

## EFFECTS OF EL NIÑO AND LA NIÑA ON LOCAL INVERTEBRATE SETTLEMENT IN NORTHERN CALIFORNIA

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### ABSTRACT

During the spring and summer upwelling season (April–August) of the years 1997–99, we monitored settlement of juvenile crabs and sea urchins in northern California. Oceanographic conditions during these three years included El Niño in 1997–98, and La Niña in 1999. Prior data had shown strong annual settlement in years during which an intra-annual upwelling/relaxation mechanism was dominant. During active upwelling, invertebrate and fish larvae were retained south of Point Reyes. When winds relaxed, larvae could be transported northward and onshore in warm, less saline water, and settle on our collectors at the Bodega Marine Laboratory. During years in which this upwelling/relaxation mechanism dominated and salinity was inversely correlated with temperature, higher temperatures, which represented relaxation flow, were associated with cancrid crab settlement. The settlement response in 1997 and 1998 was similar to that of earlier years, but 1999 was quite different. In 1997, the lack of an inverse correlation between temperature and salinity indicated that wind-driven upwelling/relaxation was not dominant, and cancrid crab settlement was not correlated with temperature. In 1998, temperature and salinity were inversely correlated, but wind and temperature were not as highly correlated as in years prior to 1997. Settlement appeared to be driven by relaxation, but the relationship was not as strong as in previous years. Although they appeared to settle during relaxation events, neither sea urchins nor non-cancrid crabs settled in relation to temperature in 1997–99, nor in most earlier years. In 1999, strong, constant upwelling winds resulted in no relaxation events, and settlement was an order of magnitude lower than in any previous year. On interannual scales, data from 1997–99 were consistent with previous data for cancrid crabs, showing a negative correlation with wind stress,

but 1999 was not consistent with previous findings of a negative correlation between temperature and settlement of non-cancrid crabs.

### INTRODUCTION

The dramatic changes in physical oceanographic conditions and biological productivity in the California Current system (CCS) during El Niño events are well documented (Chelton et al. 1982; Tegner and Dayton 1987; Glynn 1988). The general biological effect of El Niño–Southern Oscillation (ENSO) events on marine animals in the CCS is reduced productivity at all trophic levels. Reduced chlorophyll levels indicate lower primary productivity (Lenarz et al. 1995). A negative correlation between zooplankton biomass in California Cooperative Oceanic Fisheries Investigations (CalCOFI) surveys (Chelton et al. 1982) and lower abundance in more northern waters (Brodeur et al. 1992) indicate lower secondary productivity. Effects at higher trophic levels include smaller size and lower catches of salmon (Johnson 1988; Kope and Botsford 1992; Pearcy 1992), reduced survival of Pacific mackerel (Sinclair et al. 1985), reduced recruitment in rockfish species (Ralston and Howard 1995; Yoklavich 1996), and decreased reproductive success of seabird colonies (Ainley et al. 1995).

While ENSO-related effects on productivity have received much attention, the effect of ENSO events (both anomalously warm El Niño and cold La Niña events) on settlement of planktonic larvae has rarely been documented. A few relatively short time series for settlement of benthic invertebrates in the CCS provide some insight into how individual species respond to oceanographic conditions, including ENSO events. Sea urchins exhibit patchy and episodic settlement (Ebert et al. 1994) and recruitment (Pearse and Hines 1987; Sloan et al. 1987). During El Niño years, sea urchins have recruited or settled at lower levels in southern California (Tegner and Dayton 1987; Ebert et al. 1994), but at higher levels

in northern California compared to prior, non-ENSO years (Ebert et al. 1994). Larval rockfish have shown low abundances during both strong El Niño and La Niña events, and appear to have highest survival in years of intermediate temperature (Ralston and Howard 1995; Yoklavich 1996).

Upwelling winds in the CCS are generally higher during non-ENSO years. Moreover, the time series of upwelling index, ocean temperature, and sea level in central California can be represented by a single time series of its first principal component (empirical orthogonal function), which represents ENSO/non-ENSO conditions (approximately equal loading of positive temperature, negative upwelling, and positive sea level; Kope and Botsford 1992). However, a relation between the intra-annual, weekly time-scale wind patterns of interest here, and ENSO conditions has not been identified. On annual time scales, successful nearshore settlement of larvae of benthic and intertidal invertebrates is generally greater during periods of lower upwelling winds (Roughgarden et al. 1988; Ebert et al. 1994; Connolly and Roughgarden 1999). However, the sampling in these studies covers short time periods, although one study did encompass both ENSO and non-ENSO conditions over 3.5 years (Ebert et al. 1994).

Here we compare settlement of marine invertebrates at Bodega Marine Laboratory (BML) during the 1997–99 period with results from sampling in 1992–96, described in Wing et al. 2000.<sup>1</sup> This comparison can be naturally phrased in terms of ENSO effects on settlement at this location because a strong El Niño occurred during 1997 and 1998, and there was a strong La Niña in 1999. In the earlier sampling of invertebrate settlement, we identified a mechanism by which larvae were retained in the lee (south) of Point Reyes (fig. 1) during active upwelling (Wing et al. 1998) and were transported poleward and settled onshore during occasional relaxations or reversals of upwelling winds (Send et al. 1987; Wing, Botsford et al. 1995; Wing, Largier et al. 1995). Examination of interannual variability in this mechanism during the years 1992–96 revealed that this mechanism did not operate consistently each year (see footnote 1).

