

Synchronous settlement of barnacle larvae at small spatial scales correlates with both internal waves and onshore surface winds

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ABSTRACT: Larval settlement of *Chthamalus* spp. barnacles was measured daily at small spatial scales (~1 km) at 3 sites in Baja California, Mexico, along with water-column temperature, currents, and coastal winds. Synchronous settlement occurred at all sites throughout the 2 mo study. In general, no significant spatial pattern in settlement rate was detected, but on occasions when spatial differences occurred, the exposed and bay sites showed significantly greater settlement than the reef site. Autocorrelation artifacts in the environmental and settlement time series were removed with autoregressive integrated moving average analyses and their residuals were used in a principal component analysis to determine the independent modes of variability in environmental factors that explained the settlement patterns at each site. We found that settlement at the exposed site was only associated with the wind, which had not been detected previously. Settlement at the 2 other sites was associated with vertical isotherm displacements, suggesting the importance of internal waves at these more southern sites. Our results suggest that (1) the offshore larval pool does not vary greatly at the small spatial scales (~1 km) of this study, resulting in generally homogeneous, synchronous settlement, (2) a complex suite of factors may interact to result in settlement at the same site, and (3) settlement may be forced by different factors at sites in very close proximity due to differences in geomorphology and/or bathymetry, resulting in alongshore variability in transport mechanisms, which may explain the occasional spatial heterogeneity in settlement detected in this study.

KEY WORDS: *Chthamalus* spp. · Larval settlement · Internal waves · Onshore winds · Spatial–temporal variability

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INTRODUCTION

Many conspicuous benthic marine invertebrates release their larvae into the water column, where they drift or swim, until they undergo metamorphosis and settle to the benthos to complete their life history (Shanks & Shearman 2009). For sessile organisms, the term settlement has been used to represent the moment when planktonic larvae establish permanent contact with the substrate (Scheltema 1986). For this process to exist, many different stimuli, including substrate quality, light intensity, turbulence, and the presence and abundance of similar species, influence

the transformation to a sessile organism (Pineda 2000, Porri et al. 2008). However, in order to reach their adult habitat and settle, most meroplanktonic invertebrate larvae require physical transport mechanisms, such as currents, to assist in the journey from the offshore environment to the coast (Roughgarden et al. 1991, Pineda 1995, Tapia & Pineda 2007, Morgan et al. 2009).

A relationship between the spatial and temporal variability of physical transport mechanisms in the nearshore, such as winds and currents, and the pattern of larval settlement at the coast, has been observed for various meroplanktonic organisms (e.g.

Alexander & Roughgarden 1996, Shanks et al. 2000, Ladah et al. 2005, Morgan et al. 2009). For example, spatial variability in the settlement of crabs has been associated with the intensity and position of upwelling currents (Wing et al. 1995), as well as with the alongshore variability of upwelling with the irregularities of the coastline (Shanks et al. 2000). Although upwelling is a mesoscale process, with a spatial range of up to several hundred kilometers (Dickey 2002), it is partly dependent on winds and wind stress curl (Nelson 1977), and on topography and bathymetry (Song et al. 2001, Diehl et al. 2007), all of which vary at smaller scales along the shore, hence potentially resulting in differential plankton transport over short distances.

Diurnal winds with spatial effects on the order of 10 km can also result in small-scale changes in water-column structure and circulation, and potentially modulate larval transport and settlement (Kaplan et al. 2003, Woodson et al. 2007, Bonicelli et al. 2014). The diurnal sea breeze creates onshore surface currents with approximate velocities of 10 cm s^{-1} over an area of influence of about 3 km (Tapia et al. 2004, Woodson et al. 2007), potentially increasing retention times in bays, which has been proposed as a mechanism to deliver neustonic larvae to the coast (Woodson et al. 2007, Jacinto & Cruz 2008, Bonicelli et al. 2014). When the sea breeze peaks, larvae may be transported onshore near the surface, and offshore near the bottom, whereas at night, when winds are weak and change direction, cross-shore exchange nears zero (Hendrickson & MacMahan 2009). Because diurnal winds may have low spatial coherence at distances greater than a few kilometers along the shore due to coastline topography, friction of surface flow, or orographic steering (Pavia & Reyes 1983, Reyes et al. 1983, Bonicelli et al. 2014, Flores-Vidal et al. 2015), they can potentially also result in the differential arrival of plankton at these same scales.

