LIMNOLOGY
and
OCEANOGRAPHY

ASLO

Limnol. Oceanogr. 63, 2018, 2618–2629

doi: 10.1002/lno.10964

Reduced barnacle larval abundance and settlement in response to large-scale oceanic disturbances: Temporal patterns, nearshore thermal stratification, and potential mechanisms

Jesús Pineda,[1]* **Nathalie Reyns**,[2] **Steven J. Lentz**[3]
[1]Department of Biology, Woods Hole Oceanographic Institution, Woods Hole, Massachusetts
[2]Environmental and Ocean Sciences Department, University of San Diego, San Diego, California
[3]Department of Physical Oceanography, Woods Hole Oceanographic Institution, Woods Hole, Massachusetts

Abstract

We assessed the effects of large-scale oceanic disturbances on the settlement rate of an abundant intertidal barnacle. Daily or weekly settlement, nearshore temperature, currents, and abundance of early-stage barnacle nauplii and *Chthamalus fissus* cyprids were measured in La Jolla, California, from the inception of the large-scale warm-water anomaly known as the "Blob" in 2014, to 1 yr following the 2015/2016 El Niño. We also measured over 2 yr of weekly settlement rates during the 1997/1998 El Niño in La Jolla and in two Mexican sites. Settlement was low during the Blob and the 2015/2016 El Niño, but increased dramatically after its end, and rates remained high through spring 2017. Barnacle nauplii and *C. fissus* cyprid abundances were also low during the Blob and El Niño. Nearshore water column thermal stratification and variability of the high-frequency cross-shore currents, a measure of internal wave activity, declined during the Blob and El Niño, but increased at the end of El Niño. Similarly, settlement rates in the Mexican sites were low during the 1997/1998 El Niño. The reduction in settlement during the Blob and El Niño may be related to two factors: a decrease in water column stratification, which can influence internal bore larval transport and the cross-shore distribution of larvae, and also to reduced early-stage larval abundance, potentially related to lower reproductive output or high nauplii mortality during the disturbances.

Large-scale oceanic disturbances can have profound and diverse effects on marine communities and ecosystems. Events such as El Niño and the warm-water anomaly known as the "Blob" (Bond et al. 2015), are more than temperature anomalies or heat waves, and can also influence atmospheric pressure patterns, upwelling circulation, and water column structure, from coastal stratification (Fiedler 1984; Bond et al. 2015; McClatchie et al. 2016), to nearshore thermocline depth (Dayton and Tegner 1984; Zimmerman and Robertson 1985). Forcing associated with large-scale disturbances such as El Niño can be local, through changes in wind patterns, and remote, through Kelvin wave propagation (Lynn and Bograd 2002). El Niño and the Blob have scales on the order of 1000's of km and 1 yr, and their effects on oceanic, coastal, and nearshore habitats vary with latitude, proximity from the shoreline, and the phenology of the forced ecological variables. For example, El Niño effects on nearshore benthic communities are profound off Peru (Arntz et al. 2006), but not clearly discernable in intertidal Washington populations (Paine 1986). And whereas effects on the oceanic ecosystem can be consistent among El Niño events, including a reduction in zooplankton biomass in the Southern California Bight (Lavaniegos and Ohman 2003), consequences of El Niño on nearshore chlorophyll *a* can be variable (Kim et al. 2009). The seasonal timing of El Niño in the temperate northern Eastern Pacific can be variable (e.g., McClatchie et al. 2016), but typically begins in late spring and summer of year 1, with maximum water properties and sea level anomalies following in fall and winter, fading in early spring of year 2. Consequently, the ecological response depends on the phenology of the organism or biological variable of interest and the precise timing of the event in question.

In the coastal and nearshore temperate Eastern Pacific, El Niño has been associated with significant environmental changes, including increases in temperature, sea level, frequency of large surface waves, changes in water column stratification and circulation, including significant poleward flow (Lynn and Bograd 2002), and diminished coastal upwelling and deepening of the thermocline (Fiedler 1984; Filonov and Tereshschenko 2000; Barnard et al. 2017). Impacts of El Niño on nearshore populations and communities through storm damage and reduction in nutrient supply associated with

---

*Correspondence: jpineda@whoi.edu

deepening of the thermocline can be immediate and profound (Dayton and Tegner 1984; Zimmerman and Robertson 1985). Other large-scale oceanic disturbances, such as the Blob, might have similar ecological consequences as El Niño. The Blob evolved from temperate Eastern Pacific oceanic surface waters failing to lose heat during winter 2013/2014 (Bond et al. 2015), and its spatial extent and magnitude of the temperature anomalies were unprecedented. Large patches of anomalous warm water appeared in the Eastern Pacific, from Alaska to Baja California. Effects of the Blob in the southern California Bight (~ 11 km from shore and deeper) included surface layer warming, subsurface freshening at 100 m depth, increase in water column stratification, decreased upwelling, and an overall decrease in chlorophyll *a* (Leising et al. 2015; McClatchie et al. 2016; Zaba and Rudnick 2016). Such El Niño and Blob-related changes in the hydrographic and hydrodynamic conditions may also influence nearshore larval distribution and larval transport by suppressing coastal upwelling, hypothesized to cause offshore larval drift (Brodeur et al. 1985). Ebert et al. (1994) and Connolly and Roughgarden (1999) suggested that increased settlement and recruitment of nearshore invertebrates in northern California during the 1982/1983 and 1997/1998 Niños were associated with upwelling disruption. In contrast, in some southern California locations, sea urchin settlement decreased (Tegner and Dayton 1987; Ebert et al. 1994). Recruitment of an abundant intertidal sculpin also declined during El Niño conditions (Davis and Levin 2002), whereas the abundance of the rare reef finspot increased (Davis 2000). A multiyear comparison of larval spotted sand bass settlement to estuarine habitat in southern California also observed lowest settlement during Blob conditions in 2014 (Basilio et al. 2017). These contrasting results indicate that settlement and recruitment response to large-scale oceanic disturbances can vary alongshore at regional (kilometer) scales, and be species-dependent (see also Navarrete et al. 2002), possibly related to differences in coastal upwelling (Ebert et al. 1994) or water column stratification (Pineda and López 2002). Geographic range extensions during El Niño (Cowen 1985; Newman and McConnaughey 1987), and during the Blob (Goddard et al. 2016), may result from changes in circulation, larval dispersal, larval transport, and settlement.

The effects of El Niño and the Blob on larval transport might be mediated by changes in water column stratification. As internal motions are more energetic when the water column is more stratified, and internal tidal bores are associated with larval transport (Pineda 1999), changes in stratification may result in changes in larval transport and settlement (Pineda and López 2002). El Niño- and Blob-related deepening of the thermocline may result in decreased nearshore water column stratification and diminished internal waves and tides, as suggested by Zimmerman and Robertson (1985). Further, larvae use vertically sheared flows to control their horizontal distribution (reviewed in Pineda and Reyns 2018), and these flows tend to occur more frequently in stratified waters. Thus, a decrease in water column stratification can result in a larval center of distribution farther away from the nearshore adult habitat (Hagerty et al. 2018) and potentially less settlement.

Coastal southern California was impacted by consecutive large-scale oceanic disturbances, with the appearance of the Blob in 2014 (Zaba and Rudnick 2016), that was followed by El Niño conditions from April 2015 to May 2016 (McClatchie et al. 2016, based on Oceanic Niño Index [ONI]). Like the strong 1997/1998 El Niño (Lynn and Bograd 2002), the highest sea level anomalies occurred in fall–winter 2015/2016, diminishing by spring 2016. As opposed to the 1997/1998 El Niño, which was associated with anomalous poleward flow (Lynn and Bograd 2002; Pérez-Brunius et al. 2006), at present there is no clear physical evidence for such flow in the 2015/2016 event, although the massive appearance of the Baja Californian red crab *Pleuroncodes planipes* along Californian beaches in 2015 suggests a cautious interpretation of an absence of poleward flow (McClatchie et al. 2016). Further, temperature anomalies in the 1997/1998 events were strongest in the coastal ocean, but during the 2015/2016 events, cross-shore gradients in sea surface temperature were weaker, likely because of the precedence of the Blob in the 2015/2016 event (Jacox et al. 2016).