Although intra-annual patterns in upwelling winds were not the same each year, daily temperature at BML covaried significantly with daily wind stress in each year. However, covariability between local temperature and salinity did not always indicate an upwelling/relaxation pattern; correlations were significantly negative only in 1992, 1993, 1995, and 1996. During these years, settlement of cancrid crabs was higher during periods of

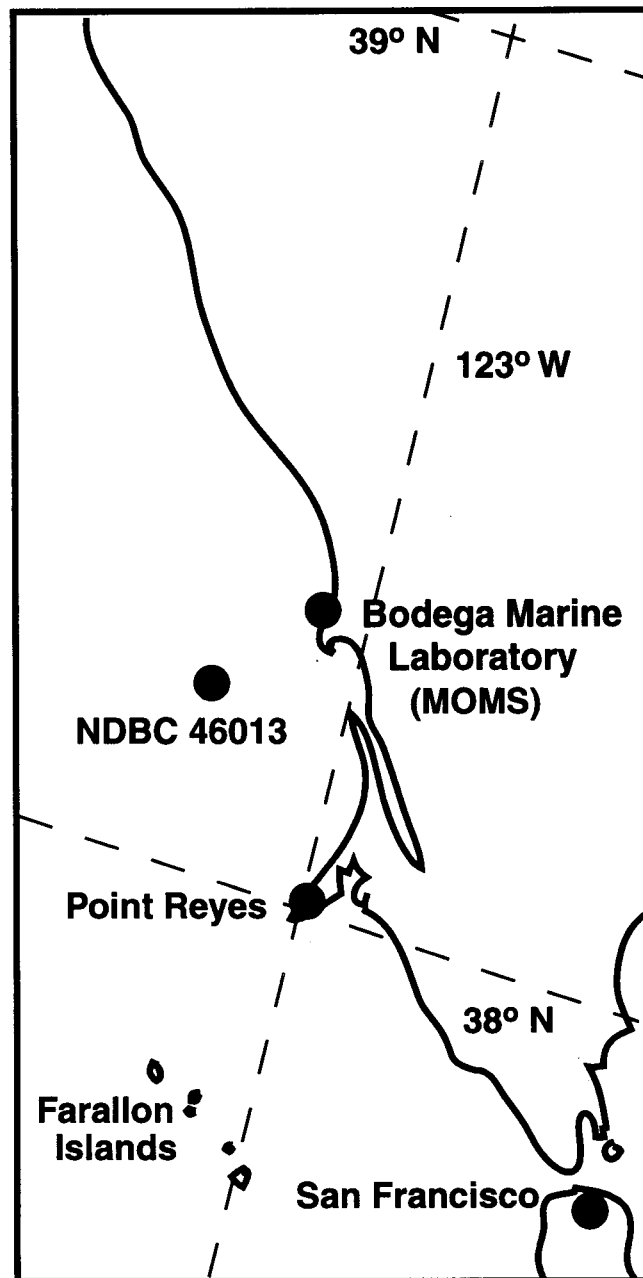


Figure 1. Map detailing location of study site at Bodega Bay, California. Meteorological observations were taken from the Bodega Marine Laboratory's Meteorological and Oceanographic Monitoring Station (MOMS) and NOAA/National Data Buoy Center (NDBC) buoy 46013.

higher BML temperature, reflecting relaxation flow, than during periods of strong upwelling winds. There was a significant correlation between weekly cancrid crab settlement and temperature, except in 1995, when samples may not have been frequent enough to identify this relation. Interannual variability in total annual settlement of cancrid crabs was negatively correlated with upwelling and alongshore wind stress. Weekly settlement of non-cancrid crabs and sea urchins was not correlated with

<sup>1</sup>Wing, S. R., L. W. Botsford, L. E. Morgan, J. M. Diehl, and C. J. Lundquist. 2000. Interannual variability in larval supply to crab and sea urchin populations in the northern California Current. (manuscript)

fluctuations in local temperature, in part because their settlement seasons are much shorter, and there were fewer opportunities to observe settlement. Interannual variability in total annual settlement of non-cancerid crabs was positively correlated with La Niña conditions; 1992 through 1994 were moderate ENSO years, and 1995 through early 1997 were moderate La Niña years.

Here we present observations of crab and sea urchin species during the anomalous 1997–99 period and examine (1) intra-annual variability in settlement due to local wind forcing and the wind relaxation mechanism as proposed by Wing, Botsford et al. (1995), Wing, Largier et al. (1995), and Wing et al. (1998); and (2) interannual variability and the effect of anomalous oceanic conditions on invertebrate settlement.

## MATERIALS AND METHODS

### Oceanographic Data

Oceanographic data used in this study were collected from multiple sources. Time series of wind velocities, temperature, and salinity were obtained from Bodega Marine Laboratory's Meteorological and Oceanographic Monitoring Station (MOMS), located offshore of BML (38°19'N, 123°04'W; fig. 1). Data from MOMS are collected as 20-minute averages for sea-surface temperature and conductivity sensors, and as 10-minute averages for wind-velocity data. Temperature time series for 1999 were obtained from NOAA buoy NDBC 46013 (38°14'N, 123°18'W), because temperature data were not continuously available from MOMS over the 1999 sampling period.

MOMS temperatures and buoy temperatures were highly correlated over periods when both data sources were available ( $r = 0.899$ ). No salinity data were available near Bodega Bay in 1999. For each settlement season (April 30–August 13, day 120–day 225) we calculated daily averages of wind velocities, temperature, and salinity. Alongshore wind stress (317°) was calculated from wind velocities (Pond and Pickard 1983), according to

$$\tau = \rho_a C_N V^2$$

where  $\tau$  = magnitude of wind stress at 317°

$\rho_a$  = density of air = 1.3 kg/m<sup>3</sup>

$C_N$  = drag coefficient

$V$  = magnitude of wind velocity at 317° (m/s).

$C_N$  was calculated per Trenberth et al. (1990) as a step function where

$$\begin{aligned} 10^3 C_N &= 0.49 + 0.065 V && \text{for } V > 10 \text{ m/s} \\ &= 1.14 && \text{for } 3 \leq V \leq 10 \text{ m/s} \\ &= 0.62 + 1.56/V && \text{for } V \leq 3 \text{ m/s} \end{aligned}$$

To reflect the variability in wind that is associated with relaxation events, we also present an index of re-

laxation strength that uses a nonlinear transformation of the alongshore wind stress values. Relaxations occur when winds cease or reverse direction from the typical alongshore (317°) direction during upwelling periods, and these events are recognizable in the wind stress time series as periods of low or negative values. Researchers have postulated that several days of wind relaxation are necessary for larvae to be transported from upwelling retention zones south of Point Reyes to the sampling location at Bodega Head (fig. 1; Send et al. 1987; Wing, Botsford et al. 1995; Wing, Largier et al. 1995). To reflect this multiday relaxation period, we calculated a 4-day running average of  $\log_{10}(\text{wind stress} + 1)$  as an indicator of relaxation flow reaching the BML site as in Wing et al. 2000 (see footnote 1). We calculated correlations among all oceanographic variables by using a standardized linear correlation statistic (Zar 1984). We calculated 95% confidence limits based on sample size during the primary settlement period (30 April–13 August, day 120–225;  $n = 106$ ).

