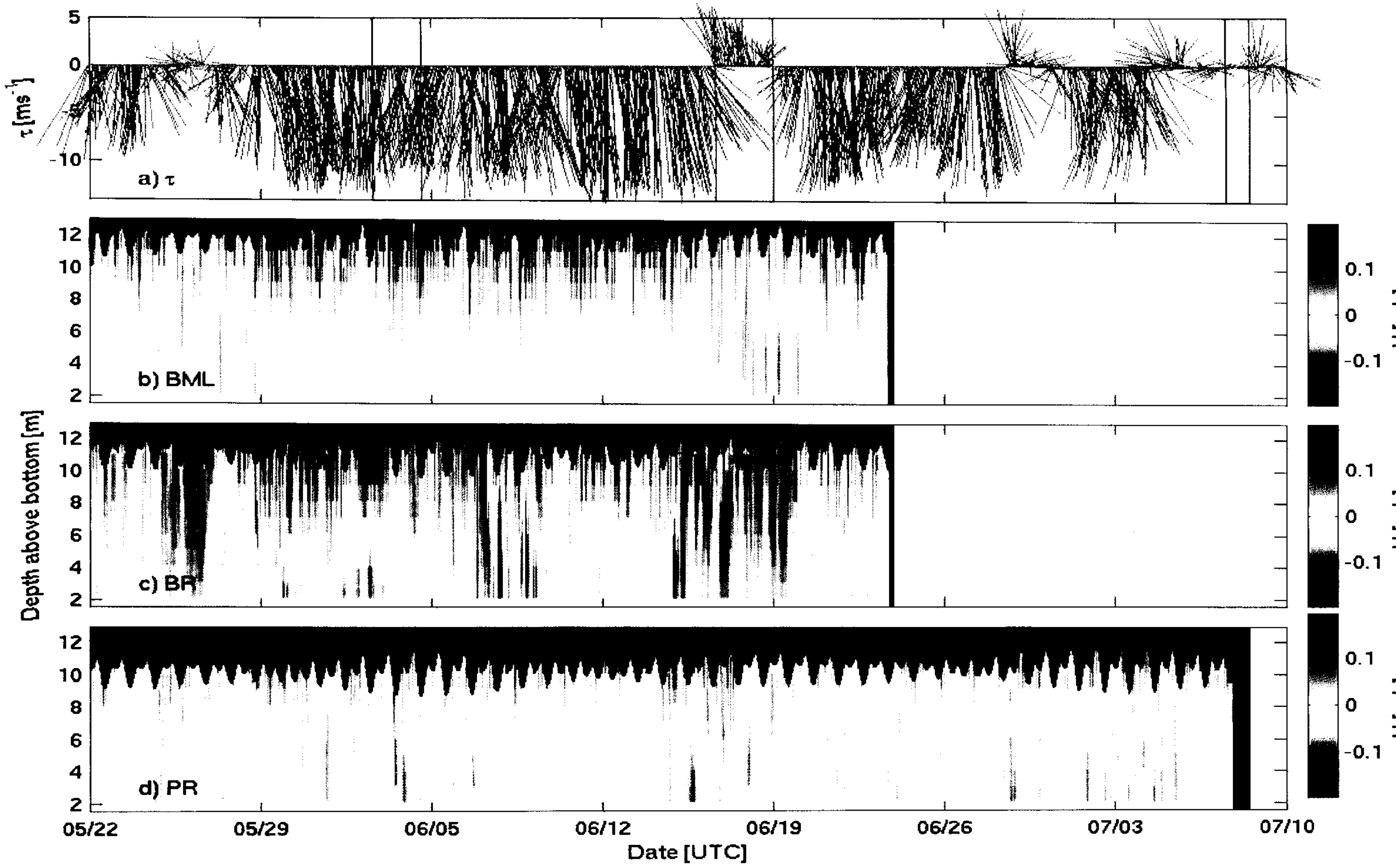

Figure 1.7. As for Figure 1.6 but the current velocities are in the across-shore direction.

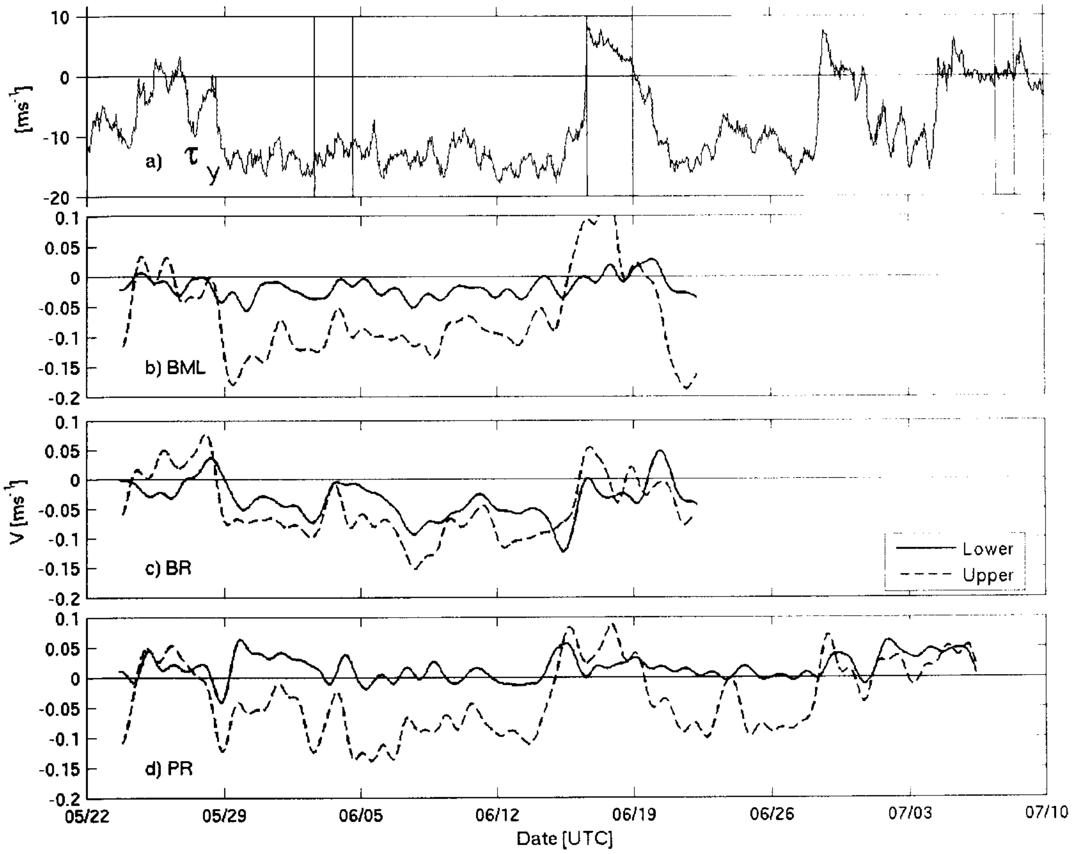

Figure 1.8. a) Alongshore component of wind (ms^{-1}), and depth averaged alongshore velocity at BML, BR and PR (b–d) respectively. Depth averaged velocities are calculated for an upper layer (8–10 m above the bottom) and a lower layer (2–6 m above the bottom).

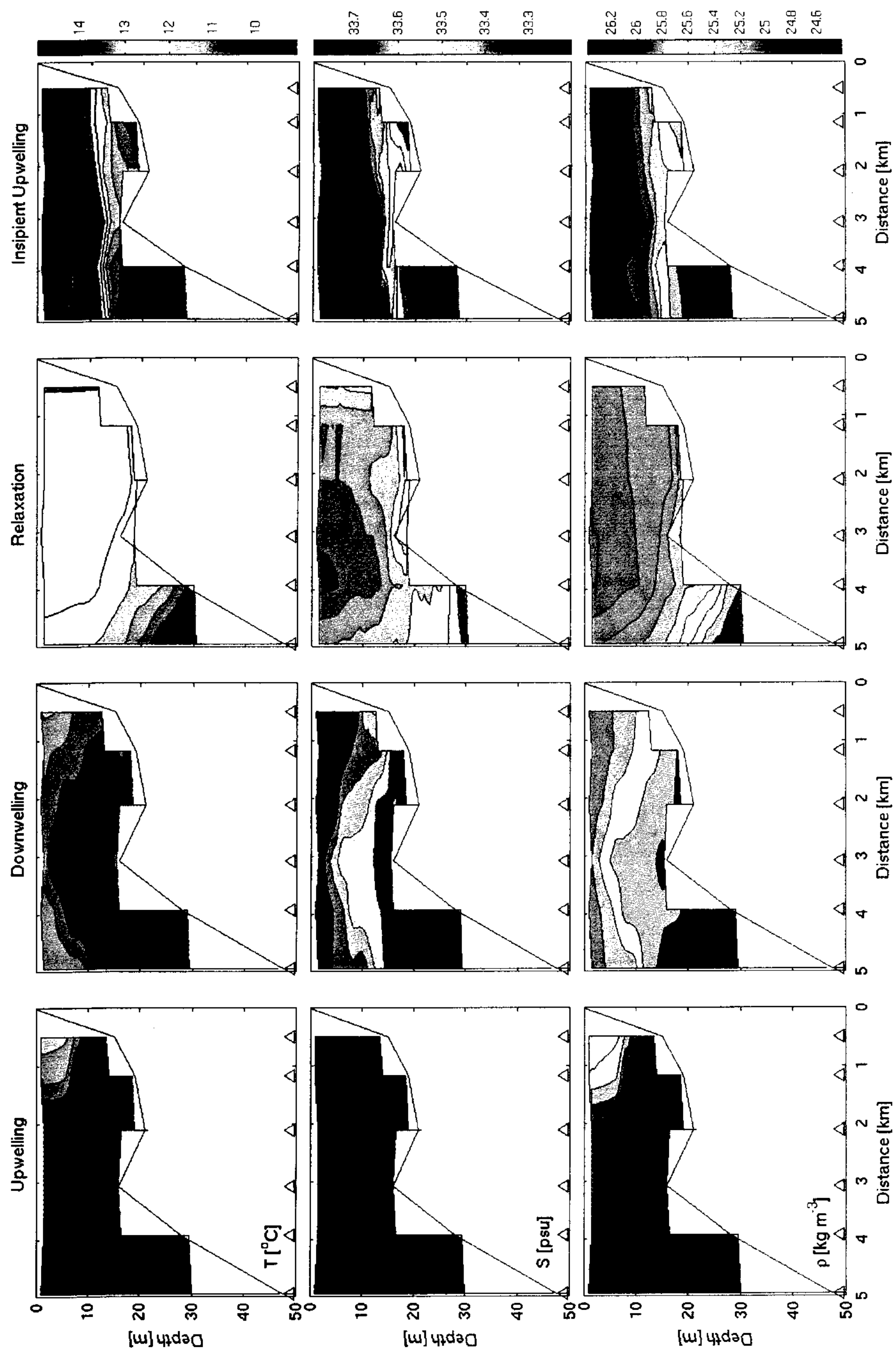

Figure 1.9. Cross sections of temperature (°C) (top row), salinity (psu) (middle row) and density (kgm^{-3}) (bottom row) along CTD transect 3 (mid-bay perpendicular to shore, Figure 1.1) during upwelling, downwelling, relaxation, and incipient upwelling conditions (L–R respectively).

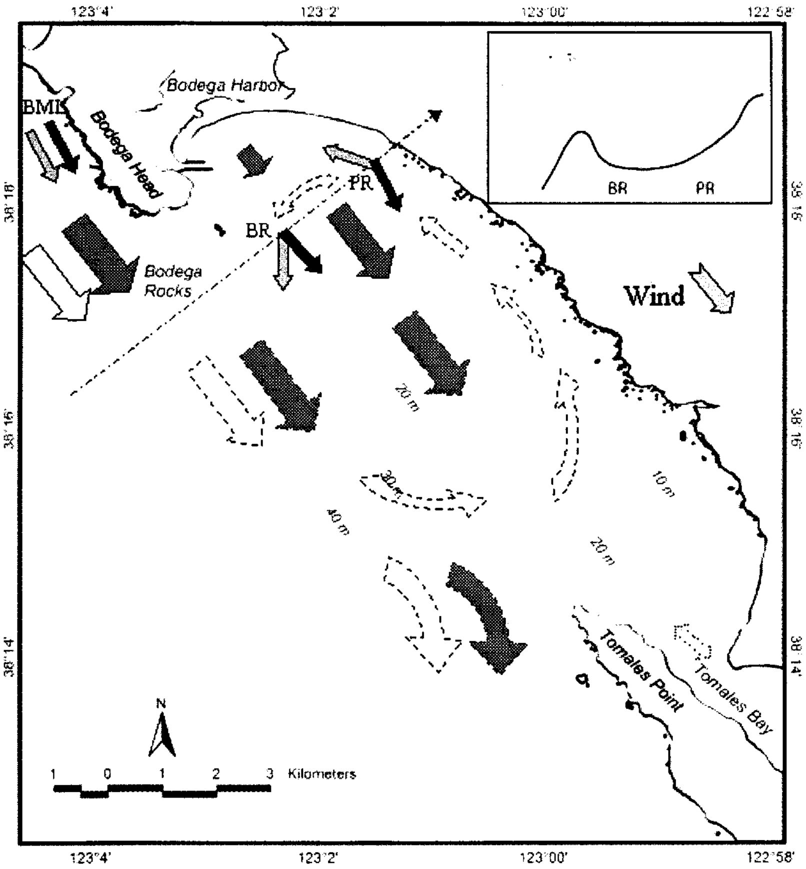

Figure 1.10. Schematic diagram of flow patterns observed in Bodega Bay under upwelling conditions. Smaller arrows at BML, BR and PR sites show direction of observed near-surface (dark) and near-bottom (light) currents, whereas larger arrows show postulated circulation patterns near-surface (dark) and near-bottom (light). Arrows with dashed outlines indicate a flow pattern that is suggested by a combination of observed currents at ADCP sites, drifter tracks on 3–4 June 2004, and gradients in water temperature. Arrows with solid outlines represent flow patterns in which we have confidence due to their proximity to direct ADCP or drifter observations. Arrow length/size is not intended to reflect current speed. The inset shows a cross-section of flow in the bay, with vertical shear along the eastern shore and equatorward flow at all depths in the outer bay.

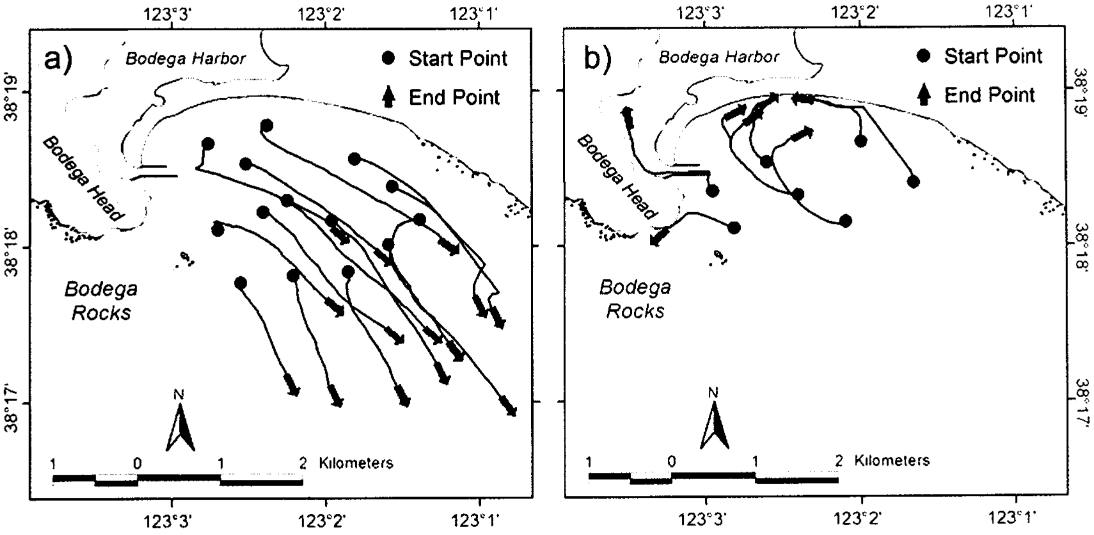

Figure 1.11. Surface drifter tracks during a) upwelling conditions (3 and 4 June 2004) and b) downwelling conditions (19 June 2004).