Resolving the effects of interannual disturbances is difficult, as measurements should be sustained for years. How large-scale oceanic disturbances affect larval transport, dispersal and settlement in the nearshore, and the mechanisms explaining latitudinal variability are open questions. Because these phenomena operate over large spatial scales, responses may vary with latitude, and are time-dependent. Observing patterns and resolving how these processes influence settlement can help elucidate the basic mechanisms governing larval transport and settlement. In this study, we measured settlement of the most abundant barnacle in southern California shores, *Chthamalus fissus*, from the onset of the Blob in 2014 through mid-2017, after the end of the 2014/2015 El Niño, in La Jolla, California, U.S.A. Barnacle settlement was also compared to data collected during the 1997/1998 El Niño in La Jolla, California and in two locations in Northern Baja California, Mexico. We tested the hypothesis that *C. fissus* settlement would be reduced during El Niño. We also measured nearshore larval barnacle abundance, moored temperature and currents, and obtained Conductivity Temperature Depth (CTD) profiles in 2014–2016. We hypothesize that a reduction in stratification associated with El Niño would result in reduction of larval transport by internal tides. Hagerty et al. (2018) found that the center of distribution of barnacle cyprids was more distant from the intertidal adult habitat when the water column was less thermally stratified, possibly because decreased stratification would result in reduced ability for the larvae to control their horizontal distribution. Therefore, in addition to decreased larval transport by internal motions, reduced water column stratification by El Niño may also influence larval supply and settlement. We would also expect larval transport and settlement to decrease during the Blob, if nearshore thermal stratification decreased during this event. We addressed the questions: Are settlement and thermal stratification different during and after El Niño and during the Blob? Is there a reduction in internal waves associated with El Niño and the Blob?

Materials and methods

Settlement was measured in the intertidal of Bird Rock, La Jolla, from 2014 to 2017. The rocky shore consists of large sedimentary ledges interspaced with rocks and boulders (~ 50–200 cm). The gentle intertidal slope provides abundant *C. fissus* habitat, which extends alongshore ~ 575 m, ending to the south with a long sandy beach and to the north in a cobble beach that continues in a series of rocky shores and pocket beaches. The study site was selected because of its large *C. fissus* population and for its simple slope bathymetry (Fig. 1). In 1997–1999, settlement measurements were taken at Dike Rock, La Jolla (7 km N of Bird Rock), and near Medio Camino and La Salina, Baja California, Mexico (78 km S and 92 km S; descriptions in Pineda 1994; Pineda and López 2002).

Settlement was measured on halved polyvinyl chloride pipes, 2.5 cm inner diameter by 11 cm long, cut through the pipe's longitudinal axis. Three sharp grooves were machined on the interior surface of the plates (Pineda and López 2002), and a hole in the middle secured the plate to the rock substrate, with a bolt embedded in the rock with marine epoxy resin. Fourteen plates separated ~ 5–50 m were installed near the middle of *C. fissus* intertidal vertical distribution in Bird Rock, and six in Dike Rock, Medio Camino, and La Salina. *C. fissus* is very small (~ 300 μm) at settlement, and cannot be counted accurately in the field even on plates with a white background. Thus, plates were collected and replaced with fresh plates, taken to the laboratory, and cyprids and metamorphs were counted using a dissecting microscope. Only barnacle larvae that settled along the corner of the base and wall of the grooves were counted. Settlement of other barnacle species, *Pollicipes polymerus* and *Balanus glandula* was very rare (< 0.05% in Bird Rock) and are not reported here.

Daily and weekly sampling interval measurements

Settlement was measured daily near Bird Rock, and weekly near La Salina, Medio Camino, and Dike Rock, and during times when moorings were not deployed near Bird Rock. On a handful of occasions, plates could not be collected because of adverse conditions, and settlement was not measured in July–August 1997. All settlement rates are reported as number cm^{-2} d^{-1} by dividing counts of unmetamorphosed cyprid larvae and metamorphs by area of plate inspected and sampling interval in days.

From 06 April to 21 November 2016, both daily and weekly settlement measurements were taken at Bird Rock, to relate settlement rates derived from daily and weekly sampling. A weekly mean of the daily measurements was derived by first calculating the mean of 14 plates (e.g., spatial averaging), and then obtaining a 7-d mean (temporal averaging):

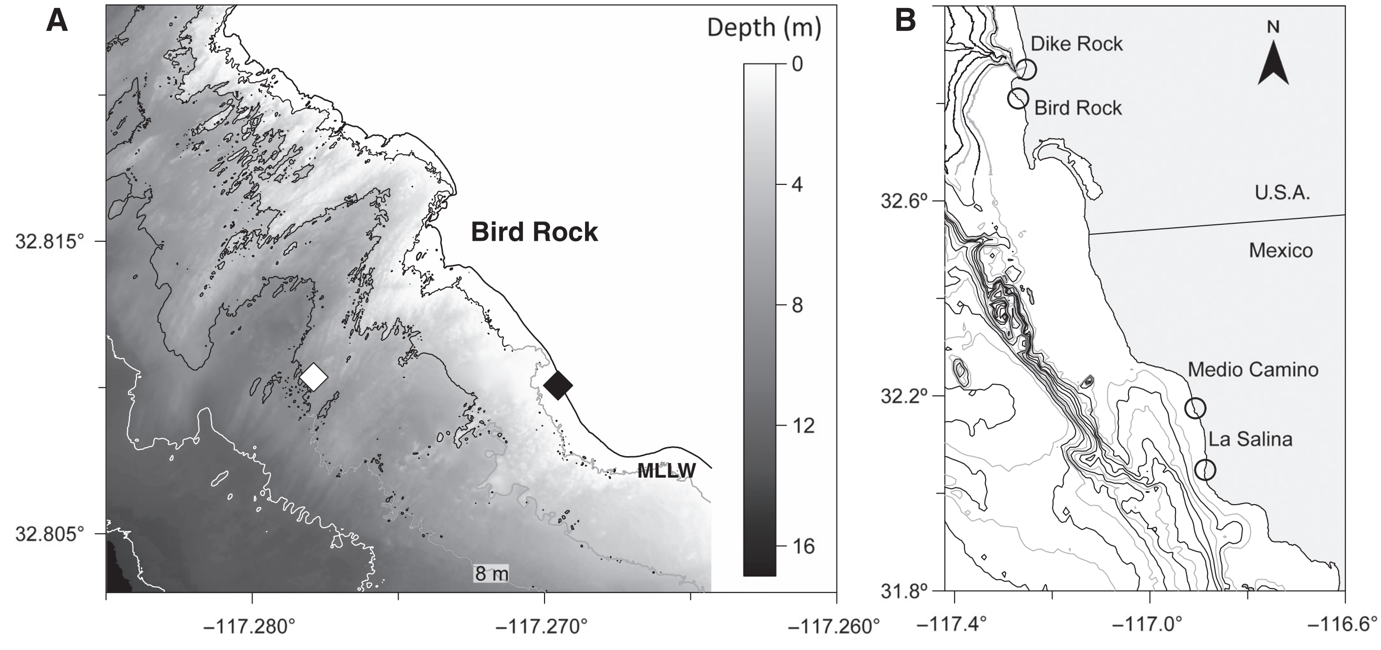

Fig. 1. (**A**) Bird Rock, La Jolla, California field site, with approximate temperature mooring and Doppler current meter positions (white square), and location of plates (black square). Distance between symbols is ~ 791 m. Depth contours relative to MLLW (Mean Lower Low Water), at MLLW, 4 m, 8 m, 12 m, and 16 m. Lidar data from the 2013 NOAA Coastal California TopoBathy Merge Project, https://data.noaa.gov/dataset/2013-noaa-coastal-california-topobathy-merge-project. (**B**) All barnacle settlement field sites (open circles), ranging from Dike Rock, U.S.A. to La Salina, Mexico (~ 97.4 km distance). Contours every 100 m. Bathymetric data from GEBCO (General Bathymetric Charts of the Oceans), and from NOAA (Carignan et al. 2012).

$$\frac{1}{n}\sum_{i=1}^{n}\left(\frac{1}{m}\sum_{j=1}^{m}x_j\right)_i$$

where x is number of settlers, i is days 1–7, $n = 7$; j is plate number 1–14 and $m = 14$. For weekly sampling, mean values were obtained as:

$$\frac{1}{m}\sum_{j=1}^{m}x_i$$

where $m = 6$. Henceforth, we call these data "daily" and "weekly" settlement. Thus, daily and weekly settlement rates should be comparable, assuming no processes other than accumulation with time influence number of settlers. Several studies have found, however, that settlement measured daily and at longer time intervals yield different per-day settlement rates, because of behavioral and postsettlement mortality processes (discussed in Pineda 2000). Consequently, a relationship between daily and weekly settlement rates was derived using regression analyses. Although weekly measurements should be referred to as "recruitment" (Connell 1985), here we use "weekly settlement" for simplicity, and because we derive a relationship between the weekly and the daily measurements.