To put the influence of local oceanographic conditions on settlement in the context of anomalous ENSO events, we compared annual settlement to ocean basin-scale and other large-scale indices of ENSO and upwelling. Daily Bakun upwelling indices were obtained from the National Oceanic and Atmospheric Administration (NOAA) for latitude 36°N. Monthly standardized Southern Oscillation Indices (SOI) were obtained from the NOAA Climate Prediction Center. The SOI is the standardized monthly mean pressure difference between Darwin, Australia, and Tahiti, French Polynesia. Negative values correspond to warm, El Niño events; positive values correspond to cold, La Niña events. An extratropical analog to the SOI has recently been created to more accurately describe the strength of ENSO events in midlatitude Northern Hemisphere regions.<sup>2</sup> Data for this alternative index, the Northern Oscillation Index (NOIx), were obtained from the NOAA Pacific Fisheries Environmental Laboratory. The NOIx is the standardized monthly mean pressure difference between the North Pacific High (35°N, 135°W) and Darwin, Australia.

### Invertebrate Settlement Data

In spring and summer of 1997–99 at the Bodega Marine Laboratory (38.19°N, 123.04°W; fig. 1) we sampled settlement of crabs and sea urchins approximately weekly. The general characteristics of our collection site include an exposed coastline and a rocky substrate. Each year we placed an array of three collector moorings at 10–12 m depth separated by approximately 100 m.

<sup>2</sup>Schwing, F. B., T. Murphree, and P. M. Green. 2000. A climate index for the northeast Pacific. (manuscript)

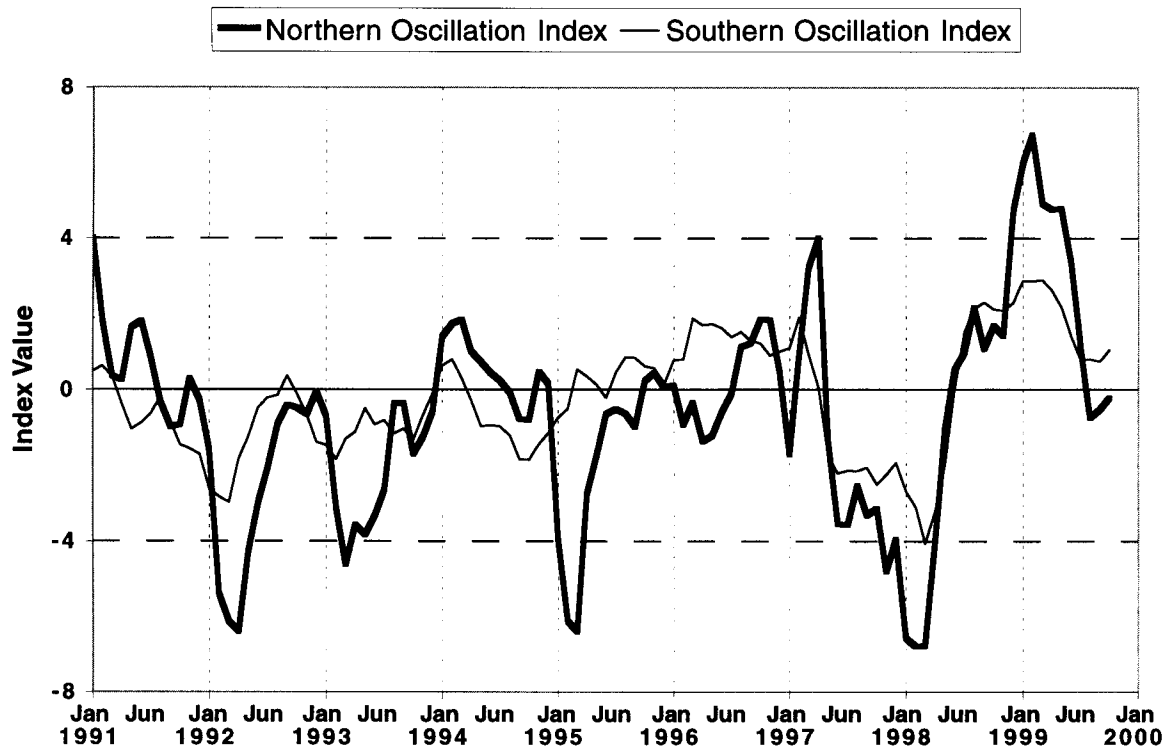


Figure 2. Time series of monthly extratropical Northern Oscillation Index (NOI) and Southern Oscillation Index (SOI). Positive values indicate La Niña conditions; negative values indicate El Niño conditions. Time series are presented as 3-month running averages.

Collections generally were made weekly, but several were delayed because of inclement weather, and periods between samples were sometimes two weeks; one period in 1999 was one month. Because of this, some important variability on weekly (or shorter) time scales may have been unresolved for some time periods.

We sampled juvenile invertebrates with two types of settlement collectors. “Brush” collectors consisted of four, 7-inch-long, wood-backed scrub brushes with polypropylene bristles, based on methods of Ebert and colleagues (Ebert and Russell 1988; Ebert et al. 1994). “Bag” collectors were constructed from half-inch Nytex plastic mesh, forming a 75 cm-long bag with a 30 cm-wide opening that contained a 1 m by 5 m section of #30 3/4 inch nylon mesh trawl netting, based on methods of Wing et al. 2000 (see footnote 1). Each collector was moored by a polypropylene line with net floats for buoyancy, anchored to the bottom with a 25 kg cement anchor. One brush and one bag collector were attached to each mooring line so that the collectors floated approximately 0.5 to 1 m above the bottom. After weekly exchange, we rinsed the collectors in fresh water, and fixed the resulting material in ethanol for later enumeration and identification of newly settled crabs and sea urchins.