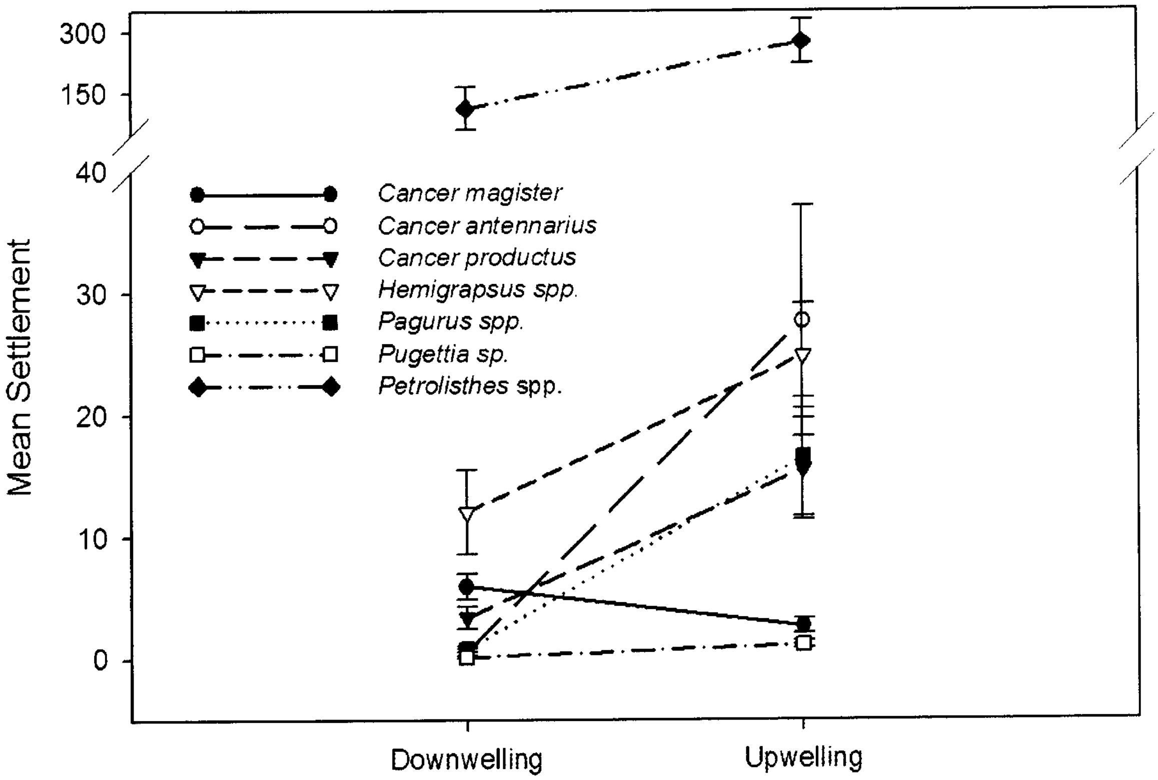

Figure 1.12. Postlarval settlement of 7 crab taxa (± SE) at the PR site during upwelling and downwelling conditions. Note that higher settlement occurred during upwelling for all taxa except *Cancer magister*.

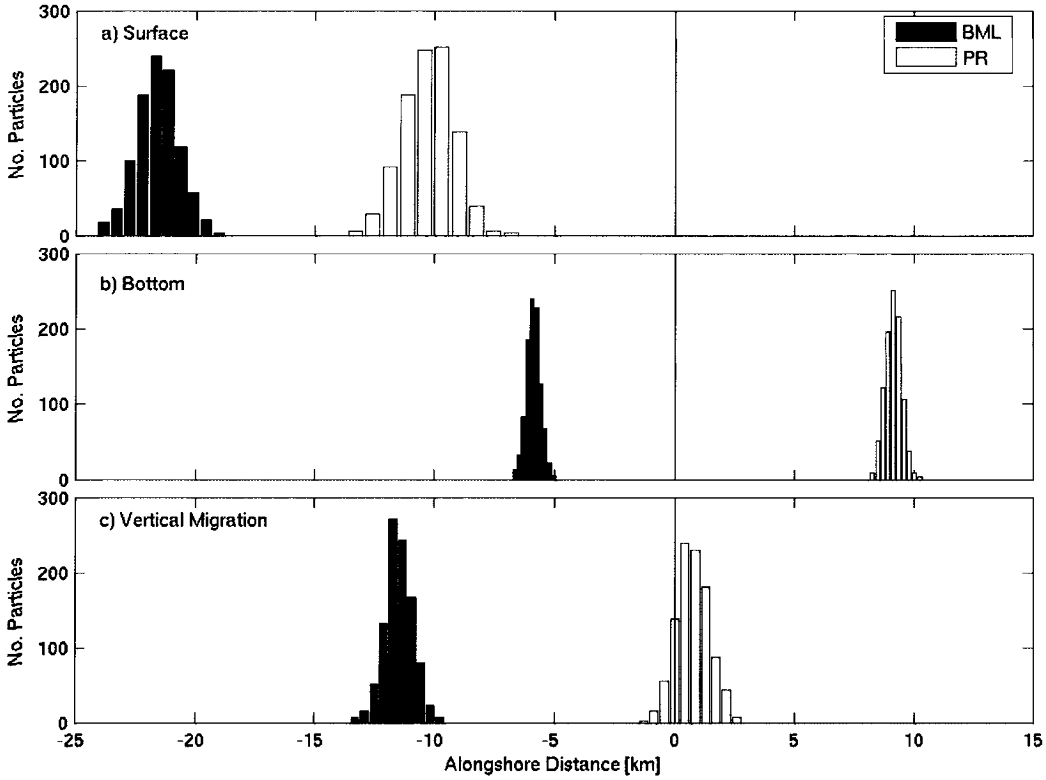

Figure 1.13. Histogram of the alongshore displacement of particles ('larvae') advected for 3 days by depth averaged velocities observed at the BML and PR sites during upwelling conditions. Results are shown for the transport of 1000 particles in a) the upper layer, b) the lower layer, and c) a combination of the two layers through diurnal vertical migration with each particle experiencing 9 hours at the surface overnight and 15 hours at depth during daylight hours. The vertical line delineates zero displacement.

Table 1.1. Details of ADCP and thermistor deployment May to July 2004. Latitude and Longitude are in WGS 84. Three Optic StowAway TidbiT® thermistors were located on each temperature mooring: 1 m off the bottom, mid water column, and 1 m below the surface. Temperature ± 0.2°C was recorded every 2 min. *short record length because moorings were lost.

Instrument type	Mooring Name	Date Deployed	Record Length (days)	Latitude °N	Longitude °W	Water Depth (m)
ADCP	PR	19-May	49	38 18.3612	123 1.6800	12.2
ADCP	BML	21-May	33	38 18.8478	123 4.4598	11.6
ADCP	BR	21-May	33	38 17.6070	123 2.5308	13.1
Temperature	T1	20-May	73	38 18.4150	123 1.7030	13.7
Temperature	T2	20-May	73	38 18.1640	123 4.2360	13.7
Temperature	T4	20-May	73	38 18.5920	123 2.6260	7.6
Temperature	T5	20-May	73	38 17.2699	123 0.3060	16.8
Temperature	T6	20-May	73	38 16.1639	122 59.6000	13.7
Temperature	T7	20-May	73	38 15.4199	122 58.8700	13.7
Temperature	T8	20-May	31*	38 15.1580	123 0.2400	21.3
Temperature	T9	20-May	31*	38 13.9000	123 0.1290	15.2
Temperature	T10	20-May	73	38 15.9890	123 0.9710	24.4
Temperature	T11	20-May	31*	38 17.2490	123 2.4190	18.3

Table 1.2. Wind forcing, dates, wind strength and stage of the tide during each of the 4 CTD surveys.

Developed Upwelling	3 June 2004	Wind NW 10-15 ms^{-1}	Flood tide, range 1.5 m
Downwelling	19 June 2004	Wind S 6-12 ms^{-1}	Flood tide, range 0.9 m
Relaxation	7 July 2004	Wind Variable < 3 ms^{-1}	Slack tide, range 1 m
Insipient Upwelling	11 July 2004	Wind NW 8-12 ms^{-1}	Weak Ebb, range 0.5 m

Larval accumulation in the lee of a small headland: Implications for the design of marine reserves

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Key words: larval retention, larval dispersal, headland eddy, recirculation, marine reserve, meroplankton

ABSTRACT

Oceanic currents and larval accumulation potentially have large impacts on the choice of locations for marine reserves. Larval settlement of benthic invertebrates was greater in the lee than the windward side of a small headland during the height of upwelling in central California during 2001 and 2002. Strong upwelling during the study was indicated by mean annual Bakun indices of 149–176 m^3 s^{-1} per 100 m of coastline in 2001–2002. Weekly sampling of near-surface and near-bottom settlement in the lee of Bodega Head from August 2000–September 2001 revealed that most larvae of seven crab taxa settled during spring and summer when upwelling was strongest. Comparison of sites in the protected (lee) and the exposed (windward) side of the headland (two sites each) during the peak settlement season in 2001 showed most larvae settled in the lee of the headland, including 91% of crabs, 89% of barnacles, and 80% of mussels in weekly samples. During 2002, weekly sampling at one protected and one exposed site also demonstrated that most settlement occurred in the lee of the headland, including 74% of crabs, 82% of barnacles, and 65% of mussels. Crabs settled mostly at the surface, whereas barnacles and mussels primarily settled near the bottom. Larval accumulation zones should be included in networks of marine reserves to supply adult populations with propagules in recruitment-limited upwelling regions.

INTRODUCTION

The distribution and abundance of benthic organisms have often been attributed to postsettlement mortality from competition, predation, physical disturbance, and environmental stress (reviewed by Duffy & Hay 2001, Sousa 2001) as well as enhanced survival from facilitation (reviewed by Bruno & Bertness 2001). Most species of benthic marine organisms produce planktonic larvae that spend several months at sea transported by currents, and larvae must return to suitable adult habitat before they face these postrecruitment challenges. After a long history of focusing on the adult phase of the life cycle, there has been a resurgence of interest in identifying where and how larvae accumulate in space and time, which is key to understanding the dynamics of benthic marine populations and communities (reviewed by Morgan 2001, Underwood & Keough 2001). This is particularly important in recruitment-limited areas where larval supply may be more important than postsettlement mortality in structuring the distribution and abundance of adults. In general, the distribution and abundance of adults may be determined primarily by postrecruitment processes in areas where settlement is high and largely by spatial and temporal variation in larval abundance where settlement is low (Connell 1985, Gaines & Roughgarden 1985, Minchinton & Scheibling 1991, Menge 2000a).

Along the Pacific coast of the USA, larval supply of barnacles and mussels was higher along the coast of Oregon and Washington than California, possibly due to a gradient of increasing upwelling strength from north to south (Connolly et al. 2001). High larval settlement in the northern latitudes intensified post-settlement processes and increased mortality, thereby dampening the community-level effects of temporal and spatial variation in larval abundance (Menge 2000b). In contrast, recruitment limitation from the strong offshore transport of surface waters and larvae occurred along the California coast, reportedly holding adult populations below carrying capacity (Gaines & Roughgarden 1985). Consequently, episodic increases in the supply of larvae may increase adult populations.

At a smaller spatial scale, topographic features of shorelines appear to generate predictable variation in the larval supply to adult populations and communities (Ebert & Russell 1988). Several studies have observed increased zooplankton abundance and larval settlement in the lee of headlands (Caffey 1985, Murdoch 1989, Gaines & Bertness 1992, Rankin et al. 1994, Wing et al. 1995b, Graham & Largier 1997, Wing et al. 1998, Archambault & Bourget 1999, Lagos et al. 2002). In upwelling regions, larval supply was greater on the leeward side of major headlands, where larvae may be entrained into waters that are retained there (Wing et al. 1995a, Wing et al. 1995b), than on the windward side where strong upwelling jets may advect larvae far offshore (Wing et al. 1995a, Wing et al. 1995b). When winds relax, the larvae-rich waters in the lee of the headland may flow poleward around the headland allowing for settlement of larvae on the poleward side of the headland. Although upwelling generally decreases during the El Niño Southern Oscillation events, settlement along the poleward side of a major headland was observed to decrease rather than increase, perhaps due to the decline in productivity of the California Current System (Lundquist et al. 2000) or due to the absence of this upwelling-related larval accumulation and poleward transport mechanism. Previous studies of headlands have generally been on a scale of 10-100 km (Murdoch 1989, Rankin et al. 1994, Graham & Largier 1997, Wing et al. 1998), except for a recent study around Point Loma in San Diego, California (Roughan et al. in press). It is unclear whether this mechanism operates around small headlands, which are much more common and relevant to the establishment of marine reserves (no-take zones), which typically are less than 10 km long. Information on large-scale processes (> 100 km) must be coupled with an understanding of processes at a smaller scale (< 10 km) in the nearshore environment to design an effective network of marine reserves, which should include areas that export larvae to adjacent reserves as well as areas that are hotspots of larval settlement.

Larvae that accumulate in the lee of small headlands may have been produced there or may have immigrated from elsewhere, and therefore we refer to such areas of high larval concentration as accumulation rather than retention zones, which indicate areas where larvae have been locally produced and retained (Warner et al. 2000). Small headlands may allow populations with planktonic larvae to persist by (1) increasing the retention of local larvae nearshore (Roughan et al. in review), (2) entraining remotely spawned larvae (Gaylord & Gaines 2000), and (3) accelerating larval development through elevated concentrations of food and warmer water, thereby reducing the pelagic larval duration and exposure to predation (Castilla et al. 2002, Lagos et al. 2002, Largier 2004).

Larval behavior also plays a role in keeping larvae near parental (and natal) habitats during development or by returning larvae to suitable settlement sites late in development (Morgan 1995, Shanks 1995, Kingsford et al. 2002, Sponaugle et al. 2002). Depth preferences coupled with vertical migrations between opposing stratified currents enable larvae to regulate alongshore and cross-shelf movements (reviewed in Morgan

1995). Onshore transport of late stage larvae may occur by winds, internal waves, and other physical mechanisms coupled with an ontogenetic shift in depth preference. Because multiple mechanisms may return larvae to shallow water habitats, both interspecific and congeneric differences in the timing of larval settlement to shallow water habitats may occur because larvae may exploit multiple onshore delivery mechanisms.

Larval accumulation and retention may be more common than once thought (Morgan 1995, Jones et al. 1999, Cowen et al. 2000, Hughes et al. 2000, Morgan 2001, Swearer et al. 2002). This results in a stronger link between stock and recruitment, greater vulnerability to reductions in recruitment from overfishing, greater possibility for local adaptation, and greater local benefit from marine reserves (Strathmann et al. 2002). Larval retention and cross-shelf migrations between adult habitats and larval nursery areas are critical to the success of a widespread reproductive strategy that involves the development of weakly swimming microscopic larvae in upwelling regions of a dynamic ocean (Roy 1998).