Larval abundance

We sampled plankton in the nearshore of Bird Rock from early October to late December 2014 (six cruises, $n = 108$ samples; Blob conditions), and late May to early October 2015 (six cruises, $n = 94$ samples) and 2016 (seven cruises, $n = 139$) (El Niño and post El Niño). Samples were taken in water depths of 4 m, 6 m, 8 m, 10 m, and 12 m, ~ 280 m, 460 m, 640 m, 820 m, and 1000 m from the shore. We used a semivortex, submergible pump (Ebara 50DXU6) to filter 2 m^3 through 118 μm Nitex mesh, and plankton were preserved in 100% ethanol. At each station, we sampled 2 m vertical depth bins by slowly oscillating the pump within the sample depth interval, and thus the entire water column was sequentially sampled. Nauplii and cyprid mean concentrations for each cruise were calculated by averaging concentrations of all samples in a cruise. On a few dates, rough seas prevented sampling all stations. Samples were sorted for *C. fissus* and nauplii barnacle larvae, and identified morphologically in the lab. Over 98% of the nauplii were early-stages II and III, and could not be identified to species due to shape degradation. In culture, *C. fissus* stage IV nauplii appear at 7 d (Miller et al. 1989) and thus the majority of the II–III larvae were likely < 7 d old.

Physical measurements

Daily La Jolla sea level data collected by National Oceanic and Atmospheric Administration (NOAA) was obtained from the Sea Level Center in Hawaii (Caldwell et al. 2015), 7-d low-pass filtered, and 5-d block averaged (Lynn and Bograd 2002). Sea level anomalies for the 1997/1998 and 2015/2016 El Niño events were calculated by subtracting the average seasonal cycles for the periods 1983–1999 and 2000–2016 from the time series. Profiles of temperature, conductivity, and pressure were taken at the five stations where plankton were sampled using a Sontek CastAway-CTD. Casts were taken from early October through the end of November in 2014 ($n = 5$ dates) and 2015 ($n = 4$ dates), and mid-April to early October in 2015 ($n = 9$ dates) and 2016 ($n = 9$ dates), and the majority of stations were sampled on each date. Thermal stratification from CTD profiles was calculated as surface minus bottom temperature divided by depth (°C per meter). Temperature and currents were also sampled from October 2014 to January 2015, April to August and September to December 2015, and April to October 2016, at a subsurface mooring deployed ~ 700 m offshore in ~ 9 m water depth (Fig. 1). Temperature was measured every 5 s with 5 SBE56 loggers (Sea-Bird Scientific) spaced ~ 1.2 m, from 1.2 m to ~ 6.8 m above bottom, plus one SBE 39 sampling every 60 s at ~ 5.3 m above bottom. Time series of thermal stratification of hourly data (°C per meter) were calculated from these data by subtracting bottom from surface temperature and dividing by logger separation. Monthly means were derived from 1-d averages of the hourly data.

Currents were measured with an upward-looking acoustic Doppler current meter (1200 kHz ADCP Workhorse Sentinel, Teledyne RDI), deployed on a tripod near the subsurface temperature mooring, and sampling every 2 s (in 2014–2015) or 5 s (in 2016) in 0.4 m layers (bins) from 1.5 m above the bottom to 1.6 m below the surface. The ADCP nominal standard deviation of these currents measurements is 0.089 m s^{-1}. We used longer sampling intervals, and these yield lower standard deviations (e.g., 0.002 for 2014–2015 m s^{-1}, and 0.003 for 2016 m s^{-1} for hourly data). However, there are other sources of noise associated with the acoustics, including the compass, the properties of particles in the water, and surface wave aliasing. Some of these are bias errors, and they do not average out.

Currents were rotated in the predominant cross-shore and alongshore directions. To evaluate current variability associated with high-frequency internal motions, high-frequency cross-shore currents were obtained by subtracting 33-h low-pass currents from the hourly time series. These currents include both baroclinic and barotropic currents, and some of the barotropic variance may be associated with internal wave shoaling in this shallow water column. We then calculated the daily standard deviation of the cross-shore currents for each layer, obtained monthly means, and averaged all layers. The standard deviation of the high-frequency currents is assumed to be a measure of currents associated with high-frequency internal waves.

Results

Weekly averages of daily *C. fissus* settlement rates were higher than weekly settlement rates, and their relationship differed for values higher and lower than ~ 30 cm^{-2} d^{-1}

(Fig. 2). Thus, we fit two linear regressions to the data, and used the equations to estimate daily or weekly settlement rates in the 2014–2017 data. (A nonlinear hyperbolic regression approach yielded unrealistic high values, and thus was discounted.) The *x*–*y* points where the two regression lines intercepted demarcated the regression equations to use for low and high values. Settlement rates from weekly sampling were converted to settlement rates from daily sampling when both sampling frequencies were used in 2016 using the regression models indicated above, and the correlation between daily values from the regression model, and observed daily values was high ($r = 0.93$).

Sea level anomalies in La Jolla were high from mid-August through fall 2014 with peaks in mid-September and mid-October. Thus, we assume the Blob was first observed in the nearshore in late August 2014. Sea level decreased in November 2015, but increased in December, and remained high through 2015, with high, sustained positive anomalies in fall 2015 (Fig. 3).

The precise timing of the transition from the Blob to El Niño in Southern California in 2015 is undetermined (e.g., Jacox et al. 2016; Zaba and Rudnick 2016). Based on the seasonal timing of notable past events (e.g., the 1997/1998 event, Lynn and Bograd 2002), El Niño started sometime in the spring. Assuming roughly a 1-yr duration, and that El Niño 2015/2016 ended when the positive sea level anomalies switched from positive to negative, we assume the event started at the beginning of April 2015 and concluded at the end of March 2016. This is consistent with the timing and duration of the 2015/2016 El Niño based on the ONI index (McClatchie et al. 2016).

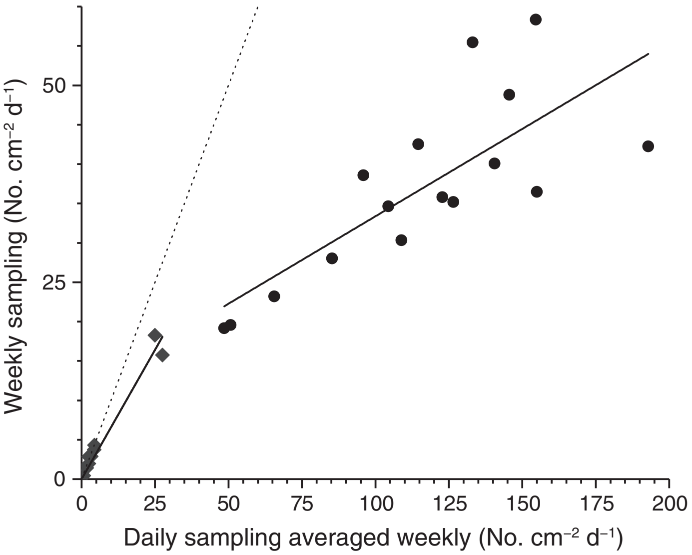

Fig. 2. *Chthamalus fissus* settlement rates from daily and weekly sampling. Dotted line is the hypothetical relationship if no other processes other than accumulation with time would influence number of settlers, i.e., if settlement rate from daily and weekly sampling were equal. Regression equations are $y = 0 + 0.657 \times x$ for weekly values ≤ 25.70 (daily samples averaged weekly), and $y = 11.17 + 0.\ 222 \times x$ for weekly values > 25.70. The 25.70 value is where the two regression lines intercept.

C. fissus settlement rates in Bird Rock were low in early 2014, and increased in late spring (Fig. 3), but in fall 2014, during the Blob in coastal Southern California, settlement rates decreased, and were the lowest in our observations. Settlement rates increased slightly in April 2015, when the Blob transitioned to El Niño, but remained relatively low through the spring, summer and fall of 2015 compared to 2016. Low settlement rates in early 2016 continued for 3 months after the end of El Niño through June 2016 (i.e., after sea level decreased to below mean conditions). Settlement increased sharply in July 2015, and remained high for the rest of the fall and winter. In spring 2017, we measured the highest settlement rates in the three and a half year sampling interval.