We used a dissecting microscope to identify crab and sea urchin species to the lowest taxon possible. Sea urchin

species included the red sea urchin (*Strongylocentrotus franciscanus*) and the purple sea urchin (*S. purpuratus*). Cancrid crab species included larval and juvenile crabs of primarily *Cancer antennarius* and *C. productus*, but also some individuals of *C. magister* and *C. gracilis*. Other crab species included primarily porcellanid crab megalopae and juveniles (*Petrolisthes* spp.) and also various majid (*Pugettia producta*, *Loxorhynchus crispatus*), pagurid (*Pagurus* spp.), and grapsid (*Hemigrapsus nudus*) species.

To analyze patterns, we considered settlement of all sea urchin species combined, and settlement of cancrid crabs and settlement of non-cancrid crabs separately. We reported cancrid and non-cancrid (primarily porcellanid) crab species separately because of their different larval periods (cancrid crabs: 3–6 months, porcellanid species: 4–6 weeks) and different times of larval release (cancrid crabs: winter, before spring transition; porcellanid crabs: near the spring transition; Strathmann 1987), which may cause these different larvae to be transported in different water masses and subject to different local conditions for transport and settlement.

Settlement rates were calculated as the average number of settlers per brush collector per day of the collection period for each taxon. Bag collector data were not used in the average calculation so that we could make comparisons to prior years of settlement data at BML (Wing, Botsford et al. 1995; Wing, Largier et al. 1995;

Wing et al. 2000<sup>3</sup>). Average daily settlement rates were calculated for each collection period from 30 April to 13 August (day 120–225) each year.

### Intra-annual Correlations of Settlement with Physical Variables

To determine correlations between oceanographic variables and invertebrate settlement, we calculated average values of temperature, salinity, alongshore wind stress,  $\log_{10}(\text{wind stress}+1)$ , and upwelling over each sampling period. We calculated correlations between these oceanographic values and average settlement on brush collectors of sea urchins, cancrid crabs, and non-cancrid crabs during each sampling period at Bodega Head by using a standard linear correlation statistic (Zar 1984). We calculated 95% confidence intervals based on sample size (number of sampling periods) for each year.

### Interannual Correlations of Settlement with Physical Variables

Annual settlement rates for cancrid crabs, non-cancrid crabs, and sea urchins were calculated for each year (1997–99) of settlement collection. We calculated these as the average settlement rate over the period 30 April–13 August (days 120–225) of each year. Annual values of oceanographic variables—temperature, salinity, wind stress,  $\log_{10}(\text{wind stress}+1)$ , and upwelling index—were calculated as the mean value of daily time series over the period from day 120 to day 225. We calculated annual values of the NOIx and SOI as the mean value of the monthly time series from April to August.

## RESULTS

### Intra-annual Variability in Settlement and Oceanographic Conditions

The years 1997–99 included more extreme values of basin-scale indicators of ENSO conditions than the 1991–96 time series. Time series of NOIx and SOI indicate that 1997–99 were anomalous years with extremely low values in late 1997 and early 1998, representing strong El Niño conditions of much longer duration than El Niño events in 1992 and 1995, and extremely high values in 1999, representing strong La Niña conditions (fig. 2). During previous settlement monitoring at BML, 1992 and 1993 appear as mild El Niño years in both indices, whereas 1994 represents a transitional year of moderate conditions for both indices. The NOIx shows early 1995 to be an El Niño event of similar magnitude to that of 1992–93, but the SOI gives no implication of anomalous conditions. A mild La Niña event is apparent in both indices from 1996 through early 1997.

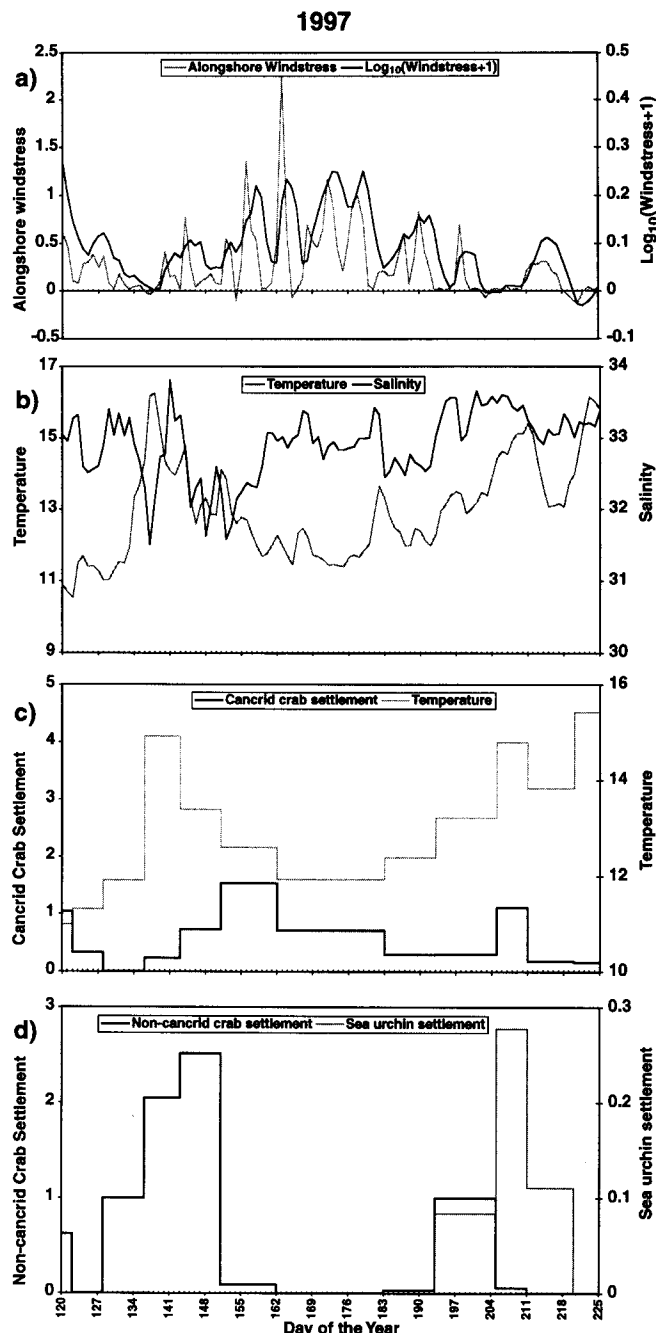


Figure 3. 1997 time series at Bodega Head of a, alongshore wind stress (dynes/cm<sup>2</sup>, pale line) and  $\log_{10}(\text{wind stress}+1)$ ; b, temperature (°C, pale line) and salinity (ppt, bold line); c, settlement per brush-collector-day of cancrid crabs (bold line) and average temperature per sampling period (pale line); d, settlement per brush-collector-day of non-cancrid crabs (bold line) and sea urchins (pale line). In c and d, lines extend over the entire settlement period, but this does not imply constant settlement.