Evidence for larval accumulation in the lee of headlands comes from correlating settlement or recruitment of marine invertebrates such as crabs, barnacles, and urchins with physical water column measurements (Ebert & Russell 1988, Wing et al. 1995b, Lagos et al. 2002). However, depth preferences also may play a role in the accumulation of larvae in the lee of headlands. Therefore, to test the effect of coastal topographical features on larval supply, we investigated settlement of larvae around Bodega Head, a small headland in a strong upwelling region, for 3 years. In a concurrent study we found that cyclonic recirculation in Bodega Bay at depth, provides a potential mechanism for retaining larvae and accumulating postlarvae (Roughan et al. in review). Cyclonic recirculation was strongest during upwelling due to the increased equatorward alongshore flow past Bodega Head. Recirculation weakens during relaxation or downwelling, potentially exporting larvae north of the headland. The objectives of the present study were to determine (1) the strength of upwelling, (2) seasonal patterns of larval settlement by benthic invertebrates, (3) settlement at exposed and protected sites around the headland, and (4) the synchrony of larval supply to exposed and protected sites. We then draw inferences for the design of marine reserves.

MATERIALS AND METHODS

Study area

The study was conducted around Bodega Head (38°18' N 123°04' W) in central California, which is characterized by persistent equatorward winds during spring and summer (Fig. 2.1). Bodega Bay occurs on the leeward side of this small headland and is a shallow, broad, southwest-facing embayment. The bay mouth is approximately 11 km wide from the northern tip at Bodega Head to the southern tip at Tomales Point, expanding to 15 km wide landward of the mouth, and is approximately 3.5 km from mouth to shore. The rocky outcrops of Bodega Head and Tomales Point continue as a shallow (< 15 m deep) submarine ridge across the mouth of the bay. The ridge rises to the surface to form Bodega Rocks toward the northern end of the bay. The bay is 20–25 m deep, and depths steeply increase to more than 40 m seaward of the ridge. Tides are mixed semi-diurnal with a tidal range of 1.2–2.9 m.

Upwelling

Offshore wind speed and direction were obtained from the National Data Buoy Center (NDBC 46013, 38°13'30" N 123°19'00" W; http://www.ndbc.noaa.gov/) and local wind velocities were obtained from a land-based site at Bodega Marine Laboratory (BML, 38° 19' 03.35" N 123° 04' 17.20" W, http://bml.ucdavis.edu/boon/). Alongshore winds at BML and the NDBC buoy were correlated to 95% confidence with r = 0.88 and a lag of 2 hours (BML leads NDBC) (Roughan et al. in review). Wind data from the offshore buoy were used because they are more representative of larger scale wind forcing events. Alongshore windstress was calculated (Large & Pond 1981) from 10-min averaged data that was adjusted to a height of 10 m above sea level using a neutral stability wind profile and rotated to a principal axis of 317° T. Negative values indicate equatorward windstress and larger negative values reflect stronger upwelling-favorable winds. Low or positive values are associated with relaxation or downwelling conditions.

Upwelling indices (from 39°N 125°W) were obtained from the National Oceanographic and Atmospheric Administration's Pacific Fisheries Environmental Laboratory (PFEL), Pacific Grove, California (http://www.pfeg.noaa.gov/). Positive values indicate upwelling and offshore transport of surface waters resulting from equatorward windstress, and low values indicate relaxation of upwelling. Negative values indicate downwelling and the onshore advection of surface waters due to poleward windstress. Average of mean daily values of upwelling indices for April 30 to August 13, 1995–2004 were compared to those obtained during 2001–2002 (Lundquist et al. 2000).

Daily averages of temperature were obtained from two Optic StowAway TidbiT® thermistors, which were attached to a settlement mooring at each site. On each mooring thermistors were placed 1 m off the bottom (approximately 9 m deep) and 1 m below the surface. Temperature ± 0.2 °C was recorded every 6 min. Daily averages of salinity ± 0.005 psu were obtained from a Sea-Bird Electronics thermosalinograph (SBE 45 MicroTSG) that was situated in the seawater intake line at BML (http://bml.ucdavis.edu/boon/). The correlation between alongshore windstress and temperature was calculated to determine if there was an upwelling response to wind variability, and the correlation between local temperature and salinity was calculated to determine the local response to changes in wind conditions.

Larval settlement

Larval settlement by benthic invertebrates was monitored year-round (August 2000–September 2001) at the Jetty site (JT) to assess how settlement varied through the year (Fig. 2.1). During 2001 and 2002 larval settlement was monitored weekly around Bodega Head 1 m below the surface and 1 m above the bottom during the peak settlement season, which was determined during the first year of the study to extend from April to September (see also Wing et al. 1995b, Lundquist et al. 2000, Wing et al. 2003). During 2001, settlement was monitored at two sites on the windward (exposed) side of the headland at Bodega Marine Laboratory (BML) and Bodega Head (BH), and at two sites in the lee (protected) side of the headland at Jetty (JT) and Pinnacle Rock (PR) (Fig. 2.1). Three of these sites (BML, JT, PR) were situated adjacent to onshore long-term monitoring of rocky intertidal communities by the Gulf of the Farallones National Marine Sanctuary or Bodega Marine Laboratory. Larval settlement has been monitored at the

BML site since 1992 (Wing et al. 1995b, Lundquist et al. 2000, Wing et al. 2003). During 2002, only one exposed (BML) and one protected site (PR) were sampled.

Each site consisted of an array of three moorings with attached collectors spaced approximately 50 m apart along the 10 m isobath. For comparison among sites, collectors were placed at similar depths (10 m) and habitats (sandy substrate adjacent to submerged rocks). Settlement substrate for crabs, mussels, and echinoderms consisted of two mesh 10 × 30 cm bags each containing three Tuffy® kitchen scrub pads. Artificial settlement substrate for barnacles was a 10 × 10 cm polyvinylchloride plate covered on both sides with black 3M® safety walk tape. Collectors were rinsed in fresh water, and settlers were fixed in 50% ethanol. Postlarvae and juveniles were identified to species when possible using available keys (Lough 1974, Shanks 2001). *Cancer productus* and *Cancer antennarius* were distinguished as juveniles but not as postlarvae. These species were collectively called *Cancer antennarius/productus,* even though 79% of the juveniles were *C. antennarius*. Similarly, *Pugettia producta* and *Pugettia richii* were not distinguished at the postlarval stage, although 95% of the juveniles collected were identified as *P. producta*. Sea stars (*Pisaster* spp. and *Leptasterias* spp.), urchins (*Stronglyocentrotus franciscanus* and *S. purpuratus*), and barnacles were combined (except *Lepas* spp.) due to difficulty of correctly identifying new recruits.

Data analysis

Because protected and exposed sites may be influenced by mesoscale oceanographic features, they may be environmentally correlated and would not meet the primary assumption of standard parametric analysis: independent replicates. Thus randomization tests were used to determine whether settler abundance differed between exposure (sites), settlement depth, and year. A distribution of F-ratios was generated via parametric bootstrapping and used to test whether the observed differences were statistically significant. Random samples of 1000 $\log_{10}$-transformed abundance of settlers were drawn, with replacement, to generate a distribution of F-ratios and p-values. A factorial model was used considering site (protected vs. exposed), year (2001 vs. 2002), depth (surface vs. bottom), and all interactions. Because two sites (BML and PR) were monitored in 2002, only two (BML and PR) of the four sites from 2001 were included in the analysis.

To determine if settlers arrived at the same time on each side of the headland during 2001 and 2002, the abundance of settlers at a protected site (PR) were correlated with those at an exposed site (BML) ($n = 129$). A positive relationship would indicate that a mesoscale oceanographic feature consistently delivered larvae to exposed and protected sites in similar numbers, whereas a negative relationship would indicate that while one site received larvae during a specific condition the other site received larvae only under other conditions. Alternatively, no relationship would be found if larval retention or accumulation resulted in settlement in the lee of the headland independent of the settlement at the exposed site.

RESULTS

Upwelling

Characteristic upwelling winds with brief periods of weaker wind occurred during the spring and summer, and the strength and duration of these cycles varied among years. Upwelling was strong during 2001–2002 and was strongest in 2002 (Fig. 2.2). The average upwelling index (m^3 s^{-1} per 100 m coastline) for 2001 and 2002 was 149 ± 9 SE, and 176 ± 11 SE respectively. Long periods of upwelling were punctuated by brief periods of relaxation (Fig. 2.3). One upwelling event in 2001 lasted more than a month (late May to late June). When windstress increased (larger negative values) temperature decreased and salinity typically increased indicating the arrival of newly upwelled water, though the response was not as pronounced for salinity. Hence, there was an inverse relationship between windstress and temperature and a positive relationship between windstress and salinity. There was little inter-annual variation in the response of temperature and salinity to windstress as indicated by the similar high correlation values for 2001 and 2002 (Table 2.1).

Larval settlement

Sampling at site JT from August 2000 to September 2001 revealed that more larvae settled during the spring and summer than during the fall and winter (Fig. 2.4). During this year, 88% of crabs settled between May and August. Cancrids, porcellanids, and majids were most abundant, followed by small numbers of grapsids and pagurids. The three most abundant taxa settled throughout much of the year. However, cancrids were most abundant from January to July with a peak in May and June, porcellanids peaked in July and August, and majids were most abundant between May and August with a peak in June. No crabs settled during August 2000.

Twenty-one taxa of meroplankton, including species of crabs, barnacles, mussels, and urchins, settled during the upwelling season in 2001 and 2002 (Table 2.2), however (to avoid analysis of species with small sample sizes) only the 9 most abundant taxa were included in analyses. During 2001, higher settlement occurred at the protected sites (PR, JT) than the exposed sites (BML, BH) (Fig. 2.5); 91% of 9,722 crabs settled in the lee of Bodega Head including 98% of porcellanids, 86% of cancrids, 85% of grapsids, 71% of majids, and 57% of pagurids. Furthermore, 89% of *Balanus* spp. and 80% of *Mytilus* spp. also settled in the protected region in the lee of the headland. Higher settlement at the protected site again was apparent for most taxa during 2002, although some differences between depth distributions at protected and exposed sites were found (Table 2.3). More *Cancer antennarius/productus*, *Petrolisthes cinctipes*, *Petrolisthes eriomerus/manimaculus*, *Hemigrapsus nudus*, *Mytilus* spp., and *Balanus* spp. settled in the lee of Bodega Head than along the exposed coast (Fig. 2.6, Table 2.3). These species comprised 78% of the crab settlement in 2001 and 74% in 2002. Settlement of *Cancer magister*, *Pagurus* spp., and *Pugettia producta/richii* was similar at exposed and protected sites during 2001 and 2002 (Fig. 2.6, Table 2.3). The abundance of settlers was similar between years for six taxa, however more *Pagurus* spp., *Mytilus* spp., and *Balanus* spp. settled in 2002 (Fig. 2.6, Table 2.3).

Vertical stratification of settlers differed among and within taxonomic groups. Crabs predominately settled near the surface (*Cancer magister*, *Pagurus* spp., *Petrolisthes cinctipes*, *Hemigrapsus nudus, Pugettia producta/richii*), but there was no statistical difference between depths for *Cancer antennarius/productus* and *Petrolisthes eriomerus/manimaculus* (Fig. 2.6, Table 2.3). More *P. producta/richii* and *Pagurus* spp. settled at the surface in years of high abundance. In contrast to most crabs, *Mytilus* spp. and *Balanus* spp. consistently settled in much higher densities near the bottom.

The strongest positive relationship between the abundance of settlers at an exposed and protected site during 2001 and 2002 combined was obtained for *Cancer* *magister*, *Pugettia producta/richii*, *Pagurus* spp. and *Mytilus* spp., suggesting that these taxa may sometimes arrive at both sites at the same time (Table 2.4). The other five taxa showed a very weak relationship and all of them settled more abundantly in the lee of the headland.

DISCUSSION

Larval accumulation in the lee of headlands

Most larvae settled in the lee of Bodega Head during both years in which spatial patterns were investigated. Similar patterns have been observed around larger headlands, including Point Reyes (Wing et al. 1995a, 1995b) and Año Nuevo (Graham & Largier 1997) in central California and the Otago Peninsula in New Zealand (Murdoch 1989), but this is the first evidence that retention may occur in the lee of small headlands. In upwelling regions, upwelling shadows form in the lee of large headlands and are characterized by reduced local wind forcing, localized reversal of alongshore flow, and warm surface waters (Graham & Largier 1997). A variation of a typical upwelling shadow was seen in Bodega Bay (Roughan et al. in review). Upwelling-favorable winds were not sufficiently diminished by the low-lying headland to preclude upwelling and alongshore transport of surface waters in the bay, but recirculation of bottom waters did occur at depth, below the direct effect of the wind (Roughan et al. in review). This recirculation feature increased with increased upwelling (Graham & Largier 1997, Penven et al. 2000, Roughan et al. in review). Consequently, larvae that remained deep in the water column, or that vertically migrated between northward-flowing surface waters and southward-flowing bottom waters, may remain in the bay during upwelling conditions. Roughan et al. (in review) explored particle displacement during upwelling using water velocities observed at two of our settlement sites inside and outside of the bay (PR in the bay, BML outside the bay) and found that larvae undertaking diel vertical migrations would experience near-zero alongshore advection in the bay, while those at BML would be transported approximately 12 km alongshore over a 3-day period (Roughan et al. in review). Species of crab larvae collected during our study are known to undertake diel vertical migrations (Wing et al. 1998), which likely contributed to their accumulation and high settlement inside the bay.

Although the recirculation of bottom waters during upwelling may be the most likely mechanism responsible for the high settlement observed in the lee of Bodega Head, other explanations may be postulated. Though these alternative explanations cannot be evaluated, they are unlikely to yield such clear results and we do not explore these any further here. These include (1) reduced velocities observed in the bay, (2) wind or tidally generated fronts that may occur at the mouth of the bay which reduce exchange between bay and oceanic water, (3) greater transport into the bay due to non-linear internal waves either because of stratification in the bay or because of internal wave generation over the ridge at the mouth of the bay, (4) greater availability of rocky substrate outside the bay causing larvae to bypass collectors in favor of more suitable settlement sites nearby. Although fronts at the mouth of the bay may concentrate larvae and enhance residence time in the bay (Rankin et al. 1994), observations are anecdotal and fronts are likely to be transient. The observed recirculation of bottom waters would be more effective and reliable at retaining larvae at the consistently high levels found during this study. Furthermore, internal waves are more active during relaxation conditions (Rosenfeld

1990), but larvae of most species settled in the bay in high abundances during both upwelling and relaxation (Mace 2005). Differences in habitat availability inside and outside of the bay are also an unlikely explanation for higher settlement inside the bay, because all collectors were moored in sand next to a rocky shore.

Consistent interspecific differences in the vertical distributions of settlers were found, indicating that larvae regulated their position in the water column. Most species of crabs settled at the surface, and at least some of these species are known to be transported onshore in surface waters (Shanks 1985). A later companion study found that the vertical distributions of settlers was maintained during upwelling conditions even when the water column was well mixed; 85% of crab postlarvae settled at the surface during upwelling and 84% settled at the surface during downwelling (Roughan et al. in review). In contrast, barnacles and mussels settled in higher abundance near the bottom, indicating that they are transported onshore or settle in preferred habitats deeper in the water column (Grosberg 1982, Miron et al. 1995, Pineda & Caswell 1997, Miron et al. 1999). Despite interspecific differences in the vertical distributions of larvae, most taxa settled in the lee of the headland in greater abundances indicating that they are being entrained into the bay at all depths.