During the 1997/1998 event, similar to other El Niños, positive sea level anomalies were at their maximum during the fall and winter, and sea level returned to mean conditions at the end of February 1998 (Fig. 4), when we assume the El Niño ended. Based on the dates of the positive anomalies, El Niño spanned from early May 1997 to mid-February 1998. Settlement rates were higher near Dike Rock than at the Mexican sites and higher near Medio Camino than near La Salina (Fig. 4). Settlement was high at all sites prior to and at the beginning of the El Niño (May 1997). Sea level increased in May 1997, at the beginning of El Niño, but decreased from late June to late July. Settlement rates decreased at Dike Rock and La Salina and remained low at the peak of the sea level anomalies from August–September 1997 to February 1998. After the end of El Niño, settlement rates increased sharply at Dike Rock, with more modest increases after 1 month at Medio Camino and La Salina.

Median settlement rates during El Niño at La Salina, Medio Camino, and Bird Rock were lower than post El Niño (Fig. 5, Wilcoxon sign rank test on matched weekly sampling dates: La Salina, $z = 3.58$, $p < 0.001$, Medio Camino $z = 2.12$, $p < 0.05$, and Bird Rock $z = 3.90$, $p < 0.001$). However, no evidence of significant differences in settlement during and post El Niño were found for Dike Rock ($z = -0.38$, $p > 0.05$). Results for Dike Rock might have been sensitive to the periods defined for comparison (Fig. 4). In Bird Rock, October settlement during the Blob (2014) and El Niño (2015) was lower than during the post El Niño period, and differences in settlement rates were significant (Friedman test on matched sampling dates, Friedman test statistic = 12.2, df = 2, $p < 0.01$).

During the Blob, nauplii and cyprid concentrations tended to be low (Fig. 6), although results are not directly comparable with the El Niño and post El Niño results, as the periods compared are different (October–December vs. May–October). Nauplii and cyprid larvae of *C. fissus* were less abundant during El Niño in 2015 than post El Niño in 2016 (Fig. 6; *t*-test on cruise means for 2015 and 2016, $t = -5.10$, df = 7.36, $p < 0.01$ for nauplii, $t = -2.70$, df = 6.11, $p < 0.05$ for *C. fissus* cyprids).

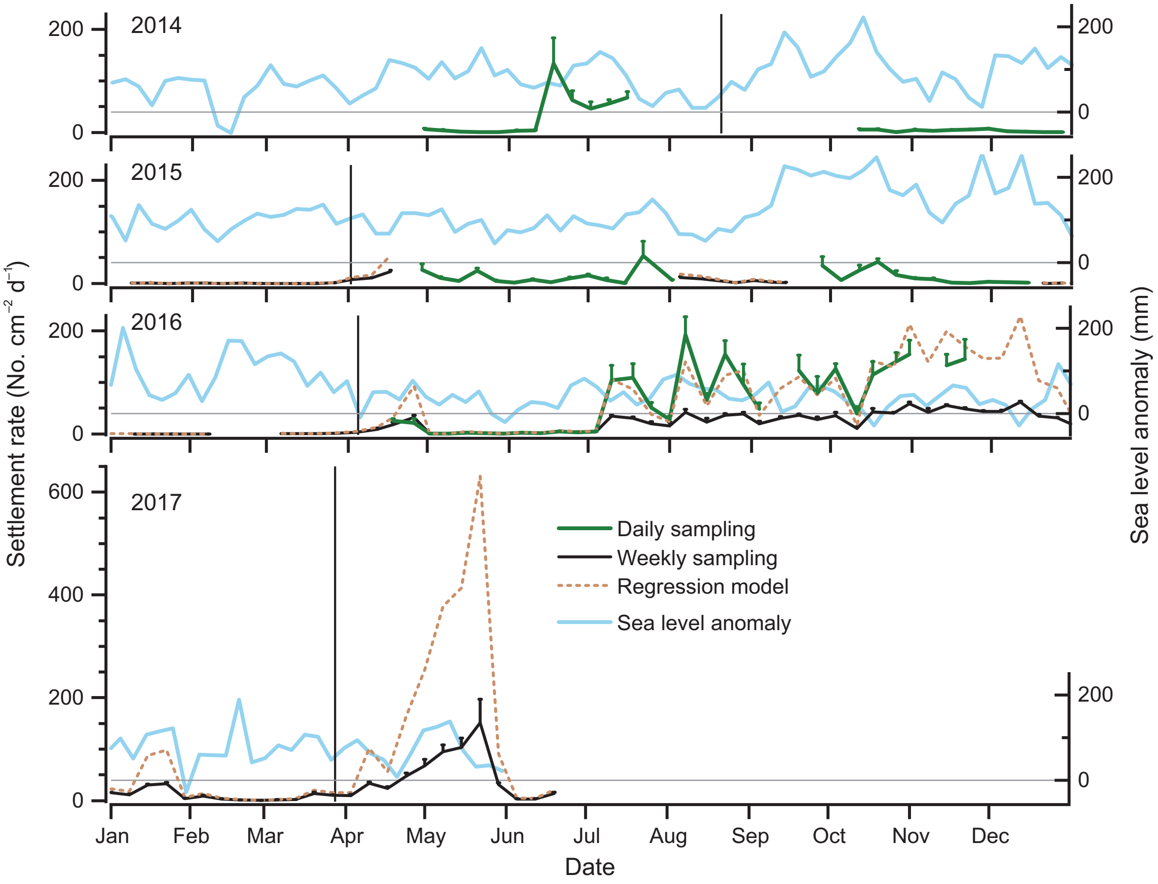

Fig. 3. Daily, weekly, and regression output of *Chthamalus fissus* settlement rate for Bird Rock, and sea level anomaly. Means and standard error. Daily settlement rates are means plus standard error. Regression predictions estimate settlement rates from daily sampling, after settlement rates derived by weekly sampling. Vertical lines on *x*-axes denote the start of the Blob (2014), the start of El Niño (2015), end of El Niño and start of the post El Niño periods (2016), and end of the post El Niño period (2017). Ticks in the *x*-axis are the first day of the month.

Thermal stratification (from CTD profiles) increased with distance offshore (increasing water depth) and was consistently weaker during El Niño than in the post El Niño period (Fig. 7A). Monthly mean thermal stratification from mooring data during spring tended to be similar for El Niño and post El Niño periods, except in May, when thermal stratification was higher post El Niño. During summer and fall, thermal stratification was weaker during the El Niño period than during the Post El Niño periods (Fig. 7B). The lowest thermal stratification from CTD profile data were observed in the fall, but were similar when comparing Blob and El Niño conditions (e.g., 0.07 ± 0.02 in 2014, and 0.09 ± 0.03 in 2015, for 10 m [mean ± SE]). Moored temperature data also indicated weaker thermal stratification during the Blob (October 2014) than during El Niño (October 2015), and post El Niño (October 2016, Fig. 7B).

The standard deviations of the high-frequency cross-shore currents were consistently lower during El Niño than post El Niño (Fig. 8). Observations for the Blob were only available for October, and these indicate lower values in 2014 than during El Niño. (No observations were available for October post El Niño.) These results indicate that high-frequency internal waves were more energetic post El Niño than during El Niño.

Discussion

Settlement rates vary at short temporal scales, and thus, to estimate larval supply, measurements must be taken tidally or daily (Cruz et al. 2005, discussed in Pineda 2000), although they are often collected at longer intervals. Daily and weekly measurements of settlement tend to produce different per-day settlement rates (Michener and Kenny 1991; Pineda 2000; Shanks 2009; South 2016). Over an 8-month sampling period, *C. fissus* settlement rates from daily sampling yielded higher values than weekly sampling. The relationship between daily and weekly settlement rates was nonlinear, with a more depressed accumulation of barnacles at higher densities, i.e., settlement rate was density-dependent. Postsettlement mortality and settler repulsion of other recent settlers might explain this result (Crisp 1961). Connell (1985) found that mortality in the first weeks after settlement was independent of recruitment for two barnacle species (i.e., density-