Internal wave transport is another mechanism by which plankton may reach the shore. Internal tidal waves are energetic internal motions often forced by the tide, which oscillate at high frequencies (from minutes to about a day), and are modulated by the stratification of the water column (Leichter et al. 2005, Cudaback & McPhee-Shaw 2009). Internal waves are generated by the interaction of tidal (or wind) forcing with sharp bathymetric features near the coast, such as platforms or banks (Filonov et al. 2014). When internal waves propagate across the shelf and break, energy is dissipated either through mixing or through non-linear transformations, which can result in cross-shelf currents and transport of par-

ticles (Shanks & Wright 1987, Pineda 1995). Internal waves have been linked with onshore transport and settlement of barnacle larvae (i.e. Shanks & Wright 1987, Pineda 1999, Pineda & Lopez 2002, Ladah et al. 2005), and their varying flow regimes can result in heterogeneity in plankton abundance on small scales of hundreds of meters (Lennert-Cody & Franks 1999). The generation, propagation, and disintegration of internal waves depend on bathymetry and stratification (Levine et al. 1983), which can vary substantially at kilometer and smaller scales, resulting in significant differences in internal wave velocity, strength, and vertical displacement over short distances (Rayson et al. 2012, Filonov et al. 2014), therefore also potentially modulating the amount of larval transport and settlement at small scales.

Combined with the varying scales of physical mechanisms, there are suites of other factors that may explain settlement patterns. For example, zones with strong wave action are thought to have greater settlement due to increased water exchange (Shanks et al. 2010), although there is contradictory evidence for this (Todd 1998, Todd et al. 2006). These differences in settlement could be due to surf zone exchange processes that might vary with beach morphology and wave conditions, thereby affecting onshore transport of larvae (Shanks et al. 2015). Physical processes can also interact with larval behavior (LeFevre & Bourget 1992, Shanks et al. 2014) and the availability of suitable substrate (Raimondi 1988, Minchinton & Scheibling 1993, Pineda 1994) to alter settlement rates. The nearshore larval pool may also vary spatially and temporally (Gaines et al. 1985), partly due to occurrence of adult reproduction (Pineda 2000, Macho et al. 2005), behavior, and small-scale hydrodynamics (e.g. Butman 1987, Pineda 1994, Helfrich & Pineda 2003, Scotti & Pineda 2007, Fujimura et al. 2014), as well as the survival and feeding of larvae in the plankton (Rumrill 1990, Boidron-Metairon 1995, Morgan 1995). Because larvae show contrasting horizontal and vertical distribution and abundance patterns along and across the shore between early and late developmental stages (Tapia & Pineda 2007, Tapia et al. 2010, Shanks et al. 2014), this may translate into differential spatial and temporal settlement.

Meroplanktonic invertebrates have long been used as model organisms for the study of the coastal zone, and there exist many examples of small-scale variability in the settlement rates of these larvae. For example, the settlement rates of both barnacles (Ladah et al. 2005) and mussels (Porri et al. 2008) vary spatially at small scales (<300 m). Low spatial coherence in settlement may be due to small-scale