Settlement at exposed and protected sites was best correlated for *Pugettia producta/richii*, *Pagurus* spp., *Cancer magister,* and *Mytilus* spp., suggesting that larvae may be delivered to the nearshore environment by a single large-scale oceanographic event, however the weekly sampling interval prevented resolution of potential mechanisms. For example, Wing et al. (1995a) showed that larvae accumulated in the lee of Point Reyes during upwelling and were advected northward to Bodega Bay during relaxation periods, which may account for the fairly synchronous settlement of the 4 taxa at our study sites. Three of these taxa settled in similar numbers at exposed and protected sites high in the water column, whereas *Mytilus* spp. primarily settled in the lee of the headland low in the water column, suggesting that *Mytilus* spp. may have been more likely to become entrained in the bay at depth. A very poor relationship between settlement at exposed and protected sites was found for the remaining five taxa and all of them primarily settled in the lee of the headland, suggesting that they were entrained by the subsurface recirculation feature in the bay during upwelling events. It is likely that both of these large-scale and small-scale scenarios operate to varying degrees throughout the season and their effects on settlement are modulated by availability of competent larvae in the plankton, because settlement was only weakly synchronous for some taxa.

Temporal variation in larval accumulation

Prior to this study, seasonal variation in larval settlement by benthic invertebrates on the West Coast was not well known for many species (Strathmann 1987). We found that most crab species in this study settled throughout much of the year with peaks occurring from May through August. It is counterintuitive that larvae of shallow-water benthic invertebrates develop during the upwelling season (April–August) when offshore transport is most likely to occur (Parrish et al. 1981), because larvae must return to shore to replenish adult populations. Larval entrainment in the lee of both small and large headlands is most effective during upwelling (Graham & Largier 1997, Wing et al. 1998, Roughan et al. in review) and may facilitate larval settlement at many sites along the coast especially during strong upwelling years. During our study, larvae accumulated in the lee of Bodega Head during two strong upwelling years, and larvae of 3 taxa (*Pagurus* spp., *Mytilus* spp., *Balanus* spp.) settled more during the year of strongest upwelling. Moreover, an 8-year record of larval settlement at the BML site leading up to our study demonstrated that settlement increased during upwelling years, except in 1999, an exceptionally strong upwelling (La Niña) year that followed a strong El Niño year (Lundquist et al. 2000, Wing et al. 2003). However, the average upwelling index in 1999 was also similar to that recorded in 2002 (Fig. 2.2) when higher larval settlement occurred in the lee of the headland than at this exposed site.

Implications for the design of marine reserves

Our study demonstrated that larvae accumulated in the lee of a small headland, increasing larval settlement during the height of the upwelling season in two consecutive years of strong upwelling. Postlarvae were likely to be entrained in recirculating bottom waters and may be exported to adjacent areas along the exposed coast during relaxation events. The recirculation of bottom waters may have been facilitated by a submarine ridge that extended across the mouth of the bay, adding to the growing number of ways that accumulation zones may form in the lee of headlands. In addition to surface recirculation observed in upwelling shadows forming in the lee of large headlands, sub-surface recirculation cells may form behind small or low-altitude headlands. Further investigations are needed to identify other topographic features of coastlines that facilitate the accumulation of planktonic organisms. Meanwhile, we suggest that both small and large headlands predictably accumulate larvae and are particularly effective during periods of strong upwelling.

The leeward sides of headlands not only accumulate larvae, but are deposition zones that favor soft-bottom communities. Larvae of hard-bottom species may settle densely on available rocky habitat or disperse to adjacent exposed coasts during relaxation events.

Currently, discussion of the relevance of larvae in reserve design primarily involves the spacing of reserves based on dispersal distances and the seeding of surrounding areas (Largier 2003, Shanks et al. 2003). Incorporating potential accumulation zones into the design of reserve networks in recruitment limited regions with intense upwelling is important because (1) these areas are replenished by abundant settlers and (2) larval dispersal from accumulation zones to adjacent areas is likely during relaxation events. Thus the spatial predictability of larval accumulation zones and habitat types may be used to inform the establishment of a network of marine reserves in upwelling regions.

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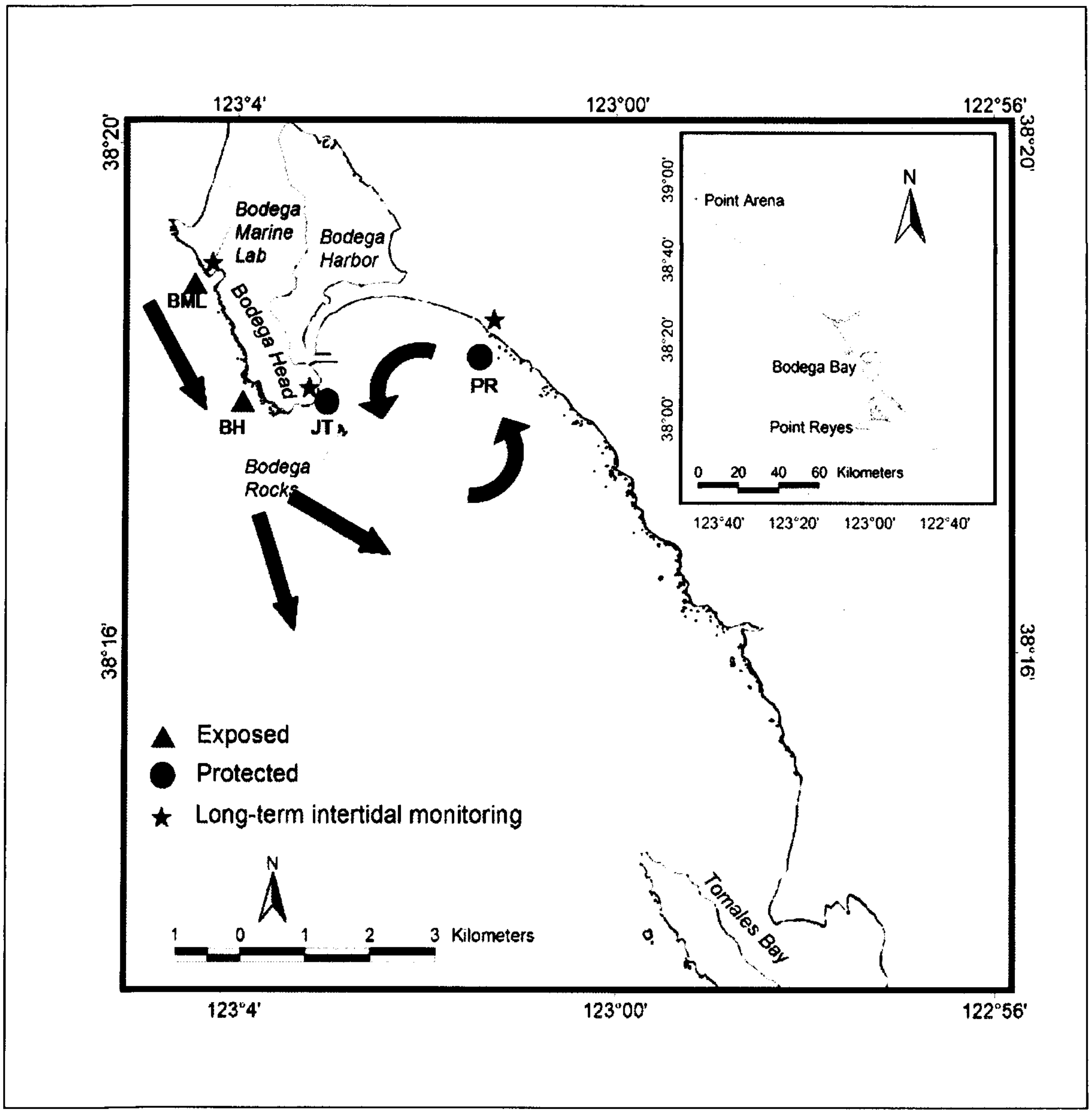

Figure 2.1 Exposed and protected sampling sites. All four sites were sampled in 2001. Only BML and PR were sampled in 2002. Arrows indicate simplified flow around Bodega Head.

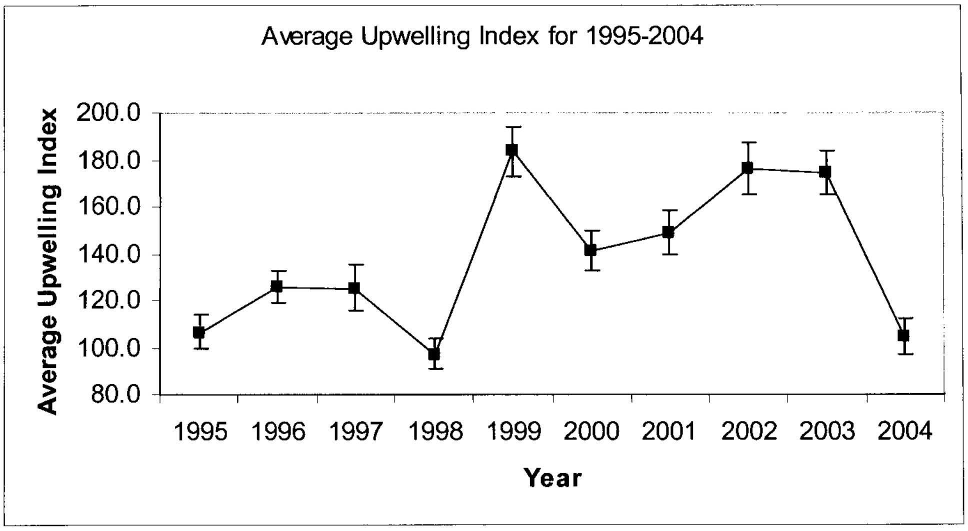

Figure 2.2 Bakun upwelling index from 1995 to 2004 showing mean of daily values ± SE for the upwelling season (April 30 to August 13) from 39°N latitude.

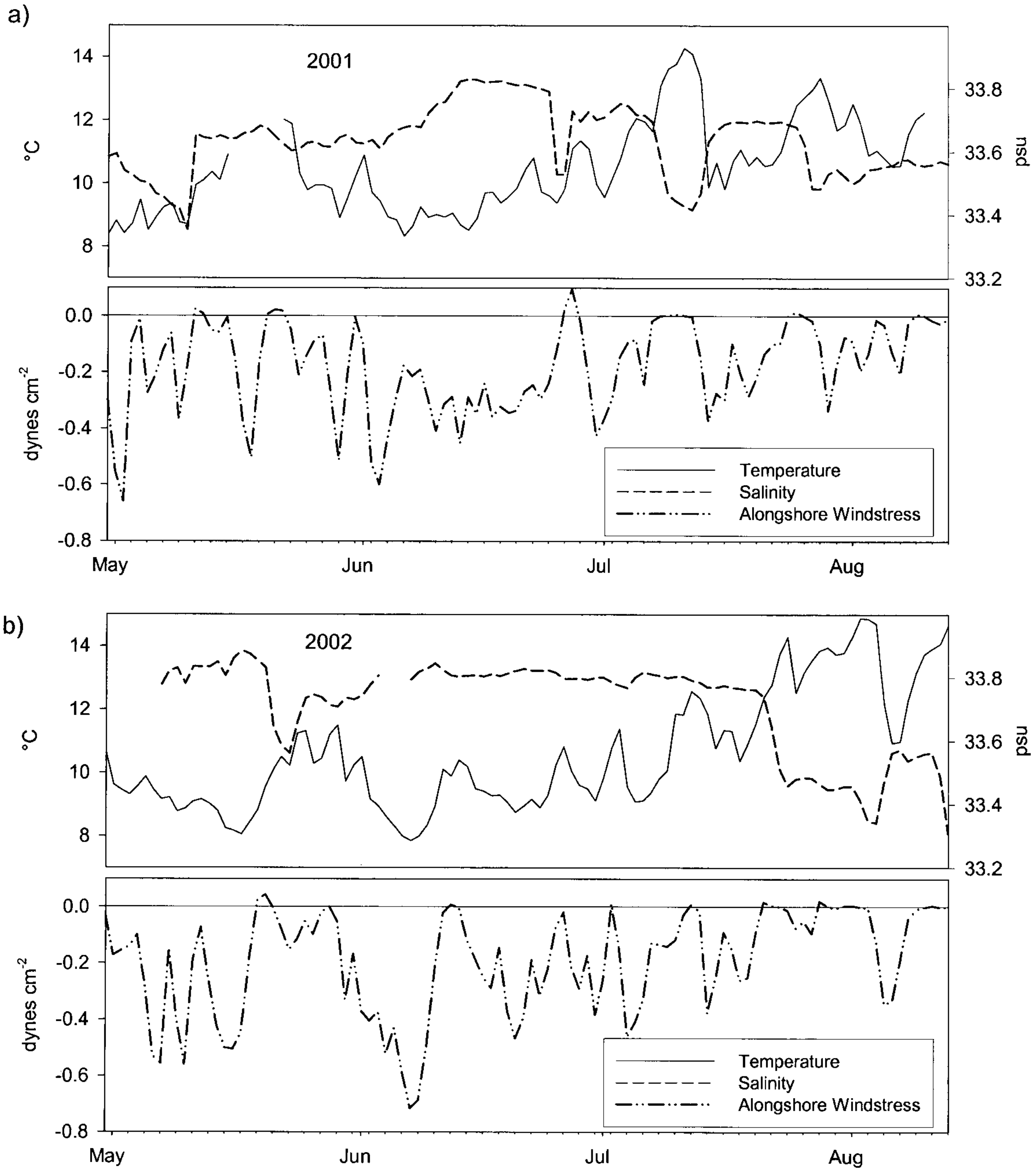

Figure 2.3 Figure 2.3. a) 2001 and b) 2002 time series at Bodega Marine Laboratory of daily averages of: temperature (°C) and salinity (psu, dashed line), and alongshore windstress (dyn cm^{-2}) rotated to 317° (negative values indicate increasing equatorward windstress).

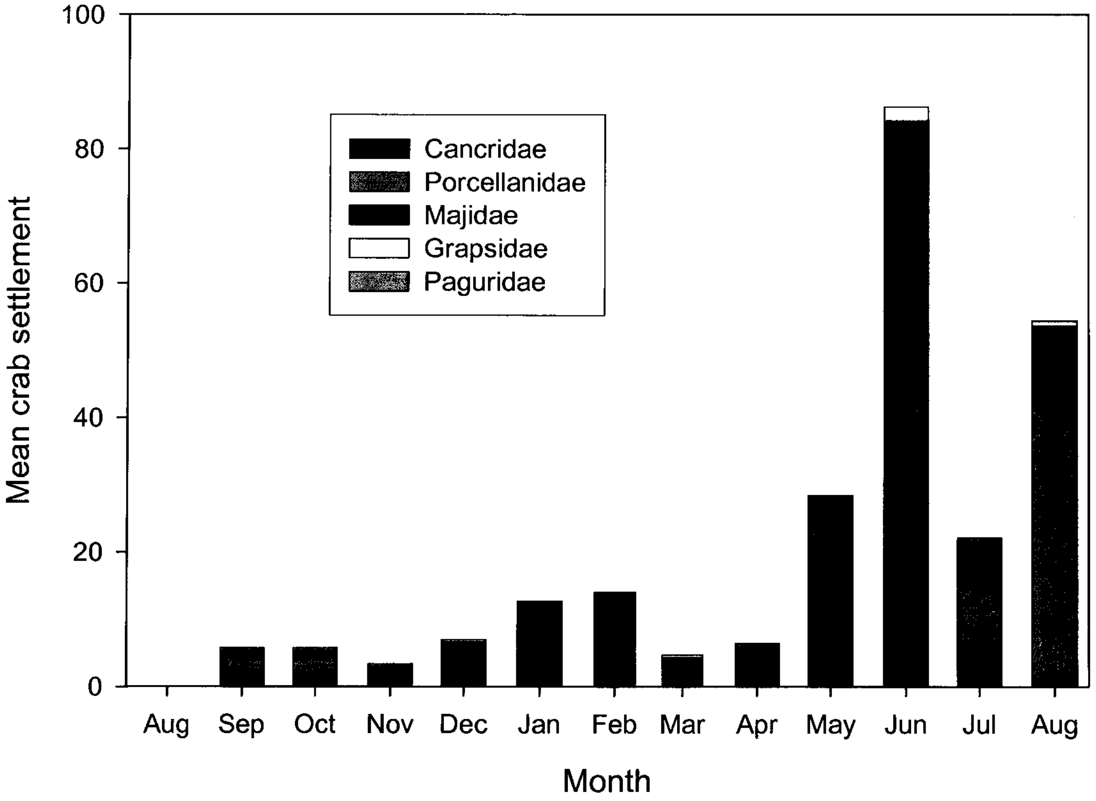

Figure 2.4 Figure 2.4. Stacked mean monthly settlement of five families of crabs: Cancridae, Porcellanidae, Majidae, Paguridae, Grapsidae, at the Jetty site from August 2000 through August 2001.