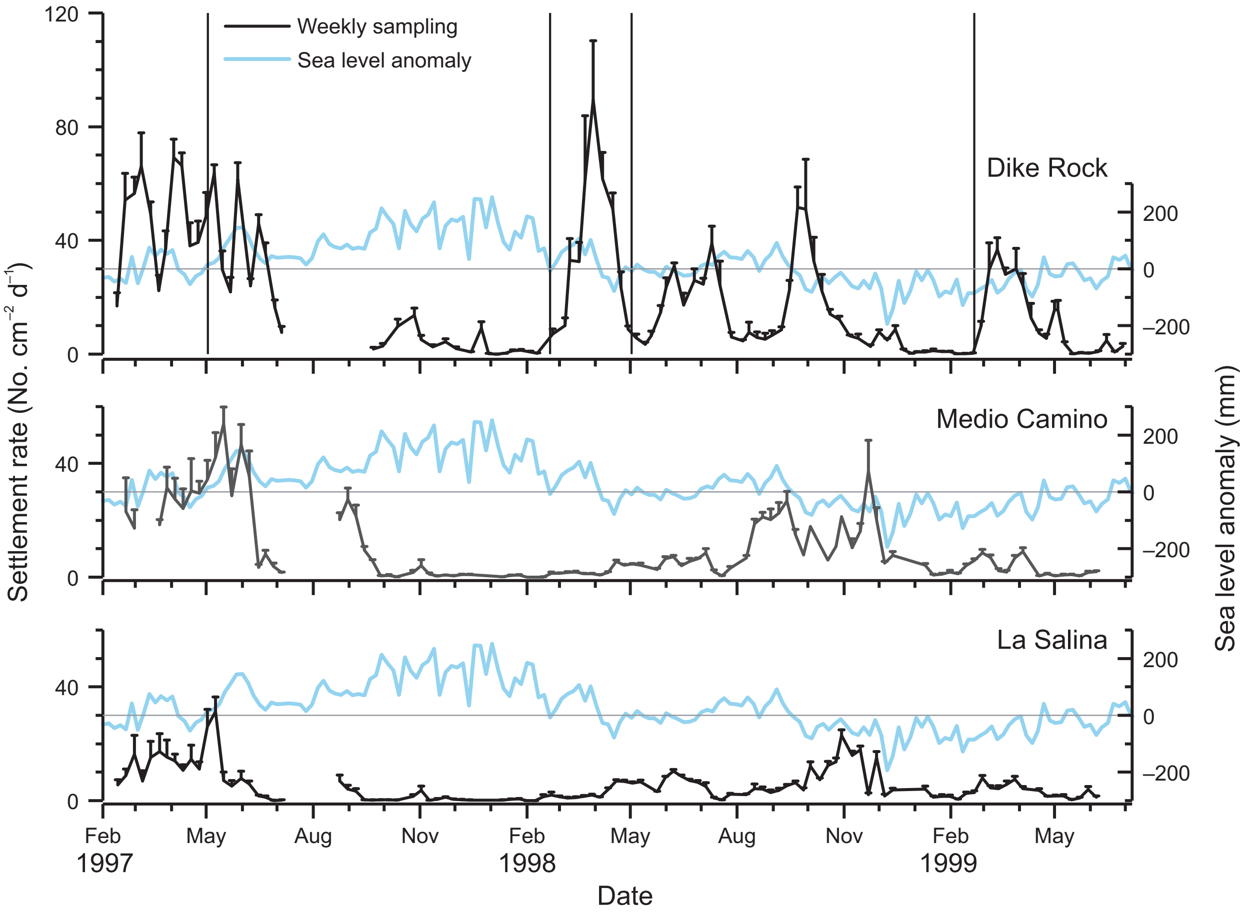

Fig. 4. Weekly, *Chthamalus fissus* settlement rate in 1997–1999 for Dike Rock (La Jolla, California), Medio Camino and La Salina (Baja California, Mexico), and sea level anomaly. Mean and standard error. Vertical lines on *x*-axes for Dike Rock denote the start of El Niño (May 1997), its end (February 1998), and, the start of the post El Niño period (May 1998), and its end (January 1999). Ticks in the *x*-axis are the first day of the month.

independent). Shanks (2009) found that *B. glandula* settlement rate varied, with "enhanced" settlement at low recruit densities, but depressed settlement at higher recruit densities. High post-settlement mortality is common in benthic organisms (Hunt and Scheibling 1997), and it might be the norm for barnacles (e.g., Gosselin and Qian 1996). Settler repulsion on substrates with high densities of recent settlers may also explain density-dependence in settlement rate. Barnacles are gregarious settlers (Knight-Jones and Stevenson 1950), and thus absolute repulsion is unlikely, although repulsion might be dependent on density and spacing of settled individuals. *C. fissus* cyprids and metamorphs saturate settlement habitat at about ~ 900 individuals per square centimeter (J. Pineda pers. obs.). Higher settlement in *C. fissus* is very rare, but possible when larvae settle on top of each other (e.g., in spring 2017, N. Reyns pers. obs.). The nonlinearity in our data is apparent at settler densities less than 200 per square centimeter (daily sampling averaged weekly, Fig. 2) and thus suitable substrate for settlement was not limiting. Undersaturation of the substrate suggests that the nonlinear accumulation of settlers may relate to settling behavior and density-dependent mortality.

The two large-scale events that influenced coastal habitats in the temperate northern Eastern Pacific from 2014 to 2016, including in southern California, were both associated with warm surface waters. The Blob was detected offshore of our study area in early 2014, as a warm-water anomaly that extended up to 100 m deep (Zaba and Rudnick 2016). Thus, a static adjustment would suggest a small elevation of sea level, and would partially explain the anomalously high sea level we observed during the fall of 2014 (Fig. 3). Furthermore, nearshore thermal stratification was lower in October 2014 during the Blob, than in 2016. The Blob transitioned to El Niño conditions in spring 2015, based on the ONI index (McClatchie et al. 2016) with peak sustained sea level anomalies in fall–winter 2015. The 1997/1998 El Niño followed a similar trajectory (Lynn and Bograd 2002), with highest sea level anomalies in fall–winter 1997/1998, although conditions before this event were not anomalous. El Niño causes warming, higher sea level, deepening of the thermocline, and thickening of the surface mixed layer in the coastal Eastern Pacific (Filonov and Tereshschenko 2000; Lynn and Bograd 2002), and the thickening of the surface mixed layer may cause a decrease in

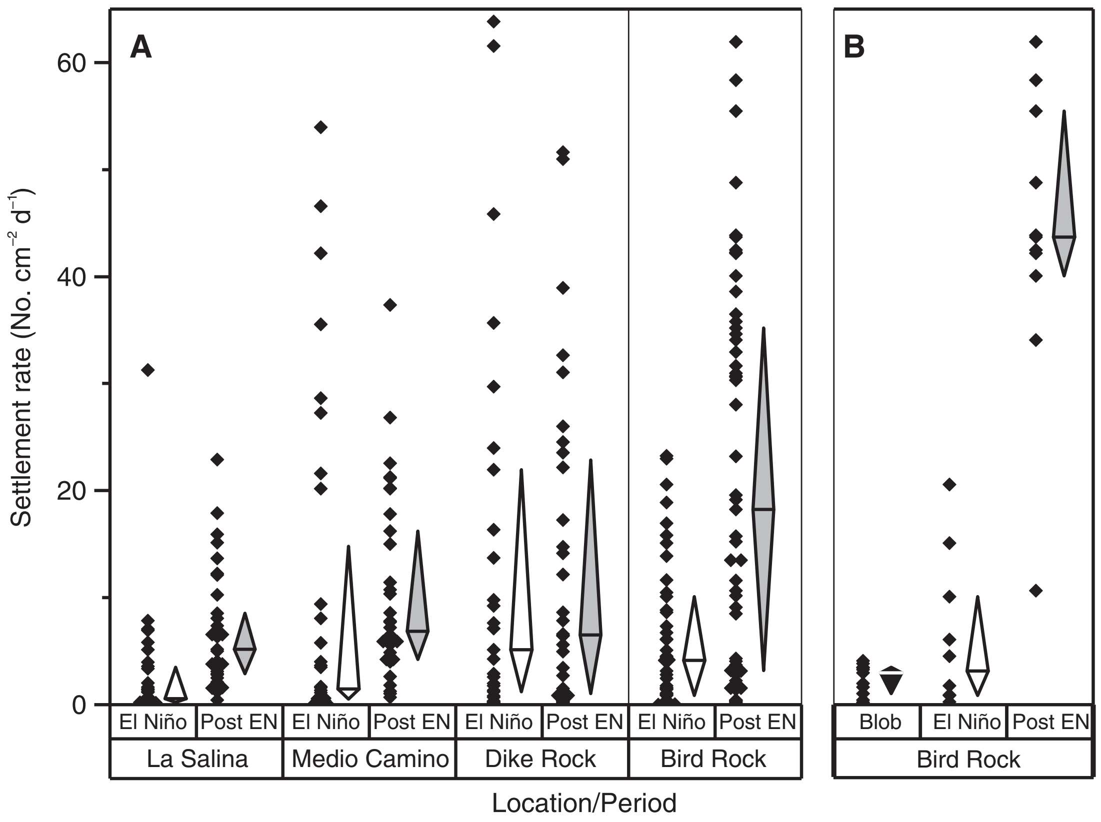

Fig. 5. (**A**) Raw settlement values (black filled symbols), and box plots with median *Chthamalus fissus* settlement rate (horizontal line) and 25% (bottom triangle) and 75% (top triangle) percentiles during El Niño and post El Niño (Post EN) periods in 1997–1998 (from south to north: La Salina, Medio Camino, and Dike Rock), and 2015–2016 (Bird Rock). Dates: El Niño: 08 May 1997–23 February 1998, and 02 April 2015–28 March 2016. Post El Niño: 10 May 1998–21 February 1999, and 04 April 2016–27 March 2017. (**B**) Blob conditions, along with comparable periods in 2015 and 2016 in Bird Rock. Blob conditions: 12 October–21 December 2014. El Niño: 12 October–21 December 2015. Post El Niño: 11 October–19 December 2016. Note: For Bird Rock, weekly settlement was estimated using linear regressions of daily data when only daily data were available. When raw settlement rates were the same during a given time period, filled symbols are presented side-by-side.