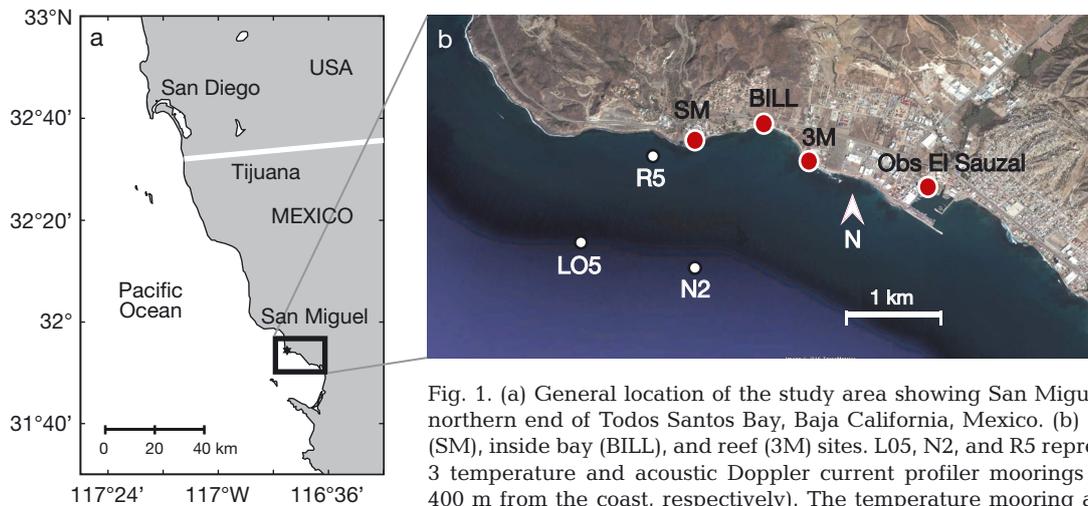


Fig. 1. (a) General location of the study area showing San Miguel (black box) at the northern end of Todos Santos Bay, Baja California, Mexico. (b) Study sites: exposed (SM), inside bay (BILL), and reef (3M) sites. L05, N2, and R5 represent the locations of 3 temperature and acoustic Doppler current profiler moorings (at 1600, 1400, and 400 m from the coast, respectively). The temperature mooring at L05 was deployed during the entire sampling period (18 July to 18 September 2009). Wind velocity and direction at 10 m above sea level were recorded at the El Sauzal Tsunami Observatory ('Obs. El Sauzal'). Image taken from Google Earth Pro (map data ©2016 DigitalGlobe)

complex flows caused by topography, bathymetry, or geomorphology of the coastline, such as bays or outcroppings (Tapia & Pineda 2007, Cowen & Sponaugle 2009). As mentioned above, larval behavior, suitable substrate availability, predation, and varying nearshore cyprid concentrations are other processes that may explain spatial heterogeneity (Gaines et al. 1985, Pineda 1994, 2000).

For *Chthamalus*, the most conspicuous barnacle genus in Baja California, Mexico, settlement occurs in the middle and upper intertidal zone. Two species have been reported along the west coast of North America and Mexico: *C. dalli* and *C. fissus*; however, they overlap in distribution and show similar external morphology, making it difficult to identify them to the species level (Miller et al. 1989, Wares & Castañeda 2005). Larvae are planktonic and are generally retained near the coast (<6 km), showing vertical segregation patterns between developmental stages, with later stages concentrated in mid-water and bottom layers of the water column (Tapia & Pineda 2007, Morgan et al. 2009, Shanks & Shearman 2009, Tapia et al. 2010).

The objective of this study was to quantify and compare the daily rate of settlement of *Chthamalus* spp. barnacle larvae during strong internal tidal forcing, at 3 sites separated by small spatial scales (<1 km), encompassing (from north to south) a wave-exposed point, a protected bay, and a semi-exposed reef, along a semidiurnal internal wave exposure gradient, where the strength of semidiurnal internal waves decreases moving south (Filonov et al. 2014). We also aimed to determine whether the settlement rate at each site correlated with the physical trans-

port mechanisms operating in the area, and focused on winds and internal wave forcing. These mechanisms are the 2 most frequently invoked transport mechanisms for barnacle larvae in this area.

We predicted that settlement would be synchronous and would correlate to strong summer internal wave activity (and not to wind) at all sites, as has been previously detected for the spring season at this study region (Ladah et al. 2005), and that spatial differences would show consistently higher settlement at the exposed site due to the quantity of water exchanged with the nearshore ocean and the stronger internal wave exposure there.

MATERIALS AND METHODS

This study was carried out in the northern part of Todos Santos Bay, Baja California (Fig. 1). This bay is characterized by a semidiurnal mixed tide, depths <50 m, and strong spatial variability in the strength of the semidiurnal internal tide. The semidiurnal signal is strongest in summer (Ladah et al. 2012), ranging from very strong at San Miguel (exposed site) and reducing drastically (to one-tenth the intensity) within a short distance moving south and into the bay (Filonov et al. 2014). Semidiurnal internal tidal waves dissipate rather quickly near the northern end of the bay, whereas in the southern part, a weaker diurnal signal, most likely forced by the sea breeze, becomes dominant (Filonov et al. 2014).