**1997.** During the early settlement period of 1997 (day 120 to approximately day 150), covariability among oceanographic variables—temperature, salinity, alongshore wind stress, and  $\log_{10}(\text{wind stress}+1)$ —showed conditions typical of the upwelling/relaxation season at this location (fig. 3a, b). High wind stress values were

<sup>3</sup>See footnote 1 on p. 168.

TABLE 1  
 Intra-annual Correlations between Daily Values for  
 Oceanographic Variables (30 April to 13 August)

Year	Wind stress vs. temperature	Log <sub>10</sub> (wind stress+1) vs. temperature	Temperature vs. salinity
1997	<b>-0.354</b>	<b>-0.733</b>	0.087
1998	<b>-0.217</b>	<b>-0.334</b>	<b>-0.737</b>
1999	<b>-0.377</b>	<b>-0.584</b>	NA

Significant correlations ( $p < 0.05$ ) are in bold.

associated with low temperatures and high salinities, due to Ekman transport of warm surface water layers offshore, and replacement by cold, upwelled water. When the winds relaxed, however, as on days 135–140, oceanographic conditions reversed, resulting in a rapid rise in temperature and a decrease in salinity that has been associated with alongshore transport during wind relaxation periods (Send et al. 1987; Wing, Botsford et al. 1995; Wing, Largier et al. 1995). Water transported from south of Point Reyes is fresher and warmer than upwelled water (Schwing et al. 1991; Wing et al. 1998).

High winds from day 150 to day 180 led to constant low temperature and high salinity. After day 180, there appeared to be a shift from a system dominated by upwelling and relaxation to one in which wind relaxation events raised temperature, but temperature appeared to be positively correlated with salinity on a daily scale (days 180, 195, 200). The remainder of the settlement period of 1997 was marked by increasing temperature and salinity, and decreasing alongshore wind stress, atypical of conditions in the upwelling season in northern California, but more common of late summer and early fall in this region—the relaxation season described by Largier et al. (1993).

Wind stress was negatively correlated with temperature, as expected in this system, where upwelling conditions are generated by strong wind forcing (table 1). A stronger correlation was seen between temperature and the smoothed log of wind stress, which is also expected, because this index reflects the degree of relaxation. Salinity, however, was not correlated with temperature, indicating that there was no wind-forced upwelling/relaxation variability in 1997, particularly later in the season (table 1).

In 1997, there were no significant correlations between any of the three taxa (cancrid crabs, non-cancrid crabs, and sea urchins) and temperature during the settlement period (table 2). This was consistent with earlier years (e.g., 1994) in which the upwelling/relaxation mechanism was not dominant.<sup>4</sup> Cancrid crabs settled after a prolonged relaxation event early in the season (approximately day 140) and once during a wind relax-

<sup>4</sup>See footnote 1 on p. 168.

TABLE 2  
 Intra-annual Correlations between Invertebrate  
 Settlement Rates and Temperature Averaged over  
 Each Settlement Collection Period, 1997–99

Year <sup>a</sup>	Taxon	Temperature
1997 ( $n = 12$ )	Cancrid crab	-0.178
	Non-cancrid crab	0.151
	Sea urchin	0.431
1998 ( $n = 12$ )	Cancrid crab	-0.302
	Non-cancrid crab	-0.084
	Sea urchin	-0.298
1999 ( $n = 12$ )	Cancrid crab	<b>-0.586</b>
	Non-cancrid crab	-0.229
	Sea urchin	-0.261

Significant correlations ( $p < 0.05$ ) are in bold.

<sup>a</sup> $n$  refers to the total number of collection periods.

ation late in the season (day 205; fig. 3c). Non-cancrid crabs settled during the early, prolonged relaxation event and once later in the season (fig. 3d). Sea urchins showed a small settlement pulse during the relaxation event at day 195 (fig. 3d).

**1998.** Although 1998 began under strong El Niño conditions, basin-scale indicators (NOIx, SOI) show a return to non-El Niño conditions in May–June, shortly after our sampling period began (fig. 2). Although temperatures were 2°–3°C above normal, the typical pattern of upwelling periods punctuated by wind relaxation events occurred in 1998 (fig. 4a). All events in 1998 were associated with temperature increase and salinity decrease, although the magnitude of the change in temperature and salinity was usually related to the length of the wind relaxation period (fig. 4b). Temperature was significantly negatively correlated with both wind stress and log<sub>10</sub>(wind stress+1) in 1998 (table 1), although the low correlations (lowest of the 1992–99 time series) indicated that local wind forcing was not a strong driver of local relaxation. Temperature and salinity were significantly inversely correlated (table 1).

Cancrid crabs appeared to settle during relaxations (fig. 4c), but this response was not reliable enough to produce a significant negative correlation between temperature and settlement (table 2). Three periods of low settlement at high temperature (days 120–127, 155–161, and 210–217) appear to make the correlation between settlement and temperature negative. Although it could be argued that in each of these periods temperature is high while settlement is low because the sampling period includes the end of a relaxation event, the temperature/settlement relation is not as strong as in previous years (1992–96). The deviation from the upwelling/relaxation mechanism during 1998 is in part due to the lack of sampling resolution.