thermal stratification in the nearshore. In 2015/2016, we detected reduced thermal stratification and less energetic high-frequency flows in the nearshore, characteristic of internal waves, during the El Niño period relative to the post El Niño period. Our observations thus support previous inferences of diminished nearshore internal wave activity during El Niño (e.g., Zimmerman and Robertson 1985; Tegner and Dayton 1987). Elevated sea level, and reduced thermal stratification and high-frequency currents were also detected during the Blob, albeit comparisons were available for only 1 month.

The 1997/1998 and 2015/2016 El Niño events were associated with lower settlement to the rocky intertidal of the abundant barnacle *C. fissus*. The largest El Niño anomalies, including sea level and oceanic water properties, occur in fall/winter, and we measured the largest thermal stratification differences in Bird Rock in the fall 2015/2016. Settlement during El Niño was particularly depressed during the fall months in 1997/1998 and 2015/2016 (Figs. 3–4). In the 1997/1998 event, settlement at all sites was high during the first few months of the year, when sea level first increased (Lynn and Bograd 2002). Settlement rates at all sites decreased, however, from mid-September to November 1997, at the peak of the sea level anomaly. No statistical differences in settlement between El Niño and post El Niño periods in Dike Rock were found, however. This might relate to the high rates in settlement observed at the beginning of the 1997/1998 event or be a consequence of the March–April 1998 settlement peak that occurred after the end of El Niño, which was excluded by our calculations (Fig. 3), or may be due to a lack of response to the event in Dike Rock. Settlement rates in spring 2016 were the highest we measured in Bird Rock, and they were considerably higher than spring 2014. It is not clear whether this is related to incomplete sampling in early 2014, anomalous conditions in 2014 or 2016, or natural intraannual variability. Settlement rates tend to be higher in Dike Rock than in La Salina, and these differences have been attributed to differences in water column stratification (Pineda and López 2002). Differences might also relate to the amount of suitable area available for settlement, as settlement rate increases when suitable settlement area decreases (Pineda 1994), and suitable area appears

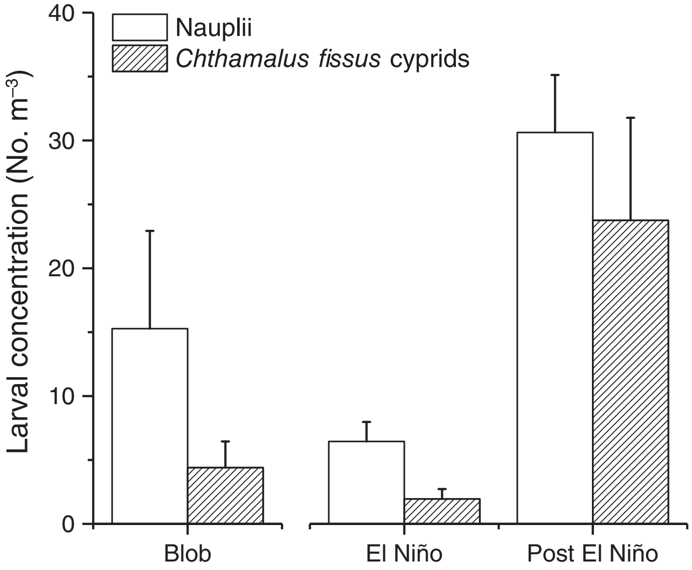

Fig. 6. Nauplii and *Chthamalus fissus* cyprid concentration in October–December 2014 (Blob conditions), May–October 2015 (El Niño), and May–October 2016 (post El Niño). Mean and standard error.

to be more abundant in La Salina than at Dike Rock (Pineda and López 2002). Similarly, suitable area for settlement appears more abundant in Bird Rock than in Dike Rock, but differences in settlement rate among the two sites are inconsistent (N. Reyns pers. obs.).

Red and purple sea urchin weekly settlement decreased during the 1991/1992 El Niño in some locations in southern California (Tegner and Dayton 1987; Ebert et al. 1994), and the abundance of a numerically dominant intertidal fish also decreased due to the lack of recruitment in the 1997/1998 event, associated with a reduction in fish fecundity (Davis and Levin 2002). In contrast, red and purple sea urchin settlement increased in northern California locations (Ebert et al. 1994). Similarly, monthly recruitment of the barnacle *B. glandula* tended to be higher in central and northern California in the 1997 El Niño, although *Chthamalus* spp. results were not consistent (Connolly and Roughgarden 1999). These authors suggest diminished wind-driven upwelling as the potential mechanism for a decrease in settlement and recruitment north of Point Conception, as the structure of the alongshore flows changes in response to change in wind patterns associated with El Niño (e.g., Fiedler 1984). However, other studies in this region found no evidence of an El Niño effect on invertebrate settlement (Lundquist et al. 2000). Further, upwelling circulation may actually transport larvae onshore, potentially resulting in an increase in settlement (Garland et al. 2002). Suppression of coastal upwelling in northern California during El Niño may cause the waters to restratify. Upwelling relaxation is associated with increased stratification and the reappearance of internal motions in the shelf (Rosenfeld 1990), and higher larval settlement and recruitment in northern California (Ebert et al. 1994; Connolly and Roughgarden 1999) might relate to increased stratification in northern California.

Thus, regional inconsistency in the response of settlement to El Niño may not necessarily indicate a lack of effect (e.g., Navarrete et al. 2002). This unpredictability may be related to alongshore differences in regional and local dynamics (e.g., coastal stratification or nearshore circulation), and even alongshore variability (few kilometers) in adult habitat characteristics. For example, a hypothetical change in the direction of the alongshore currents may cause a decrease in

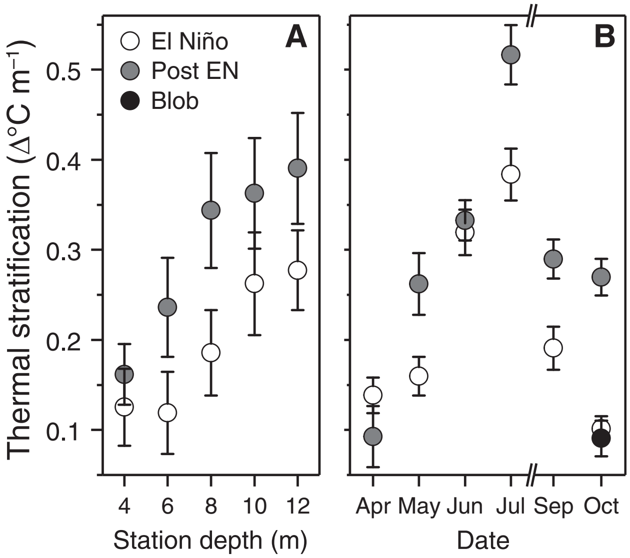

Fig. 7. (**A**) Thermal stratification at nearshore stations in Bird Rock from CTDs during El Niño and post El Niño (Post EN). Mean and ± standard error. (**B**) Monthly averages of thermal stratification from surface and bottom moored temperature loggers during El Niño (2015), post El Niño (2016), and the Blob (October 2014) periods. (Thermal stratification was 0.47 ± 0.2 for August 2016, but not available for August 2015.) Error bars are ± standard error.