The rocky shore of the northern end of Todos Santos Bay was divided into 3 sites: an exposed point (SM), an inside bay (BILL), and a reef (3M), separated by

450 m of coastline (Fig. 1b). The coastline orientation (angle relative to true north) for each site was measured using a segment of 100 m on ©Google Earth software. The northern exposed site was at 47° from geographic true north and is a reflective beach where incident waves break on large boulders on the narrow steep beach, forming a large swash zone. The site located inside the bay protected from wave action was oriented at 77° from geographic true north, is next to a pocket beach, and has dissipative characteristics with a wide and flat slope, with finer sediment and progressive waves breaking offshore. Finally, the reef site is at 132° from geographic true north, faces southwest, and is intermediate in exposure with a relatively gradual beach slope with pronounced outcroppings, merged to an attached reef bar seaward that is often exposed (fringing reef), and from where the waves break and gently roll in, except during very high tides, when water reaches the adjacent cliffs.

Various species of barnacles have been reported along the Pacific coast of Baja California, including: *Chthamalus* spp., *Balanus glandula*, *Pollicipes polymerus*, and *Tetraclita* spp. (Allen 1969); however, studies on larval settlement and abundance of adults in the intertidal zone show that *Chthamalus* is the most abundant genus in this region (Pineda & López 2002, Ladah et al. 2005, Jarrett 2008). Some species in this genus reach sexual maturity 2 mo after settlement, producing new individuals throughout the year (Hines 1978). Six naupliar stages occur in the planktonic form, until the cyprid larval form is reached, which is then ready for settlement. The duration of the planktonic larval period is approximately 2.5 wk at 15°C (Miller et al. 1989, Tapia & Pineda 2007). Along the Baja California coast, *Chthamalus* spp. settle from April to September, with a peak in summer (Ladah et al. 2005).

Evaluation of settlement: plates and sampling design

Barnacle settlement was measured daily for 2 mo in summer. At each of the 3 sites, 12 PVC settlement plates were installed in the high intertidal barnacle zone using removable screws (as per Pineda et al. 2002). The plates were made of PVC tubes cut in half, allowing for easy replication and a standardized sampling surface, reducing the variability of settlement due to natural substrate. Prior to deployment, the plates were placed in filtered seawater for 2 wk to develop a bacterial film. Deployed plates were collected and replaced at the lowest tide each day for

enumeration of cyprids and spat settlers. Counts are expressed as daily settlement rates.

Chthamalus was the most abundant barnacle settler found during this study. Although *C. fissus* is likely the most abundant species on the Pacific Baja California coast, uncertainty remains with *Chthamalus* species identification, as larvae and juveniles of both *C. dalli* and *C. fissus* show similar morphologies (Miller et al. 1989). For this reason, in the present study we refer only to *Chthamalus* spp.

Physical parameters

Water column temperature was recorded at 5 min intervals using thermistors (Stow Away@TidBits, Onset Computer, precision of $\pm 0.2^\circ\text{C}$; response time <5 min when submerged) installed every 2.5 m vertically on a line deployed at mooring site L05 (31° 53.38' N, 116° 44.56' W; Fig. 1b), 1600 m from the coast at 28 m depth. The velocity and direction of the wind at 10 m above sea level was recorded in El Sauzal (31° 53.75' N, 116° 42.22' W, www.observatorio.cicese.mx), 1300 m to the east of the study area. Wind vectors were decomposed into east–west (u) and north–south (v) Cartesian components, and then the axes were rotated and aligned along the axis of greatest variability (Emery & Thomson 2001). The axes were rotated to determine whether the greatest variability was in the offshore–onshore direction or along the shore.

Currents were measured using a 600 kHz acoustic Doppler current profiler (ADCP, Sentinel Workhorse, Teledyne RD Instruments), set to record at 1 min intervals in 1 m bins. The ADCP was bottom deployed at 3 locations for a concurrent internal wave rebound study in shallow water: at mooring sites N2 (18 July to 15 August at 24 m depth), L05 (18 to 24 August at 28 m depth), and R5 (4 to 11 September at 13 m depth). N2 (31° 53.24' N, 116° 43.69' W) was located 1400 m from the coast, whereas R5 (31° 53.87' N, 116° 44.04' W) was 400 m from shore (Fig. 1b).