Non-cancrid crabs showed highest settlement during wind relaxation periods, at approximately day 132 and day 150 early in the season, and during a later

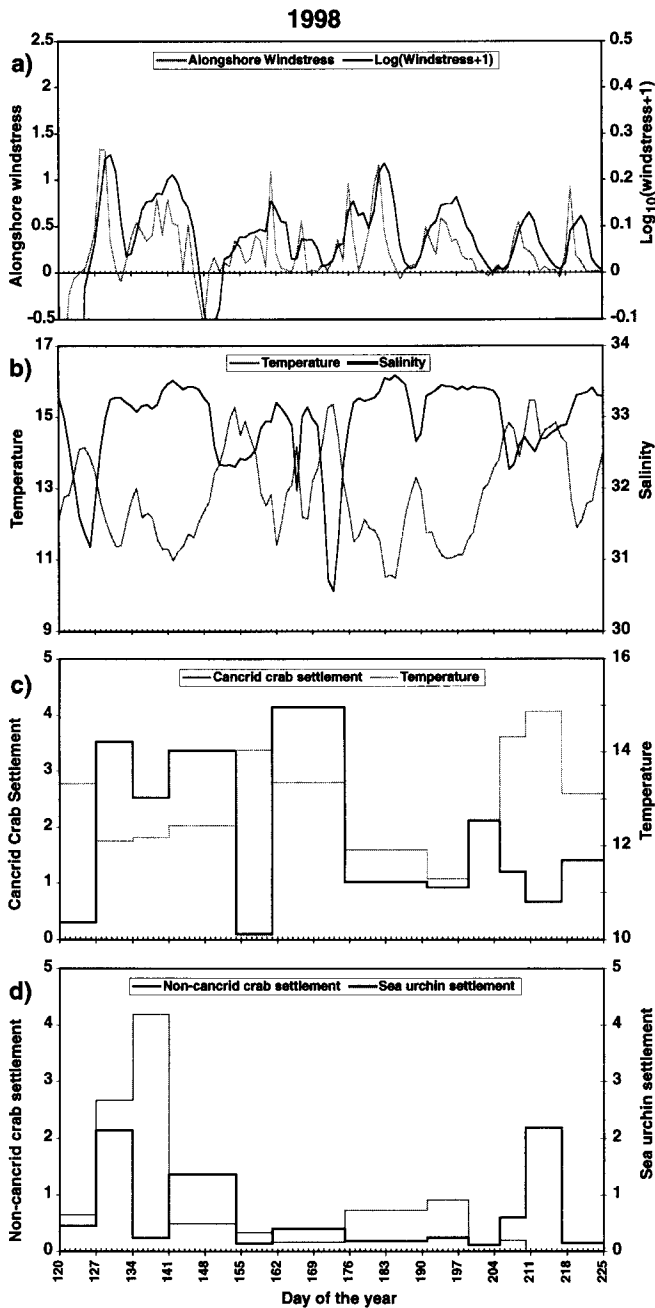


Figure 4. 1998 time series at Bodega Head of a, alongshore wind stress (dynes/cm<sup>2</sup>, pale line) and  $\log_{10}(\text{wind stress}+1)$ ; b, temperature (°C, pale line) and salinity (ppt, bold line); c, settlement per brush-collector-day of cancrid crabs (bold line) and average temperature per sampling period (pale line); d, settlement per brush-collector-day of non-cancrid crabs (bold line) and sea urchins (pale line). In c and d, lines extend over the entire settlement period, but this does not imply constant settlement.

relaxation at about day 215 (fig. 4d). Sea urchins settled unusually early in the season at high levels, overlapping a wind relaxation event at day 135, and continuing to settle the following week (fig. 4d). A smaller settlement pulse of sea urchins later in the season followed the day 175 and day 195 relaxation events. Sea urchin settlement

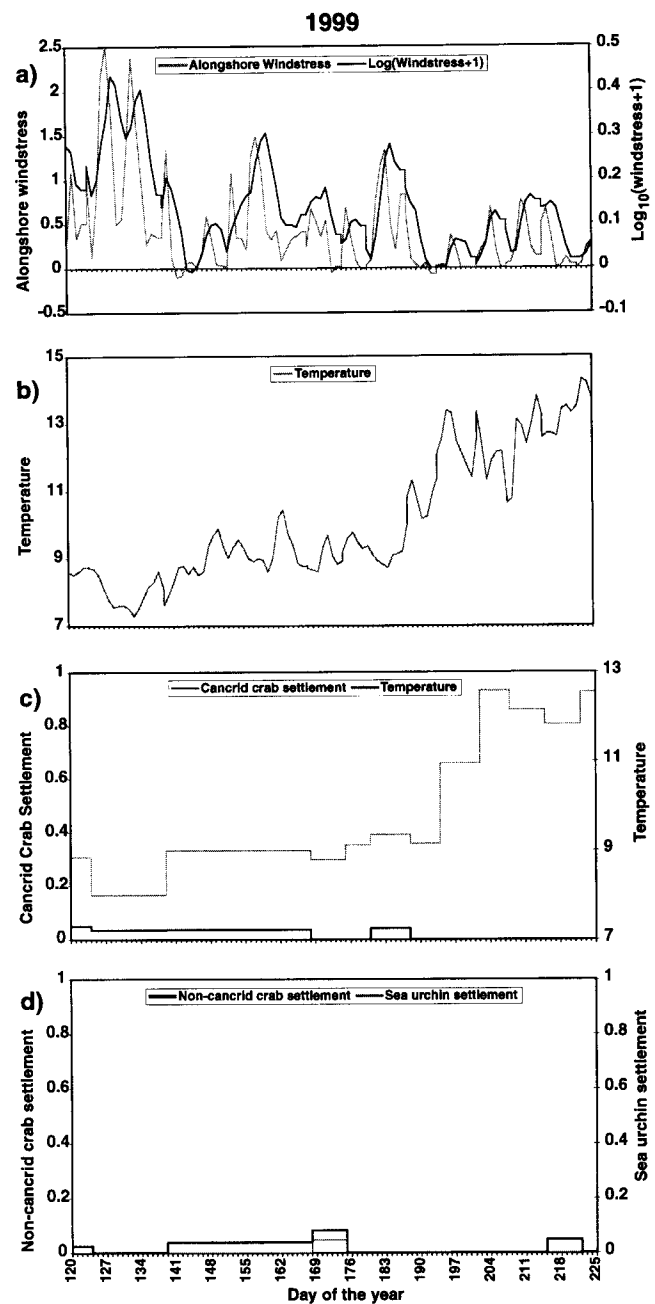


Figure 5. 1999 time series at Bodega Head of a, alongshore wind stress (dynes/cm<sup>2</sup>, pale line) and  $\log_{10}(\text{wind stress}+1)$ ; b, temperature (°C, pale line) and salinity (ppt, bold line); c, settlement per brush-collector-day of cancrid crabs (bold line) and average temperature per sampling period (pale line); d, settlement per brush-collector-day of non-cancrid crabs (bold line) and sea urchins (pale line). In c and d, lines extend over the entire settlement period, but this does not imply constant settlement.

rates were an order of magnitude higher in 1998 than in 1997.