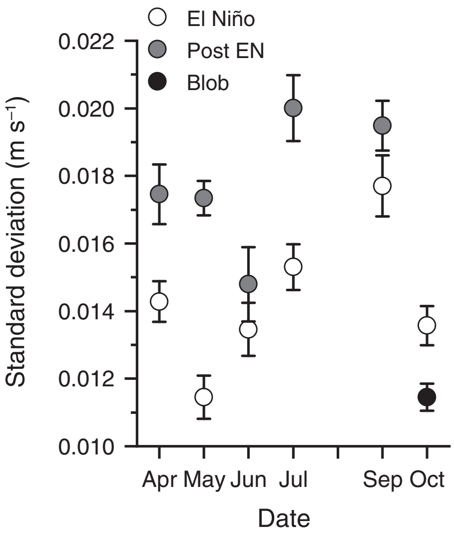

Fig. 8. Standard deviation of the high-frequency cross-shore (high-pass) currents during El Niño (2015), post El Niño (Post EN) (2016), and the Blob (comparable data only available for October 2014). Mean of daily standard deviations ± standard error.

larval supply to a given locality if the source habitat shifts from abundant barnacle rocky habitat to unsuitable habitat such as sandy beaches. Even if the currents are small, for example, 2 cm s^{-1}, a parcel of water might be transported ~ 25 km in 15 d. In studies examining impacts of circulation on larval distribution and transport of nearshore species, including the El Niño impacts on nearshore species, use of broad circulation proxies such as Ekman upwelling indices may not be justified to infer nearshore circulation. Increasing evidence suggests that larvae have cross-shore distributions constrained to the nearshore (Tapia and Pineda 2007; Morgan et al. 2009; Shanks and Shearman 2009; Hagerty et al. 2018), and thus these species will be influenced by nearshore circulation processes. Nearshore circulation is driven by a suite of processes in addition to circulation forced by alongshore winds (e.g., Lentz and Fewings 2012), that may not be represented in the often-used general upwelling indices.

Larval abundance of early nauplii and *C. fissus* cyprids, were markedly lower during the 2015/2016 El Niño than following El Niño, and abundance of these barnacle larvae were also low during the Blob, although the varying time periods that these phenomena impacted (spring vs. fall) makes direct comparisons difficult. Nauplii larvae in our samples collected in 4–12 m water depths were early-stage (II–III), and the majority were likely produced by local *C. fissus* adults (Tapia and Pineda 2007; Hagerty et al. 2018), which reproduce year round. A decrease in nauplii early stages during El Niño and the Blob suggests suppressed reproductive output in fall 2014 and 2015, that early-stage larvae were dying at higher rates, or that these larvae were rapidly advected out of the nearshore in 2014 and 2015, during the Blob and El Niño. Monthly surveys of *C. fissus* juveniles and adults in Bird Rock indicate no decline of percent live barnacle cover during El Niño, and daily larval trap data from intertidal sites also indicate less early nauplii in 2015 than in 2016 (C. Hargenrader unpubl.). This suggests that the decreased abundance in nauplii may in part relate to reduced fecundity, as in an intertidal fish (Davis and Levin 2002).

The two large-scale warm water disturbances that influenced coastal and nearshore populations in southern California, the Blob and El Niño, shared key traits. Warming and a higher sea level might affect overall productivity in the nearshore and coastal environments, including reduction of nutrient input (Zimmerman and Robertson 1985), and a reduction in phytoplankton abundance although the relationship between chlorophyll *a* and El Niño may be more complicated, with some cases of a negative correlation (1997/1998), but not for others (i.e., 1982/1983) (Kim et al. 2009). Significantly, we detected decreased nearshore thermal stratification associated with these two disturbances. Decreased stratification would reduce the energy associated with high-frequency flows that can transport larvae, and we found reduced variability in the high-frequency currents associated with internal waves during El Niño and the Blob. Further, as stratification is associated with flows that reverse with depth, and are used by larvae to control their horizontal movement (reviewed by Pineda and Reyns 2018), a decrease in stratification may limit the ability of larvae to control larval transport and cross-shore distribution. Hagerty et al. (2018) found that larval proximity to the adult habitat was related to thermal stratification, with more constrained distributions near the adult habitat in more thermally stratified waters.

Two nonmutually exclusive hypotheses may account for reduced settlement of *C. fissus* during the Blob and El Niño. First, a decrease in thermal stratification would result in reduced nearshore abundance of larvae near settlement sites (larval supply) due to a decrease in larval transport by internal motions, and a reduced ability for larvae to control their horizontal distribution. Second, a reduction in early-stage larval abundance would cause an overall decrease in larval abundance and settlement. Such a reduction could be related to increased larval mortality and a decrease in reproductive output. Our data supports the two sets of mechanisms: reduced stratification during El Niño and the Blob, and an overall decrease in nauplii abundance during El Niño and the Blob. The high larval concentrations and settlement rates shortly after the end of El Niño suggest that the potential fecundity of the barnacle populations sourcing the larvae, the reproductive population size, may not have decreased drastically during the Blob and El Niño. Instead, lower larval concentrations and settlement were likely related to processes affecting larval abundance.

In summary, our results indicate a reduction of larval abundance and settlement during the Blob and El Niño relative to post El Niño, and that large-scale oceanic disturbances can affect nearshore water column stratification, a key process that influences onshore larval transport, as well as cross-shore larval distribution (Hagerty et al. 2018). The deepening of the nearshore thermocline may also influence overall productivity, and in this way, the fecundity of adult populations and larval supply.

References

Arntz, W. E. and others 2006. El Niño and similar perturbation effects on the benthos of the Humboldt, California, and Benguela Current upwelling ecosystems. Adv. Geosci. **6**: 243–265.

Barnard, P. L. and others 2017. Extreme oceanographic forcing and coastal response due to the 2015–2016 El Niño. Nat. Commun. **8**: 14365. doi:10.1038/ncomms14365

Basilio, A., S. Searcy, and A. R. Thompson. 2017. Effects of the Blob on settlement of spotted sand bass, *Paralabrax maculatofasciatus*, to Mission Bay, San Diego, CA. PLoS One **12**: e0188449.

Bond, N. A., M. F. Cronin, H. Freeland, and N. Mantua. 2015. Causes and impacts of the 2014 warm anomaly in the NE Pacific. Geophys. Res. Lett. **42**: 2015GL063306.

Brodeur, R. D., D. M. Gadomski, W. G. Pearcy, H. P. Batchelder, and C. B. Miller. 1985. Abundance and distribution of ichthyoplankton in the upwelling zone off Oregon during anomalous El Niño conditions. Estuar. Coast. Shelf Sci. **21**: 365–378.

Caldwell, P., M. Merrfield, and P. Thompson. 2015. Sea level measured by tide gauges from global oceans—the Joint Archive for Sea Level holdings (NCEI Accession 0019568), Version 5.5, NOAA National Centers for Environmental Information, Dataset.

Carignan, K., L. Taylor, B. Eakins, D. Friday, P. Grothe, M. Love, and L. A. Taylor. 2012. Digital Elevation Models of San Diego, California: Procedures, Data Sources and Analysis, p. 32. NOAA National Geophysical Data Center Technical Report, Boulder, CO.

Connell, J. H. 1985. The consequences of variation in initial settlement vs post-settlement mortality in rocky intertidal communities. J. Exp. Mar. Biol. Ecol. **93**: 11–45.

Connolly, S. R., and J. Roughgarden. 1999. Increased recruitment of Northeast Pacific barnacles during the 1997 El Niño. Limnol. Oceanogr. **44**: 466–469.

Cowen, R. K. 1985. Large scale pattern of recruitment by the labrid, *Semicossyphus pulcher*: Causes and implications. J. Mar. Res. **43**: 719–742.

Crisp, D. 1961. Territorial behaviour in barnacle settlement. J. Exp. Biol. **38**: 429–446.

Cruz, T. and others 2005. Tidal rates of settlement of the intertidal barnacles *Chthamalus stellatus* and *Chthamalus montagui* in western Europe: The influence of the night/day cycle. J. Exp. Mar. Biol. Ecol. **318**: 51–60.

Davis, J. L. D. 2000. Changes in a tidepool fish assemblage on two scales of environmental variation: Seasonal and El Niño southern oscillation. Limnol. Oceanogr. **45**: 1368–1379.

Davis, J. L. D., and L. A. Levin. 2002. Importance of pre-recruitment life-history stages to population dynamics of the woolly sculpin *Clinocottus analis*. Mar. Ecol. Prog. Ser. **234**: 229–246.

Dayton, P. K., and M. J. Tegner. 1984. Catastrophic storms, El Niño, and patch stability in a southern California kelp community. Science **224**: 283–285.

Ebert, T. A., S. C. Schroeter, J. D. Dixon, and P. Kalvass. 1994. Settlement patterns of red and purple sea urchins (*Strongylocentrotus franciscanus* and *S. purpuratus*) in California, USA. Mar. Ecol. Prog. Ser. **111**: 41–52.