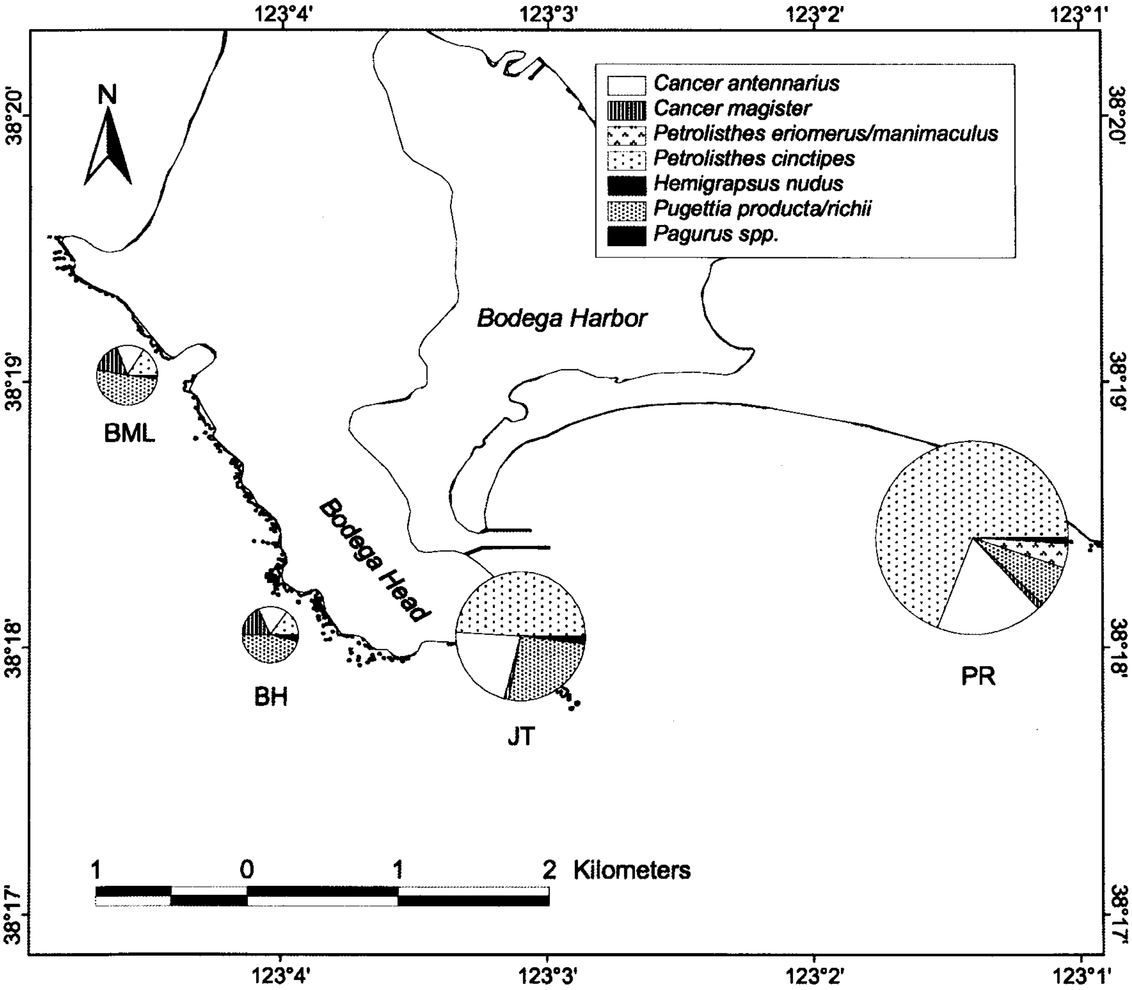

Figure 2.5 Mean crab settlement in 2001 at four sites around Bodega Head, two protected (JT and PR) and two exposed (BML and BH)

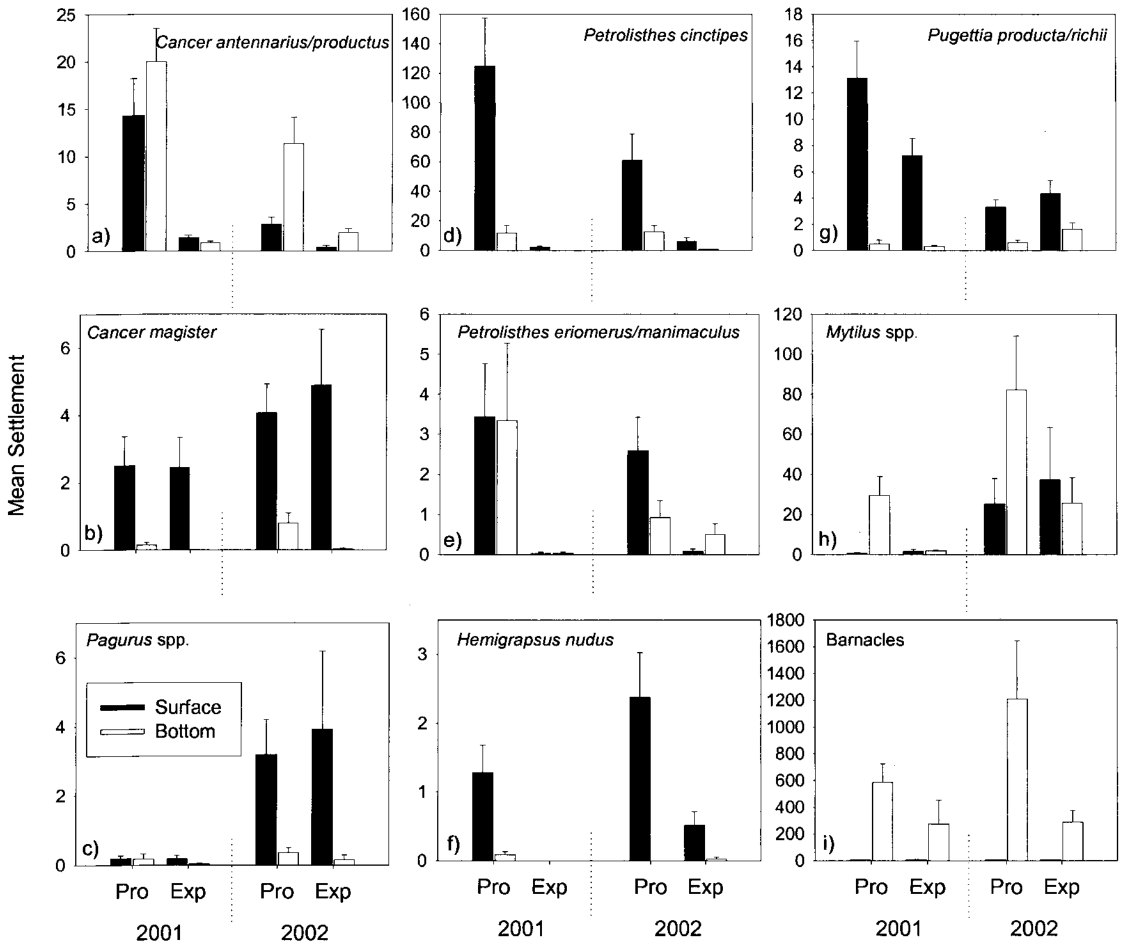

Figure 2.6 a) Cancer antennarius/productus, b) *Cancer magister,* c) *Pagurus* spp., d) *Petrolisthes cinctipes*, e) *Petrolisthes eriomerus/manimaculus*, f) *Hemigrapsus nudus. g) Pugettia producta/richii*, h) *Mytilus* spp., and i) *Balanus* spp. mean settlement ± SE

Table 2.1. Correlations between mean daily alongshore windstress (negative = increasing equatorward windstress) rotated to 317°, surface temperature from BML and PR, and salinity measured at Bodega Marine Laboratory's BOON. Values in bold are significant at 0.05

Year	Windstress vs. BML temperature	Windstress vs. PR temperature	Windstress vs. salinity	BML temperature vs. salinity	PR temperature vs. salinity
2001	**0.6551**	**0.6036**	**-0.4081**	**-0.6502**	**-0.2338**
2002	**0.663**	**0.6904**	**-0.4666**	**-0.8088**	**-0.7775**

Table 2.2. Number of settlers collected in 2001 and 2002 and percent settlement for crab species.

	Total	%
Crabs	16,020	
Petrolisthes cinctipes	8932	55.8
Cancer antennarius/productus	3387	21.1
Pugettia producta/richii	2100	13.1
Cancer magister	753	4.7
Petrolisthes eriomerus	406	2.5
Hemigrapsus nudus	199	1.2
Pagurus spp.	196	1.2
Fabia subquadrata	3	< 1.0
Loxoryncus spp.	2	< 1.0
Petrolisthes manimaculus	20	< 1.0
Pachygrapsus crassipes	16	< 1.0
Pachycheles pubescens	4	< 1.0
Barnacles		
Balanus spp.	81,565	
Lepas spp.	176	
Mussels		
Mytilus spp.	8,470	
Urchin		
Strongylocentrotus spp.	24	
Sea star		
Pisaster spp./*Leptasterias* spp.	277	

Table 2.3. Randomization results comparing exposure (Protected (PR) and Exposed (BML)), depth (Surface and Bottom), and year (2001 and 2002) with mean weekly settlement. The *p*-values are based on the probability that the data are different from randomized data.

	Exposure (E)	**Depth (Z)**	**Year (Y)**	**Y × Z**	**E × D**	**Y × E**	**Y × E × Z**
Cancer magister	0.35	**< 0.001**	0.09	0.35	0.67	0.61	0.85
Cancer antennarius/productus	**< 0.001**	0.22	0.12	0.32	0.38	0.06	0.58
Petrolisthes cinctipes	**< 0.001**	**< 0.001**	0.66	0.85	**0.01**	0.27	0.36
Petrolisthes eriomerus/manimaculus	**< 0.001**	0.11	0.99	0.99	**0.04**	0.43	0.72
Hemigrapsus nudus	**< 0.001**	**< 0.001**	0.14	0.09	**0.001**	0.98	0.68
Pagurus spp.	0.7	**< 0.001**	**0.01**	**0.03**	0.85	0.95	0.98
Pugettia producta/richii	0.94	**< 0.001**	0.14	**< 0.001**	0.37	0.42	0.86
Mytilus spp.	**0.01**	**< 0.001**	**0.001**	0.96	**0.01**	0.75	0.78
Balanus spp.	**0.004**	**< 0.001**	**0.02**	0.42	**0.04**	0.72	0.3

Table 2.4. Correlation values for comparison of timing of settlement at PR and BML for 2001 and 2002 from weekly values (n = 129).

	BML vs. PR	***p*-value**
Pagurus spp.	0.60	**< 0.001**
Pugettia producta/richii	0.57	**< 0.001**
Cancer magister	0.51	**< 0.001**
Cancer antennarius/ productus	0.17	**0.05**
Petrolisthes cinctipes	0.35	**< 0.001**
Petrolisthes eriomerus/ manimaculus	0	0.99
Hemigrapsus nudus	0.27	**0.002**
Mytilus spp.	0.50	**< 0.001**
Balanus spp.	0.37	**< 0.001**

Biological and physical coupling in the lee of a small headland: Contrasting larval transport mechanisms in an upwelling region

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Key words: headland, larval retention, meroplankton, larval dispersal, crab

Abstract

Delivery mechanisms for crab postlarvae along upwelling coasts have been inferred from weekly sampling, but have not been well-resolved. More frequent sampling is needed to directly relate highly variable oceanographic conditions indicative of transport processes (e.g. the arrival of different water masses, tidal periodicity) to postlarval settlement. Settlement of eight crab taxa was measured in Bodega Bay, California every two days from 12 May through 3 July, 2002. Using time series analysis, the abundance of postlarvae was cross-correlated with physical variables. Four upwelling and four relaxation events were recorded as fluctuations in windstress and sea temperature during this period. Transitions to and from upwelling conditions were brief and temperature changes occurred rapidly. Strongest correlations with physical variables indicative of upwelling and relaxation conditions were observed for *Cancer magister*, which settled primarily during relaxation-favorable conditions, and for *Cancer antennarius/productus*, which settled primarily during upwelling-favorable conditions. Further, *C. magister* and *C. antennarius/productus* settled at different depths and exhibited different spatial distributions, suggesting that these two congeners employ different strategies for returning to adult habitat. Weak correlations with upwelling-favorable conditions were observed for *Pugettia producta/richii* and *Pagurus* spp., and were apparently due to one or two large settlement peaks. There was little difference in settlement between upwelling and relaxation conditions for *Hemigrapsus nudus, Petrolisthes cinctipes,* and *P. eriomerus.* However, *Hemigrapsus nudus*, *Petrolisthes cinctipes*, and *P. eriomerus* exhibited significant correlations with tidal periodicity, indicating the importance of multiple taxon-specific delivery mechanisms.

INTRODUCTION

Identifying the mechanisms that deliver planktonic larvae to adult habitats is a critical link in understanding community dynamics, particularly in recruitment limited regions where larval supply more strongly influences the distribution and abundance of adults (Connell 1985, Gaines & Roughgarden 1985, Minchinton & Scheibling 1991, Menge 2000, Connolly et al. 2001). In upwelling regions, where persistent offshore and equatorward flow dominates, dynamic and energetic physical oceanographic processes are likely strong determinants of dispersal and subsequent recruitment patterns (Roegner et al. 2003). Therefore, understanding the physical mechanisms that deliver planktonic larvae to adult habitats in upwelling regions has been the focus of numerous studies (Parrish et al. 1981, Farrell et al. 1991, Roughgarden et al. 1991, Graham et al. 1992, Yoklavich et al. 1996, Shkedy & Roughgarden 1997, Pineda 1999, Lundquist et al. 2000, Botsford 2001, Wing et al. 2003).

While physical mechanisms that deliver crab postlarvae to nearshore habitats along the upwelling region of the California coastline have been postulated, they have not been well resolved. Studies suggest that depth preferences, coupled with vertical migrations between opposing stratified currents, enable larvae to regulate alongshore and cross-shelf movements (reviewed in Kingsford et al. 2002). Ontogenetic shifts in depth preference may further facilitate the onshore transport of late-stage larvae by winds, internal waves, and other physical mechanisms (reviewed in Shanks 2002). Because multiple factors play a role in larval delivery to shallow water habitats, both interspecific and intraspecific differences in the timing of larval settlement may occur.