**1999.** Basin-scale indicators (NOIx, SOI) indicate strong La Niña conditions at the beginning of our sampling period, but these conditions had declined to moderate levels by the end of the period (fig. 2). The early

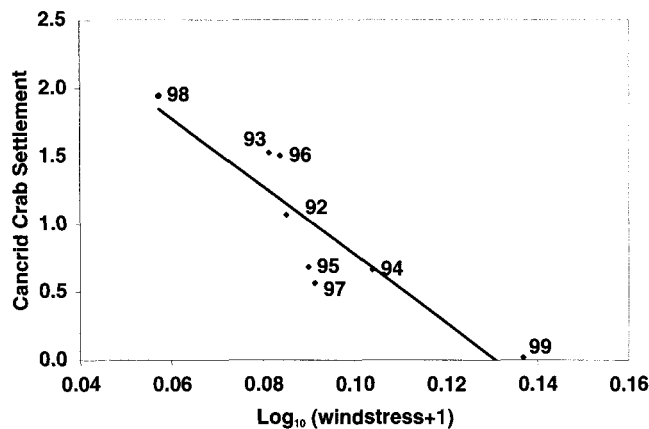


Figure 6. Linear regression of seasonal (30 April–13 August) cancrid crab settlement on brush collectors during 1992–99 at Bodega Head with seasonal average of  $\log_{10}(\text{wind stress}+1)$  ( $y = -24.37x + 3.18$ ,  $R^2 = 0.8376$ ) collected at BML MOMS.

TABLE 3  
 Interannual Correlations between Settlement  
 and Oceanographic Variables

	Cancrid crabs	Non-cancrid crabs	Sea urchins
Salinity	0.277	0.591	0.018
Temperature	0.476	0.044	0.395
Wind stress	<b>-0.777</b>	-0.140	-0.339
$\log_{10}(\text{wind stress}+1)$	<b>-0.900</b>	-0.217	-0.539
Upwelling	-0.645	-0.120	-0.423
NOIx	-0.027	0.028	0.256
SOI	0.199	-0.318	0.128

All variables are based on the years 1992–99, except for salinity (1992–98). All values are calculated as the average during the settlement period of days 120 to 225 (30 April–13 August). Significant correlations ( $p < 0.05$ ) are in bold.

part of the settlement season was dominated by strong alongshore upwelling winds, resulting in prolonged periods of lower temperatures than usual (fig. 5a, b). Low daily variability in temperature, combined with the strong alongshore winds, resulted in no clear evidence of relaxation in the temperature time series. Two atypical wind relaxation events did occur during the season, at days 145 and 190, but neither event was associated with a temperature increase of the magnitude observed during similar events in 1997 and 1998 (fig. 5b). The second relaxation event came near the beginning of a general increase in temperature that continued through the remainder of the settlement season. However, the lack of decrease in temperature as winds began after this event makes it unlikely that the temperature increase was related to wind relaxation events (fig. 5a). Correlations between daily values of temperature and wind stress and temperature and  $\log_{10}(\text{wind stress}+1)$  were significant, showing evidence of wind-forced upwelling (table 1).

In 1999, settlement of all taxa was very low, with background levels at least an order of magnitude less than

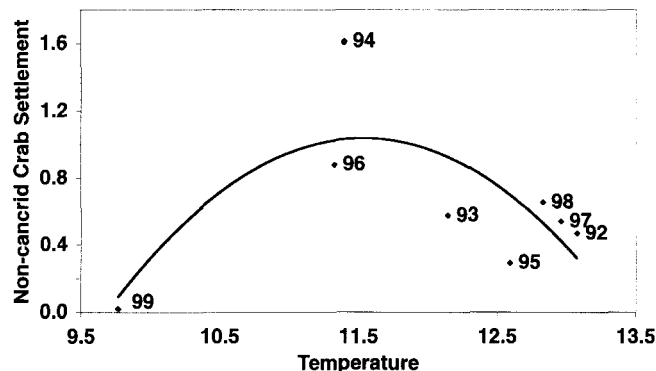


Figure 7. Nonlinear regression of seasonal (30 April–13 August) non-cancrid (porcellanid, grapsid, pagurid, and majid) crab settlement on brush collectors during 1992–99 at Bodega Head with seasonal average of the temperature ( $y = -0.3824x^2 + 8.7761x - 49.116$ ,  $R^2 = 0.6483$ ) collected at BML MOMS.

those seen in 1998 (fig. 5c, d). Settlement of cancrid crabs showed a significant negative correlation with temperature (table 2), which was probably spurious and due to the low rate of settlement occurring only during the early, colder portion of the settlement season, rather than reflecting settlement in relation to any upwelling/relaxation pattern. Settlement of non-cancrid crabs and sea urchins showed no significant correlations with temperature (table 2).

### Interannual Variability in Settlement and Oceanographic Conditions

Cancrid crabs had lower settlement in years with high seasonal alongshore wind stress,  $\log_{10}(\text{wind stress}+1)$ , and upwelling values (fig. 6, table 3). Although the previously observed negative correlation between non-cancrid crab settlement and temperature was evident for 1997 and 1998, adding 1999 to the time series resulted in no significant linear correlation, and a dome-shaped relation between settlement and temperature (fig. 7, table 3). A similar dome-shaped relation was observed between non-cancrid settlement and upwelling. Sea urchin settlement was not significantly correlated with any oceanographic variables. Sporadic settlement of sea urchins, with five of the eight years having little or no settlement, provides few data points for study, though the analysis showed relatively high negative correlations with wind stress,  $\log_{10}(\text{wind stress}+1)$ , and upwelling (table 3).