Fiedler, P. C. 1984. Satellite observations of the 1982–1983 El Niño along the US Pacific coast. Science **224**: 1251–1255.

Filonov, A., and I. Tereshschenko. 2000. El Niño 1997-98 monitoring in mixed layer at the Pacific Ocean near Mexico's West Coast. Geophys. Res. Lett. **27**: 705–707.

Garland, E. D., C. A. Zimmer, and S. J. Lentz. 2002. Larval distributions in inner-shelf waters: The roles of wind-driven cross-shelf currents and diel vertical migrations. Limnol. Oceanogr. **47**: 803–817.

Goddard, J. H., N. Treneman, W. E. Pence, D. E. Mason, P. M. Dobry, B. Green, and C. Hoover. 2016. Nudibranch range shifts associated with the 2014 warm anomaly in the Northeast Pacific. Bull. So. Calif. Acad. Sci. **115**: 15–40.

Gosselin, L. A., and P.-Y. Qian. 1996. Early post-settlement mortality of an intertidal barnacle: A critical period for survival. Mar. Ecol. Prog. Ser. **135**: 69–75.

Hagerty, M., N. Reyns, and J. Pineda. 2018. Constrained nearshore larval distributions and thermal stratification. Mar. Ecol. Prog. Ser. **595**: 105–122.

Hunt, H. L., and R. E. Scheibling. 1997. Role of early post-settlement mortality in recruitment of benthic marine invertebrates. Mar. Ecol. Prog. Ser. **155**: 269–301.

Jacox, M. G., E. L. Hazen, K. D. Zaba, D. L. Rudnick, C. A. Edwards, A. M. Moore, and S. J. Bograd. 2016. Impacts of the 2015–2016 El Niño on the California Current System: Early assessment and comparison to past events. Geophys. Res. Lett. **43**: 7072–7080.

Kim, H.-J., A. J. Miller, J. McGowan, and M. L. Carter. 2009. Coastal phytoplankton blooms in the Southern California Bight. Prog. Oceanogr. **82**: 137–147.

Knight-Jones, E., and J. Stevenson. 1950. Gregariousness during settlement in the barnacle *Elminius modestus* Darwin. J. Mar. Biol. Assoc. UK **29**: 281–297.

Lavaniegos, B. E., and M. D. Ohman. 2003. Long-term changes in pelagic tunicates of the California Current. Deep-Sea Res. **50**: 2473–2498.

Leising, A. W., and others. 2015. State of the California Current 2014–15: Impacts of the Warm-Water "Blob". Calif. Coop. Oceanic Fish. Invest. Rep. **56**: 31–68.

Lentz, S. J., and M. R. Fewings. 2012. The wind- and wave-driven inner-shelf circulation. Ann. Rev. Mar. Sci. **4**: 317–343.

Lundquist, C. J., L. W. Botsford, L. E. Morgan, J. M. Diehl, T. N. Lee, D. R. Lockwoods, and E. L. Parkson. 2000. Effects of El Niño and La Niña on local invertebrate settlement in Northern California. Calif. Coop. Oceanic Fish. Invest. Rep. **41**: 167–176.

Lynn, R., and S. Bograd. 2002. Dynamic evolution of the 1997–1999 El Niño–La Niña cycle in the southern California Current system. Prog. Oceanogr. **54**: 59–75.

McClatchie, S. and others 2016. State of the California Current 2015–16: Comparisons with the 1997–98 El Niño. CalCOFI Rep. **57**: 1–57.

Michener, W. K., and P. D. Kenny. 1991. Spatial and temporal patterns of *Crassostrea virginica* (Gmelin) recruitment: Relationship to scale and substratum. J. Exp. Mar. Biol. Ecol. **154**: 97–121.

Miller, K. M., S. M. Blower, D. Hedgecock, and J. Roughgarden. 1989. Comparison of larval and adult stages of *Chthamalus dalli* and *Chthamalus fissus*. J. Crustacean Biol. **9**: 242–256.

Morgan, S. G., J. L. Fisher, S. H. Miller, S. T. McAfee, and J. L. Largier. 2009. Nearshore larval retention in a region of strong upwelling and recruitment limitation. Ecology **90**: 3489–3502.

Navarrete, S. A., B. Broitman, E. A. Wieters, G. R. Finke, R. M. Venegas, and A. Sotomayor. 2002. Recruitment of intertidal invertebrates in the Southeast Pacific: Interannual variability and the 1997–1998 El Niño. Limnol. Oceanogr. **47**: 791–802.

Newman, W. A., and R. R. McConnaughey. 1987. A tropical eastern Pacific barnacle, *Megabalanus coccopoma* (Darwin), in Southern California, following El Niño 1982-83. Pac. Sci. **41**: 31–36.

Paine, R. T. 1986. Benthic community-water column coupling during the 1982–1983 El Niño. Are community changes at high latitudes attributable to cause or coincidence? Limnol. Oceanogr. **31**: 351–360.

Pérez-Brunius, P., M. López, and J. Pineda. 2006. Hydrographic conditions near the coast of northwestern Baja California: 1997 to 2004. Cont. Shelf Res. **26**: 885–901.

Pineda, J. 1994. Spatial and temporal patterns in barnacle settlement along a southern California rocky shore. Mar. Ecol. Prog. Ser. **107**: 125–138.

Pineda, J. 1999. Circulation and larval distribution in internal tidal bore warm fronts. Limnol. Oceanogr. **44**: 1400–1414.

Pineda, J. 2000. Linking larval settlement to larval transport: Assumptions, potentials, and pitfalls. Oceanography E. Pacif. **1**: 84–105.

Pineda, J., and M. López. 2002. Temperature, stratification and barnacle larval settlement in two Californian sites. Cont. Shelf Res. **22**: 1183–1198.

Pineda, J., and N. Reyns. 2018. Larval transport in the coastal zone: Biological and physical processes, p 141–159. *In* T. J. Carrier, A. M. Reitzel, and A. Heyland [eds.]Evolutionary ecology of marine invertebrate larvae. Oxford Univ. Press.

Rosenfeld, L. K. 1990. Baroclinic semidiurnal tidal currents over the continental shelf off northern California. J. Geophys. Res. **95**: 22153–22172.

Shanks, A. L. 2009. Barnacle settlement versus recruitment as indicators of larval delivery. I. Effects of post-settlement mortality and recruit density. Mar. Ecol. Prog. Ser. **385**: 205–216.

Shanks, A. L., and R. K. Shearman. 2009. Paradigm lost? Cross-shelf distributions of intertidal invertebrate larvae are unaffected by upwelling or downwelling. Mar. Ecol. Prog. Ser. **385**: 189–204.

South, P. M. 2016. An experimental assessment of measures of mussel settlement: Effects of temporal, procedural and spatial variations. J. Exp. Mar. Biol. Ecol. **482**: 64–74.

Tapia, F., and J. Pineda. 2007. Stage-specific distribution of barnacle larvae in nearshore waters: Potential for limited dispersal and high mortality rates. Mar. Ecol. Prog. Ser. **342**: 177–190.

Tegner, M. J., and P. K. Dayton. 1987. El Niño effects on Southern California kelp forest communities. Adv. Ecol. Res. **17**: 243–279.

Zaba, K. D., and D. L. Rudnick. 2016. The 2014–2015 warming anomaly in the Southern California Current System observed by underwater gliders. Geophys. Res. Lett. **43**: 1241–1248.

Zimmerman, R. C., and D. L. Robertson. 1985. Effects of el Niño on local hydrography and growth of the giant kelp, *Macrocystis pyrifera*, at Santa Catalina island, California. Limnol. Oceanogr. **30**: 1298–1302.

Acknowledgments

We thank Anthony Basilio, Chris Bayne, David Field, Diana Fontaine, Colin Gaylord, Malloree Hagerty, Kate Hargenrader, Jamie Irving, Héctor Lozano-Montes, Meredith Meyers, Kim Roinstead, and Patricia Rojo for field collections and sample processing. Bathymetric data in Fig. 1 from NOAA, and from the GEBCO_2014 Grid, www.gebco.net. We thank the National Science Foundation, (OCE-1357290, OCE-1357327, OCE-1630459, and OCE-1630474), the Woods Hole Oceanographic Institution, and University of San Diego for support. Over 6500 settlement plates were sampled and counted in this project.

Conflict of Interest

None declared.

Submitted 24 November 2017
Revised 13 April 2018
Accepted 04 June 2018

Associate editor: Josef Ackerman