Although multiple mechanisms are likely at play, the dynamics of wind-driven coastal upwelling are typically identified as the primary forcing mechanisms that regulate the movement of larvae along the northern and central California coast. During upwelling, cold dense nutrient rich water from depth meets lower density offshore water, sometimes forming a convergence zone at the leading edge of an upwelling front. Convergence zones (fronts) have been associated with an increased concentration of organisms (Grantham et al. 1995, Shanks et al. 2000), and the movement of these fronts during upwelling and relaxation has been identified as a mechanism for cross-shelf (Roughgarden et al. 1988, Farrell et al. 1991, Roughgarden et al. 1991) and alongshore (Wing et al. 1995b, Wing et al. 1998) movement of meroplankton. For example, the cross-shelf movement of upwelling fronts has been linked to barnacle recruitment (Farrell et al. 1991, Roughgarden et al. 1991). During active upwelling, surface waters carrying larvae are advected offshore via Ekman transport and larvae may be subsequently returned to shore by onshore flow when upwelling winds relax (e.g. Roughgarden et al. 1988, e.g. Farrell et al. 1991, Roughgarden et al. 1991).

Upwelling winds also transport warm surface waters equatorward, and the cessation of upwelling winds results in the poleward propagation of surface water (Send et al. 1987). Additionally, topographic features such as headlands provide shelter from upwelling winds, and have been shown to accumulate particles in their lee (Wing et al. 1995a, Mace 2005). Wing et al. (1995a) found that during upwelling, larvae accumulated in the lee of Point Reyes, a prominent headland just north of San Francisco Bay, CA. In this location larval settlement was more consistent and was not correlated with physical variables such as wind stress and temperature. Similarly, Mace (2005) observed higher settlement in the lee of a smaller headland (<10 km), indicating that this process is acting at multiple scales. During relaxation of upwelling winds Wing et al. (1995a) observed increased settlement of postlarvae north of Point Reyes. In this region, larval settlement was more episodic and was correlated with decreased wind stress and increased water temperature that indicated the arrival of warm larvae-laden water masses that originated in the lee of the Point Reyes. While Wing et al. (1995a) inferred that the main supply of propagules to the coastal region between Point Reyes and Point Arena (sixty miles to the north) originates from this poleward propagation of surface water, this was most apparent during years with distinct upwelling and relaxation cycles (3 out of 7 years, 1992–1999). Sampling at a finer temporal scale is needed to determine larval transport mechanisms during periods when oceanographic conditions are not as distinct. While studies have focused on upwelling processes, larvae may also be concentrated and delivered via tidally forced internal waves (internal tides) that form at the shelf break or around other complex bathymetric features such as ridges and submarine canyons (reviewed in Shanks 2002). Larvae that are concentrated in surface convergences associated with internal waves tend to be late stage larvae or post-larvae (except zoea of porcelain crabs). Such larvae may have temporal patterns of settlement with peaks every 13 to 15 days, corresponding with the spring-neap cycle (reviewed in Shanks 2002). Internal waves may be more frequent during relaxation events when the water column is more stratified (Rosenfeld 1990) and may be responsible for the observed correlations between settlement and the arrival of warm water during relaxation periods (Shanks 2002). However it is difficult to distinguish transport mechanisms during relaxation events when using data from weekly sampling, thus Wing et al. (1995a, 2003) were unable to resolve the influence of high frequency activities such as internal waves.

To better understand the possible forcing mechanisms that deliver larvae to the nearshore waters of central California, we sampled postlarval settlement every 2 days for 54 days during the upwelling season. Frequent sampling is needed to address whether highly variable oceanographic conditions (e.g. the arrival of different water masses, internal waves) can explain postlarval settlement. To address potential delivery mechanisms, we compared two-day averages of crab settlement with wind stress (along- and across-shore), temperature, salinity, tidal periodicity, and a local upwelling index.

METHODS

Study system. This study was conducted in the Bodega Bay, Sonoma Co., California, which is characterized by persistent (upwelling favorable) equatorward winds during the spring and summer months. The study site is located just offshore of Pinnacle Rocks (PR) (38°18.328 N, 123°01.435 W) along the eastern shore of northern Bodega Bay (Fig. 3.1). A more detailed description of the study area is available in Roughan et al. (in review).

Settlement patterns depend in part on the timing of larval release and developmental period. The crabs in this study spend weeks to months in the plankton, developing through two to five zoeal stages and a megalopal (postlarval) stage before returning to the benthos as juveniles. The timing of release and larval duration varies between taxa and is poorly known. More generally, release of cancrid species along the California coast is estimated to occur between December and March (Reilly 1983, Strathmann 1987). December through March is characterized by seasonal variation with wind forcing from storm events, and the nearshore flow is weakly poleward. Around March and April nearshore flow shifts equatorward, and upwelling conditions prevail (Largier et al. 1993). Cancrid settlement has been observed in Bodega Bay during all months of the year but peaked in May and June while grapsid, majid, pagurid, and porcellanid settlement in Bodega Bay peaked from May through August (Mace & Morgan in review). The larval period for *Cancer antennarius*, *C. productus,* and *C. magister* is estimated to be from 36 to >60 d, 68 to 150 d, and 75 to 180 d respectively (Reilly 1983, Strathmann 1987, Grantham et al. 2003, Shanks & Eckert in review). Larval durations for *Hemigrapsus nudus*, *Petrolisthes cinctipes*, *Pugettia producta/richii*, *P. eriomerus* and *Pagurus* spp. are estimated to be 32, 46, 49, 60, and 69 to 74 days, respectively (Grantham et al. 2003, Shanks & Eckert in review). Based on shorter larval durations, and peaks in settlement that occur between May and August, it is likely that the majority of non-cancrid crabs are released when upwelling conditions prevail.

Oceanographic data. Hourly averages of the speed and direction of surface currents offshore of Bodega Bay were obtained from a high frequency radar system (CODAR) (http://bml.ucdavis.edu/boon/). CODAR data describes the speed and direction of the surface current over 2200 km^2 area extending 50–70 km from shore with a resolution of 2 km (Kaplan & Largier in review).

Offshore wind speed and direction were obtained from the National Data Buoy Center (NDBC 46013, 38°13'30" N, 123°19'00" W; http://www.ndbc.noaa.gov/) and local wind velocities were obtained from a land-based site at the Bodega Marine Laboratory (BML, 38°19'03.35" N, 123°04'17.20" W, http://bml.ucdavis.edu/boon/). Alongshore winds at BML and the NDBC buoy were correlated to 95 % confidence with

$r = 0.88$ and a lag of 2 h (BML leads NDBC; (Roughan et al. in review). Wind data from the offshore buoy were used because they are more representative of larger scale wind forcing events. Along- and across-shore wind stress were calculated (Large & Pond 1981) from 10 min averaged data that were adjusted to a height of 10 m above sea level using a neutral stability wind profile and rotated in the alongshore direction to a principal axis of 317°T. Negative values of alongshore wind stress indicate equatorward wind stress and larger negative values reflect stronger upwelling-favorable winds. Low or positive values are associated with relaxation or downwelling conditions. Positive cross-shore wind stress values indicate eastward (onshore) wind and negative values indicate westward (offshore) wind.

Upwelling indices (from 39°N, 125°W) were obtained from the National Oceanic and Atmospheric Administration's Pacific Fisheries Environmental Laboratory (PFEL), Pacific Grove, California (http://www.pfeg.noaa.gov/). Positive values indicate upwelling and offshore transport of surface waters resulting from equatorward wind stress, and low values, indicate relaxation of upwelling. Negative values indicate downwelling and the onshore advection of surface waters due to poleward wind stress.

Sea surface temperature has been identified as a good indicator of upwelling (Shkedy & Roughgarden 1997). Shkedy and Roughgarden (1997) found that a time series model could predict SST one day ahead from the present values of temperature and wind stress which explained nearly 80% of sea surface temperature (SST) variation. Sixty percent of the variance in barnacle recruitment was explained by variance in SST (Shkedy & Roughgarden 1997). In the present study, upwelling conditions were defined by a SST at the study site of <10 ˚C in response to increased (negative) alongshore wind stress. Continuous temperature data were taken from 2 Optic StowAway TidbiT® thermistors, which were placed on 1 settlement mooring at the site: 1 m off the bottom (approximately 9 m deep) and 1 m below the surface. Temperature ± 0.2 °C was recorded every 6 min. The maximum tidal range for each 2-day sampling period was obtained from tide prediction software (Tides and Currents v.2.0a, Nautical Software Inc.). Daily averages of salinity ± 0.005 psu were obtained from a Sea-Bird Electronics thermosalinograph (SBE 45 MicroTSG) located in the seawater intake line at BML (http://bml.ucdavis.edu/boon/). Average daily rainfall was recorded at BML, which is a National Weather Service reporting station using a Hydrological Services TB4 Tipping Bucket Rain Gauge.

Larval settlement. Larval settlement of benthic invertebrates was monitored at one site (PR) every 2 days from 12 May to 3 July, 2002 (54 days, $n = 26$). The intensive schedule of sampling at a shorter time interval was conducted because settlement data from weekly sampling in 2001 (Mace & Morgan in review) was inadequate for resolving potential transport mechanisms. The PR site was selected because it is relatively protected from adverse sea conditions, facilitating regular sampling and because it consistently had higher settlement than other sites in the area. Sampling also was attempted at a site along the exposed side of Bodega Head; however high seas prevented consistent sampling here.

Three moorings, running parallel to shore along the 10 m isobath, were deployed approximately 50 m apart with settlement substrate attached 1 m below the surface. Settlement substrate consisted of 2 mesh 10 × 30 cm bags containing 3 Tuffy® kitchen scrub pads each. Collectors were deployed and retrieved every 48 h, rinsed in fresh water, and settlers were fixed in 50 % ethanol. Postlarvae and juveniles were identified to species when possible using available keys (Lough 1974, Shanks 2001). *Cancer productus* and *Cancer antennarius* were distinguished as juveniles but not as postlarvae. These species were collectively called *Cancer antennarius/productus,* even though 79 % of the juveniles were *C. antennarius*. Similarly, *Pugettia producta* and *Pugettia richii* were not distinguished at the postlarval stage, although 95 % of the juveniles collected were identified as *P. producta*.

Data analysis. Using Statistica, cross-correlations were calculated between crab settlement and physical variables when taxa were present > 80 % of the time to limit the number of significant results due to an abundance of zeros. Seven of eight taxa investigated were present > 80 % of the time and had no significant autocorrelations, thus they were used in the time series analysis. 2-day averages of physical variables were cross-correlated with mean values of crab settlement from three moorings for each 2-day sampling period, resulting in 26 samples for the 54 d period. Abundances were $\log_{10}$ transformed to meet the assumptions of normality and examined for temporal autocorrelation. No seasonal trends were apparent in the physical variables, thus de-trending was not necessary. Temperature at the bottom and the surface were highly correlated with each other (0 d lag: $r = +0.923$), because settlement was monitored at the surface, only surface temperatures were used for time series analysis. In this study, lags represent the 2-day sampling period (lag of 1 = 2 d) and the sign indicates whether peaks in settlement occurred after (positive) or before (negative) changes in the physical variables. Since the response variable of settlement must follow the physical predictor variables, only positive lags are reported, with the exception of cyclic environmental variables. Therefore, negative lags are reported for cross-correlations between settlement and maximum tidal range because of the predictable cyclic nature of tides. Only lags ≤ 3 are considered for this 26 point series because lags of up to 10 % of the time series are considered valid. Because correlations from brief time series may be due primarily to one event or only a few data points, we also qualitatively assessed whether the observed settlement patterns appeared to be in response to changes in the physical environment.

RESULTS

Physical data. 2002 was characterized by strong upwelling (Grantham et al. 2004, Mace & Morgan in review). During the sampling period, there were four upwelling and four relaxation events of varying lengths. Upwelling events ranged from 4 to 10 days with an average of 7.25 ± 1.3 days (± SE). Relaxations were typically shorter (3 to 4 days), however one relaxation event lasted 14 days (19 May to 1 June; Fig. 3.2). Surface water temperature was correlated with alongshore wind stress (0 lag: $r = 0.752$) and averaged 10.3 ± 0.2 °C (± SE) with a range of 8.4 to 13.2 °C. When equatorward wind stress increased (larger negative values) temperature decreased as was expected, indicating active upwelling. Salinity stayed fairly constant between 33.6 and 33.8 during this period except during 21 May and 5 June when it decreased to 32.9 and 33.0 respectively (Fig. 3.2). Rainfall measuring 6.1 and 8.9 mm was recorded at BML on 19 and 20 May respectively. Because relaxation conditions prevailed during this time, the low salinity levels were likely due to poleward advection of lower-salinity waters from the Gulf of the Farallones and San Francisco Bay (Fig. 3.3a). However, only 0.2 mm of rain was recorded at BML on 4 and 5 June. Upwelling conditions prevailed during this time and the low salinity values observed may have resulted in the delivery of fresher water from the Russian River plume located north of Bodega Bay (Fig. 3.3b). Positive values of the upwelling index (at 39° N, 125° W) were correlated with negative (upwelling favorable) alongshore wind stress (0 lag, r = - 0. 74).

Larval settlement. Eight crab taxa settled between 12 May and 3 July, 2002 (Table 1). *Cancer antennarius/productus* were present 96.2 % of the time, however one large peak during upwelling favorable conditions in June accounted for 42 % of the settlement (Fig. 3.4). *C. antennarius/productus* abundance was negatively cross-correlated with the arrival of cold surface water (0 lag) and negatively cross-correlated with alongshore wind stress (0 lag), therefore settlement increased with increasing (negative and upwelling favorable) equatorward wind stress (Table 2). For *C. antennarius/productus* 90 % of settlement occurred during upwelling-favorable conditions (Fig. 3.5).

Cancer magister was present in 84.6 % of samples and was positively cross-correlated with the arrival of warm surface water (0 lag) and alongshore wind stress (0 lag). Therefore settlement was greater during weaker equatorward winds (less negative) (Table 2). *C. magister* abundance was negatively correlated with upwelling indices (0 lag) and salinity (0 lag), and thus settlement increased as upwelling and salinity decreased. For *Cancer magister* 86 % of settlement occurred during relaxation events (Fig. 3.5), and 72% of settlement occurred during the first 14 d relaxation event, which may explain the significant cross-correlations with temperature, wind stress, and upwelling index. However, increases in settlement were apparent during subsequent relaxation periods (Fig 3.4). *C. magister* settlement also coincided with the decreases in salinity, which may account for the significant cross-correlation between settlement and salinity.

Hemigrapsus nudus was present in 80.8 % of samples and was positively cross-correlated with the maximum tidal range (-1 lag) suggesting that they settled about 2 days prior to peak spring tides (Table 2). For *H. nudus* 60 % of settlement occurred during upwelling (Fig. 3.5).

Pugettia producta/richii was present in 88.5% of samples, and was positively cross-correlated with cross-shore wind stress (0 and +1 lag). Therefore settlement increased 0 to 4 days after onshore wind stress increased. Two settlement events in June, representing 55 % of the total settlement (Fig. 3.4), occurred during upwelling conditions when the winds were coming more from a westerly direction, so cross-shore wind stress in the onshore direction increased and alongshore wind stress in the equatorward direction was slightly reduced (Fig. 3.2). These settlement events may be responsible for the cross-correlation between settlement and cross-shore windstress. 69 % of *P. producta/richii* settlement occurred during upwelling (Fig. 3.5).

Petrolisthes cinctipes settled in the greatest abundance (1,546.7 ± 121.5 (± SE)), representing 62.1% of crab settlement, and were present in 100 % of the samples (Table 1). *P. cinctipes* abundance was negatively cross-correlated with salinity (0 lag), therefore settlement increased as salinity decreased. *P. cinctipes* abundance was positively cross-correlated with the maximum tidal range (-2 lag) suggesting that they settled 4 days prior to peak spring tides (Table 2), particularly during low-salinity events.