### DISCUSSION

In general, settlement in 1997 and 1998 was similar to that in previous years, but 1999 was unusual because of the extremely strong upwelling winds. In 1997, the lack of inverse correlation between temperature and salinity indicated that wind-driven upwelling/relaxation was not dominant, and cancrid crab settlement was not



correlated with temperature. In 1998, temperature and salinity were inversely correlated, and settlement appeared to be driven by relaxation, with some exceptions. In 1999 strong, constant upwelling winds resulted in no relaxation events and settlement an order of magnitude lower than in any previous year.

It is somewhat surprising that our 1998 data did not show the expected positive correlations between temperature and settlement of cancrid crab and sea urchin species. This is partly due to the gaps in sampling because weather and other factors limited our ability to sample frequently. At several times in the season, sample collection was delayed, and two weeks elapsed between samples, diminishing our ability to detect responses to rapid changes in temperature. Examination of the oceanographic and settlement data on a fine scale (fig. 4) does indicate settlement following wind relaxation events; but because collection periods generally averaged over both upwelling and relaxation conditions, we cannot detect the correlation between settlement and relaxation normally evident in good settlement years. Longer collection periods also make our settlement collections more susceptible to the influence of postsettlement survival, which may bias longer-term collections. However, our 1998 (and 1999) data emphasize the necessity of examining settlement processes at the relevant temporal scale. Because settlement seems to occur over the first few days of a relaxation event (Wing, Botsford et al. 1995), weekly or even daily monitoring is much more useful for evaluating the settlement responses to local oceanographic conditions.

Settlement in 1999 was unusually low. High upwelling and only a few weak, ineffective relaxation events caused a lack of noticeable levels of settlement of any taxa. It may be that the constant, extreme upwelling winds of the early part of the season resulted in stronger alongshore and offshore transport of the warm surface layer, so that a longer relaxation event was required for nearshore temperatures to rise and for planktonic cancrid crabs from south of Point Reyes to reach BML on the coast. Another equally likely hypothesis for the lack of settlement is that larvae were transported out of the retention zone into the stronger than normal alongshore flow of the coastal jet (Hayward et al. 1999), and thus lost from the local system.

Settlement of non-cancrid crabs varied intra-annually in response to wind relaxation events, though correlations in oceanographic variables over the season do not show the same strong negative correlations between wind values and settlement. The short settlement period of non-cancrid (primarily porcellanid) crabs, with large pulses primarily early in the spring settlement season (Strathmann 1987), makes it difficult to describe direct associations of settlement with oceanographic variables

over the entire season, as noted in Wing et al. 2000.<sup>5</sup> Previous observations have shown the highest settlement in years with low temperatures, strong upwelling, and low salinity. The highest years of settlement were 1994 and 1996, years with the highest non-ENSO index values for the NOIx. Our 1999 findings modified this simple linear response between La Niña conditions and non-cancrid crab settlement to a nonlinear, dome-shaped response of settlement to both temperature and upwelling conditions (table 3). This implied that non-cancrid crabs generally settle most strongly in years of high upwelling (and presumably high CCS productivity); however, extremely high upwelling restricts settlement of these coastal crabs, possibly by transporting them offshore or southward in the coastal jet. It has also been suggested that the lack of settlement in April–August of 1999 could be explained by temperature-related disruptions in reproductive timing, because gravid porcellanid crabs were not observed until late summer (Robert Toonen, pers. comm.).

Sea urchin settlement continued to be sporadic in these years, and reasons for the exact timing and magnitude of settlement are still unknown. Other researchers have documented similar episodic settlement of sea urchin species via direct observations of settlement (Ebert et al. 1994) and indirect observations through adult size-frequency distributions (Tegner and Dayton 1981, 1987; Pearse and Hines 1987; Ebert and Russell 1988). Researchers have also documented sea urchin settlement during winter and early spring (Ebert et al. 1994), a period for which we are subject to logistical constraints (weather). Settlement of sea urchins in response to wind relaxation events has also been observed (Miller and Emler 1997). In spite of the sporadic temporal nature of sea urchin settlement, its spatial pattern indicates that sea urchins respond to the alongshore transport in the upwelling/relaxation mechanism near headlands (Wing, Botsford et al. 1995). The pattern of recent recruitment in size distributions of the red sea urchin indicates higher settlement just north of Point Reyes and Point Arena than elsewhere (Morgan et al. 2000; cf. Ebert and Russell 1988).

The findings described here represent local settlement at BML, a single point on the coast that does not necessarily reflect the coastwide settlement strength of the species we described. Settlement at BML could be influenced by two separate mechanisms: one that determines general annual strength of the year class in plankton all along the coast, and another that determines how much of that year class settles at this specific location as determined by local winds and associated circulation.

<sup>5</sup>See footnote 1 on p. 168.

Our ability to draw any of these conclusions about ENSO-related settlement effects depends critically on the long-term monitoring program in place at BML. Though the data set is, in itself, rather short (only 8 years), shorter time series often lack baseline settlement data, making it difficult to draw conclusions about the effect of relatively rare ENSO events (of the 1997–98 magnitude). There is a dire need for more long time series, to put these anomalous events in context. Although we will never know past settlement data, long-term monitoring projects will allow us to document how future anomalous events, including ENSOs and global warming, affect invertebrate settlement.

## ACKNOWLEDGMENTS

We gratefully acknowledge the Bodega Marine Laboratory for logistical support, and Steven Gough, Matthew Hickman, and others who braved the elements to collect field data for this study. We thank S. Wing for providing details of his data analysis, and J. Quinn, A. Hastings, S. Wing, and two anonymous reviewers for critical reviews of this manuscript. This study was funded by three grants from the National Sea Grant College Program, National Oceanic and Atmospheric Administration, U.S. Department of Commerce, under grant number NA36RG0537, project number R/F-157; and grant number NA66RG0477, project numbers R/F-169 and R/F-179 through the California Sea Grant College System, and in part by the California State Resources Agency. The views expressed herein are those of the authors and do not necessarily reflect the views of NOAA or any of its subagencies. The U.S. government is authorized to reproduce and distribute for governmental purposes.

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