Petrolisthes eriomerus was present in 92.3% of the samples and was negatively cross-correlated with salinity (0 lag), where settlement increased as salinity decreased. *P.*

eriomerus abundance was positively cross-correlated with the maximum tidal range (-2 lag) suggesting that they settled 4 days prior to peak spring tides (Table 2). *P. eriomerus* abundance was also negatively cross-correlated with the maximum tidal range (+2 lag) suggesting that they settled 4 days after neap tides (Table 2).

Pagurus spp. were present in 96.2 % of samples, and one settlement event during upwelling conditions in May accounted for 24% of the settlement (Fig. 3.4). *Pagurus* spp. abundance was negatively cross-correlated with the arrival of cold surface water (+2 lag) and wind stress (+2 lag), therefore settlement increased 4 days after increasing (negative and upwelling favorable) equatorward wind stress (Table 2). 53% of *Pagurus* spp. settlement occurred during upwelling favorable conditions (Fig. 3.5).

Petrolisthes manimaculus was present in 26.9 % of samples and was not considered for analysis (Table 1). 94% percent of settlement occurred during two upwelling events in June.

DISCUSSION

Interspecific differences in settlement timing. The relative importance of larval transport mechanisms can vary among years (Wing et al. 2003) and regions (Johnson et al. 1986, McConnaughey et al. 1992, Roegner et al. 2003, Miller & Shanks 2004). In Oregon, Miller and Shanks (2004) found that *Cancer magister* recruitment to light traps was positively correlated with upwelling events and tidal forcing. However, in Washington, Roegner (2003) found that *C. magister* recruitment to light traps was not significantly correlated with wind events or tidal forcing. Here, we found that *C. magister* settlement was positively correlated with relaxation events, which is consistent with previous studies in this region (Wing et al. 1995a, Wing et al. 2003), while *C.*

antennarius was positively correlated with upwelling events. *C. magister* and *C. antennarius* also had contrasting depth and spatial distributions, indicating that these congeners are returned to adult habitats via different mechanisms. Settlement of non-cancrid crabs was not as closely tied to upwelling-relaxation cycles, and therefore, variation in settlement during upwelling or relaxation events for these species may have been coincidental and influenced more by other mechanisms (e.g., tidal processes or entrainment in an accumulation zone).

Settlement during four upwelling and four relaxation events in Bodega Bay was fairly continuous, where seven of eight species were present > 80 % of the time. Regardless of oceanographic condition, larvae may settle continuously in the lee of headlands, as previously reported by Wing et al. (1995a). Bodega Bay, in the lee of Bodega Head, has been identified as a larval accumulation zone (Mace & Morgan in review) due to a sub-surface recirculating eddy that sets up during upwelling conditions (Roughan et al. in review). Larvae can be entrained in the recirculation feature and remain in the bay through vertical migratory behavior (Roughan et al. in review). Although settlement was typically continuous during the present study, most species had one or two settlement peaks that represented a large portion of total settlement during this period. Peaks in settlement during upwelling, relaxation, and tidal maximums provided evidence for multiple delivery mechanisms that vary within and among species.

Cancrid crabs had the strongest correlations with upwelling-relaxation cycles, whereby *Cancer magister* settled primarily during relaxation favorable conditions and *Cancer antennarius/productus* settled primarily during upwelling favorable conditions. *Pugettia producta/richii* and *Pagurus* spp. had weaker correlations with upwelling favorable conditions that were likely due to one or two large settlement peaks that occurred during upwelling conditions. There was little difference between total settlement during upwelling and relaxation conditions for *Hemigrapsus nudus, Petrolisthes cinctipes, P. eriomerus,* and *Pagurus* spp., even though *Pagurus* spp. settlement was correlated with upwelling conditions. These results are similar to previous findings for non-cancrid crabs from weekly sampling in this region (Wing et al. 1995a, Wing et al. 2003).

Species with nearshore distributions and shorter larval durations may be more likely to be retained in headland eddies and more likely to be influenced by transport due to internal waves and tides. While no clear signal of internal wave activity was apparent from temperature data at the settlement site, *Hemigrapsus nudus*, *Petrolisthes cinctipes*, and *P. eriomerus* abundance increased 2 to 4 d prior to spring tides and *Pagurus* spp. abundance increased 4 to 6 d after neap tides (1 to 3 days before spring tides). Thus evidence for tidal transport was apparent for all non-cancrid taxa except *Pugettia producta/richii.*

Congeneric differences in settlement timing. The 14-d relaxation event presented the best example of increasing temperature and decreasing salinity in response to decreased alongshore wind stress. Wing et al. (2003) identified coherence among these variables as important for poleward transport of larvae from the lee of Point Reyes. Poleward alongshore flow was apparent beginning 19 May (Fig. 3.3a) and continued until 23 May before it weakened and temporarily reversed. The majority of *Cancer magister* settled during this relaxation period. While it is likely that many *C. magister* postlarvae were advected poleward from the lee of Point Reyes during this 14-d period, settler abundance increased rapidly as temperature increased suggesting that there was also a more local supply of postlarvae. For example, a large pulse of crabs settled during the 2-day period between 18 and 20 May as the temperature increased.

All significant cross-correlations for *Cancer* crabs had a lag of 0 (0-2 days), which suggests that *Cancer* crabs settled with, or very soon after a change in wind stress or temperature. For example *Cancer magister* settlement increased during periods when temperature increased and *Cancer antennarius/productus* settlement increased during periods when temperature decreased. Wing et al. (1998) found higher concentrations of larvae residing in frontal zones between water masses. It is likely that crabs settle at the transition between warm and cold water because they are being transported in the leading of edge of either warm or cold fronts. Temperature increased rapidly shortly after the cessation of the wind, suggesting that a convergence zone between warm and cold water was not far from this site. It is likely that the peaks in settlement around the changes in conditions are a result of these frontal systems moving past the collectors. The presence of local larvae-laden fronts in the Bodega region may help to explain the settlement patterns in years where settlement is not correlated with the arrival of warm water from the lee of Point Reyes.

Depth distribution of different taxa may influence transport mechanisms. Larvae residing in bottom waters may be carried onshore during upwelling and larvae residing near surface waters may be carried onshore during relaxation events (Wing et al. 1995a) or via internal waves (Shanks 1998, Pineda 1999). Surface and bottom settlement data from 2001 and 2002 (Mace & Morgan in review) showed that while *Cancer magister* settled in greater abundance at the surface, *Cancer antennarius/productus* settled at both the surface and bottom. Further, peaks in *C. magister* settlement corresponded with increased temperature, suggesting that *C. magister* are delivered to shore via relaxation, while *C. antennarius/productus* settled during cold water events, suggesting that *C. antennarius/productus* are transported onshore in cold near-bottom waters. *C. antennarius/productus* settlement was primarily observed inside Bodega Bay, where recirculation at depth can accumulate larvae that spend time at depth (see Roughan et al. in review). In contrast, *C. magister* settlement occurred during relaxation, in the absence of this bay recirculation, where warm waters delivered *C. magister* postlarvae to sites both within and outside the Bay (Mace & Morgan in review).

This contrast in temporal and spatial patterns of settlement is consistent with *Cancer magister* and *Cancer antennarius/productus* adopting coherent but different strategies for the return of postlarvae to nearshore adult habitat. *C. magister*, with longer planktonic larval duration and extended larval season, adopt a "strategy" where postlarvae are concentrated in fronts (Wing et al. 1998) and are delivered to the Sonoma coast in warm waters from a nearby upwelling shadow (Wing et al. 1995b, Graham & Largier 1997) or offshore (Roughgarden et al. 1991). In contrast, *C. antennarius/productus*, with shorter planktonic larval durations confined to the upwelling season, adopt a strategy where postlarvae are delivered onshore in cold near-bottom waters during upwelling. Not only can this strategy maintain deep-dwelling *C. antennarius/productus* larvae over the shelf, but this strategy allows this species to accumulate in the lee of small low-lying headlands where recirculation during upwelling may only be observed at depth.

CONCLUSION

Settlement can exhibit extreme spatial and temporal variability at small scales, and can be related to changes in local (tidal forcing) and regional (currents and winds) scale processes. However, delivery mechanisms are difficult to resolve due to both intra- and inter-annual variations in larval availability and oceanographic conditions. Sampling on a weekly basis and grouping crabs by family is useful for providing a picture of spatial settlement at a regional scale, such as identifying the location of accumulation zones, and may be useful for designing marine reserves (Mace & Morgan in review). However, sampling at a higher frequency and distinguishing taxa to species is necessary to identify interspecific and congeneric differences (e.g. *Cancer magister* and *Cancer antennarius/productus*) in delivery mechanisms. To further resolve transport mechanisms in this highly variable environment, settlement should be monitored during multiple years over short time scales due to the rapid response of postlarvae to changes in the physical environment.

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Table 3.1. Abundance of crab postlarvae collected at Pinnacle Rock in Bodega Bay. Abundance data are presented as total mean abundance (± SE) over the 54 d sampling period (average of collectors from three moorings, $n = 3$) and mean (± SE) per sampling period (average of 3 collectors from each 2 d period, $n = 78$). The percentage of total crab settlement (% total) that each taxon represented and the percentage of days (% time) during the study that the taxa were present also is presented.

Taxon	Common name	(n = 3) Total mean	(n = 78) Mean/trip	% total	% days
Petrolisthes cinctipes	Porcelain crab	1456.7 ± 121.5	56.0 ± 9.7	62.1	100
Cancer antennarius/productus	Red crab/rock crab	375.7 ± 31.8	14.4 ± 3.5	16.1	96.2
Pagurus sp.	Hermit crab	163.3 ± 12.0	6.3 ± 1.1	7.0	96.2
Cancer magister	Dungeness crab	80 ± 6.0	3.1 ± .5	3.4	84.6
Hemigrapsus sp.	Shore crab	71 ± 4.0	2.7 ± .45	3.0	80.8
Petrolisthes eriomerus	Porcelain crab	63 ± 2.1	2.4 ± .37	2.7	92.3
Pugettia producta/richii	Kelp crab	59.7 ± 7.5	2.3 ± .52	2.5	88.5
Petrolisthes manimaculus	Porcelain crab	18.7 ± 4.4	.72 ± .27	0.8	26.9

Taxa in bold were used in analyses

Table 3.2. Time series analyses between crab postlarval abundance and physical variables at Pinnacle Rock in Bodega Bay. Lags represent the sampling period of 2 d; the sign indicates whether peaks in crab settlement occur after (positive values) or before (negative values) changes in the physical variables. Positive along shore wind stress cross-correlations indicate a relationship between crab abundance and poleward winds (relaxation favorable), and negative cross-correlations indicate a relationship with equatorward winds (upwelling favorable). Positive cross-shore wind stress cross-correlations indicate eastward (onshore) wind and negative values indicate westward (offshore) wind. Positive maximum tidal range cross-correlations indicate a relationship with spring tides and negative values indicate neap tides. Values presented are statistically significant at $p \leq 0.05$; ns = not significant.

	Along-shore wind stress	Cross-shore wind stress	Upwelling index	Temperature Surface	Salinity	Max. tidal range
Cancer antennarius/ productus	+ 0 d = -0.569	ns	ns	+0 d = -0.717	ns	ns
Cancer magister	+0 d = +0.558	ns	+0 d = -0.412	+0 d = +0.602	+0 d = -0.560	ns
Hemigrapsus spp.	ns	ns	ns	ns	ns	-1 d = +0.498
Pugettia producta/ richii	ns	+0 d = +0.472 +1 d = +0.507	ns	ns	ns	ns
Pagurus spp.	+2 d = -0.465	ns	ns	+2 d = -0.413	ns	+2 d = -0.414 +3 d = -0.420
Petrolisthes cinctipes	ns	ns	ns	ns	+0 d = -0.753	-2 d = +0.401
Petrolisthes eriomerus	ns	ns	ns	ns	+0 d = -0.630	+2 d = - 0.406 -2 d = +0.506

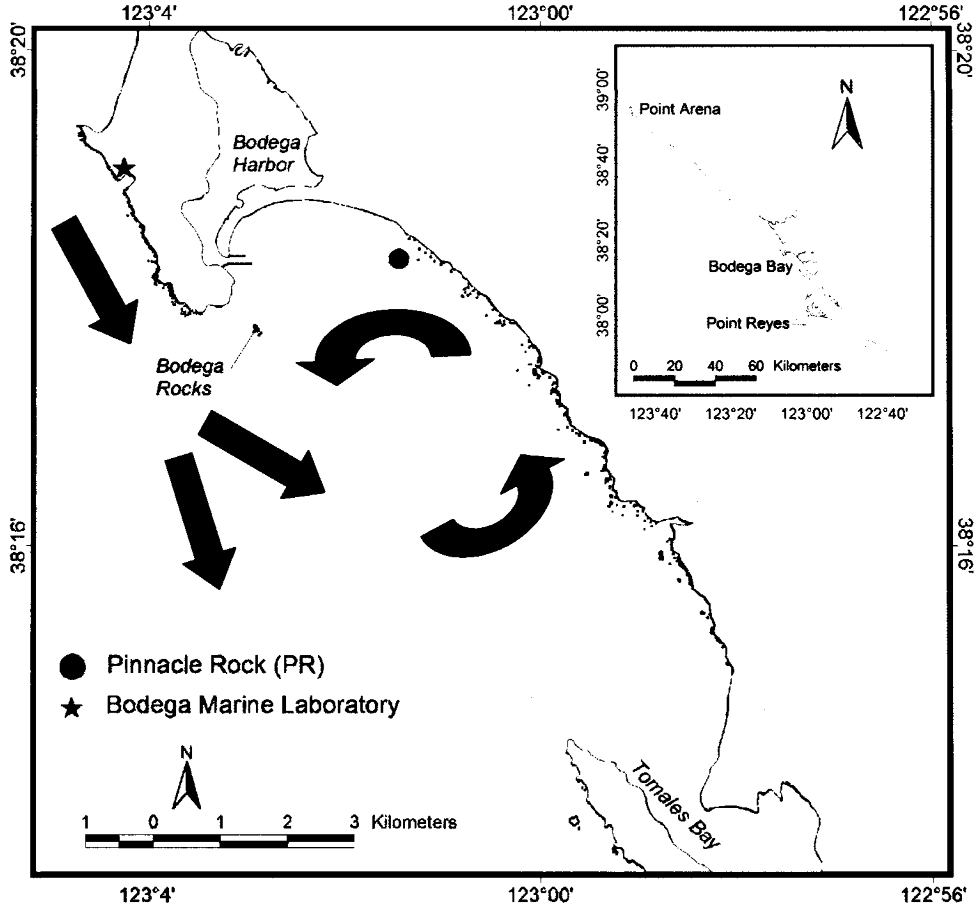

Figure 3.1. Pinnacle Rock (PR) sampling site in Bodega Bay in 2002. Arrows indicate simplified flow around Bodega Head.

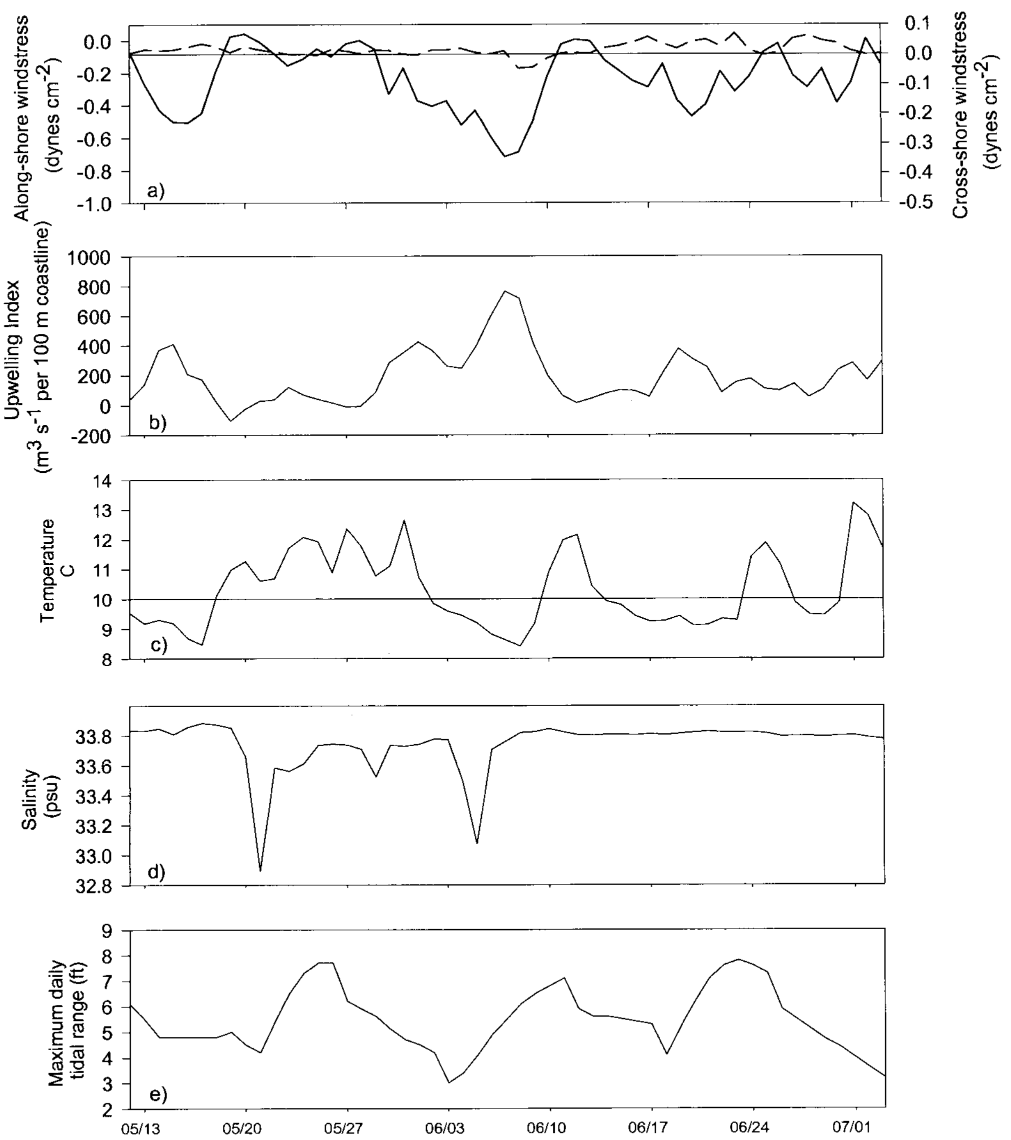

Figure 3.2. Time series at Bodega Marine Laboratory from 12 May to 3 July, 2002 of daily averages of: a) alongshore and across-shore (dashed line) wind stress (dyn cm^{-2}) rotated to 317° (negative alongshore values indicate increasing equatorward windstress); b) Bakun upwelling indices (from 39°N, 125°W) (m^{3} s^{-1} per 100 m of coastline); c) temperature (°C) with line at 10 °C indicating transitions from upwelling (< 10 °C) to relaxation (>10 °C) conditions; d) salinity (psu); and e) Maximum daily tidal range (ft).

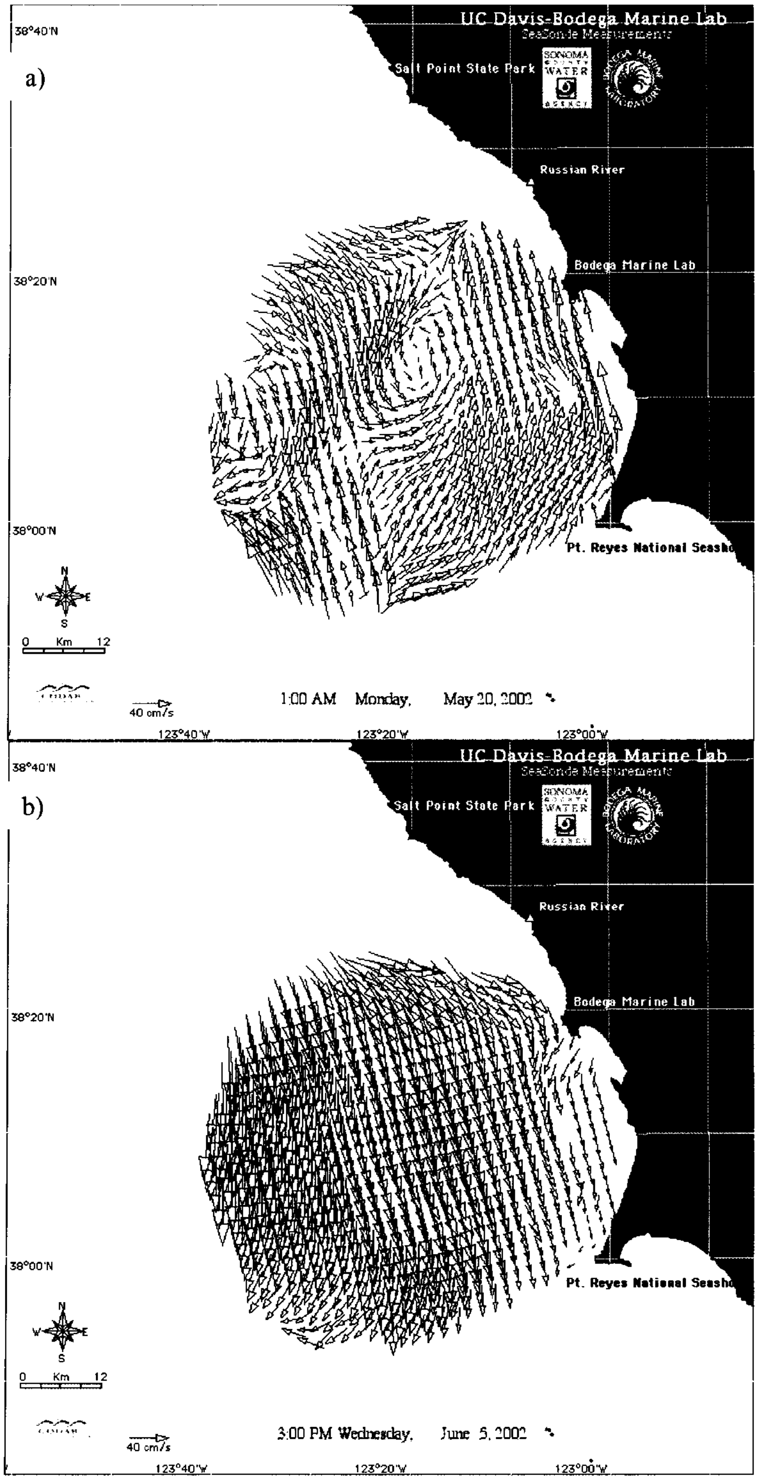

Figure 3.3. High frequency radar data showing surface current speed and direction during a) relaxation conditions with poleward flow and b) upwelling conditions with equatorward flow.

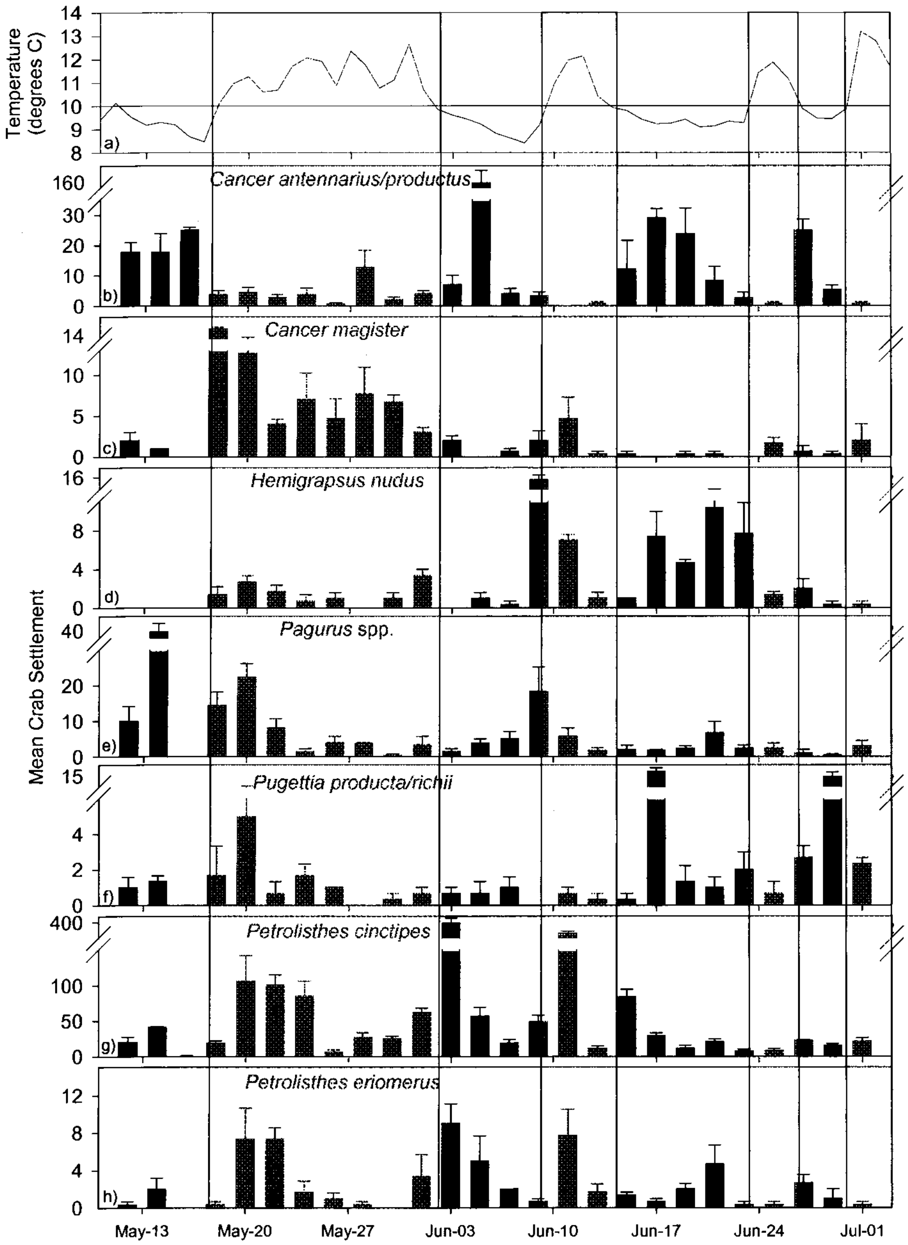

Figure 3.4. Mean settlement ± SE for each 2 d sampling period by seven taxa relative to upwelling-relaxation cycles. a) Temperature (°C) with line at 10 °C indicating transitions from upwelling (< 10 °C) to relaxation (> 10 °C) conditions. Shaded regions represent relaxation events. b) *Cancer antennarius/productus,* c) *C. magister,* d) *Hemigrapsus nudus,* e) *Pagurus* spp., f) *Pugettia producta/richii,* g) *Petrolisthes cinctipes,* and h) *P. eriomerus.*

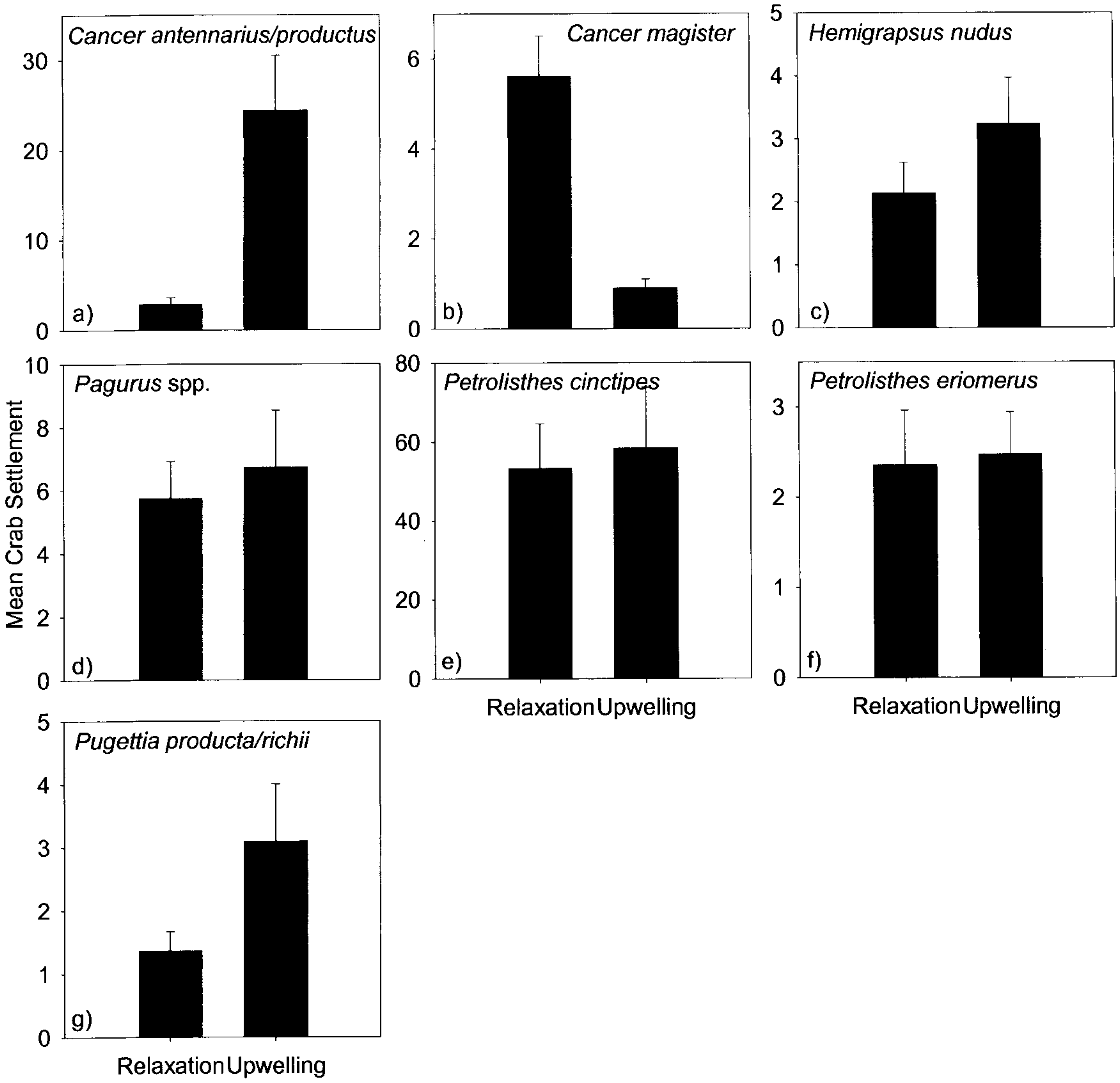

Figure 3.5. Mean settlement ± SE during relaxation (mean 2-d temperature is > 10 °C) and upwelling (mean 2-day temperature is <10 °C). a) *Cancer antennarius/productus,* b) *Cancer magister,* c) *Hemigrapsus nudus,* d) *Pagurus* spp., e) *Petrolisthes cinctipes,* f) *Petrolisthes eriomerus,* and g) *Pugettia. producta/richii.*