Data analysis

Days for which the settlement rate was greater than the average of the daily counts for the entire study plus 1 SD were considered settlement pulses. For the days of each pulse, the spatial patterns of settlement were determined using a Kruskal–Wallis nonparametric ANOVA on settlement counts. A

Spearman correlation was used to establish the degree of synchrony during the daily settlement series among the 3 sites. All plates were grouped by site, and the variation between plates was tested using the standard normal variable Z (Emery & Thomson 2001) (see Fig. S1 in the Supplement, available at www.int-res.com/articles/suppl/m552p195_supp.pdf). In addition, the maximum semidiurnal tidal range and the percent lunar illumination for each settlement day were used to determine whether there was a relationship between the overall settlement rate for all sites and the tide.

Because of the synchrony of reproduction, and the fact that coherent water mass movements often modulate larval supply, the time series of daily settlement was expected to be autocorrelated at numerous lags (Fig. S2). For our analysis, raw data were interpolated by nearest neighbor and splined to get continuous time series of settlement and physical data. We then fit an autoregressive integrated moving average (ARIMA) model to generate residuals uncorrelated in time. The appropriate structure and order of the model was determined by looking at the plots of the autocorrelation function (ACF) and partial ACF in our interpolated data (see Fig. S2). To penalize appropriately for excessive complexity in the ARIMA model, we used the Bayesian information criterion as a statistical measure of goodness-of-fit to select the best model with the fewest parameters. The residual model uses the ACF to determine whether any individual coefficients fall outside of some specified confidence interval around 0 and therefore may be more suitable for studying the influence of outside environmental factors on settlement. We quantified the variance of the time series due to the modeled autocorrelation or persistence (Table S1 in the Supplement). A principal component analysis (PCA) was then carried out on the residual ARIMA model time series of the interpolated data to determine the independent modes of variability in environmental parameters that may explain the settlement patterns, including the average vertical isotherm displacements, maximum semidiurnal tidal range, wind, and percent lunar illumination.

Quantification of the temporal relationship between number of settlers and the intensity of physical forcing

Fluctuations in currents, temperature, and stratification at tidal or lower frequencies can be indicative of internal waves within the water column. Indices of

these high-frequency changes during each settlement period were obtained by integrating the physical variables during each settlement plate deployment period. For temperature (T), we calculated the vertical isotherm displacements in the water column as part of the internal wave analysis (see Filonov 2011). Additionally, temperature differences between surface and bottom waters were calculated in order to take a measurement indicative of stratification. Previous studies have shown that density in this region is controlled mostly by temperature at our depths of interest and that temperature is a good indicator of stratification (Ladah et al. 2012, Filonov et al. 2014). These indices were calculated for the temperature mooring at L05.

The vertical isotherm displacement index was calculated using temperature profiles interpolated on a unitary depth grid for the entire period of observation. The few small inversions were removed by averaging 2 inversion-free profiles obtained by moving along the profile from top to bottom and vice versa with hysteresis jumps in the inversion layers. These monotonic profiles were used to calculate the mean temperature profile which describes the unperturbed position of isopycnal water layers, and due to the absence of inversions, the mean temperature profile uniquely defines the inverse dependence (profile) on depth. The vertical monotonic deviations of water layers were calculated by comparing each individual and mean temperature profile to obtain the vertical displacements of the water layers from the unperturbed position (expressed in meters) (see Filonov et al. 2014). Finally, we time-integrated the vertical displacements over the deployment time of the settlement plates and averaged over the water column. The negative vertical displacements were related to surface isotherms reaching bottom depths at semidiurnal frequencies due to internal waves.

The physical forcing parameter produced by the wind was established using the calculated wind stress for the 2 orthogonal horizontal components of the wind (u and v). The indices were calculated using the following equation:

$$\tau_{net} = \sum_{i=1}^t (\tau_{ui}, \tau_{vi}) \quad (1)$$

where τ_{net} indicates the net stress during the observation period, with components representing winds blowing towards or away from the coast (u), and towards the north or south (v); t represents the number of measurements taken during the sampling period. Cross-shore winds were associated with the major axis along which the variance was maximized.

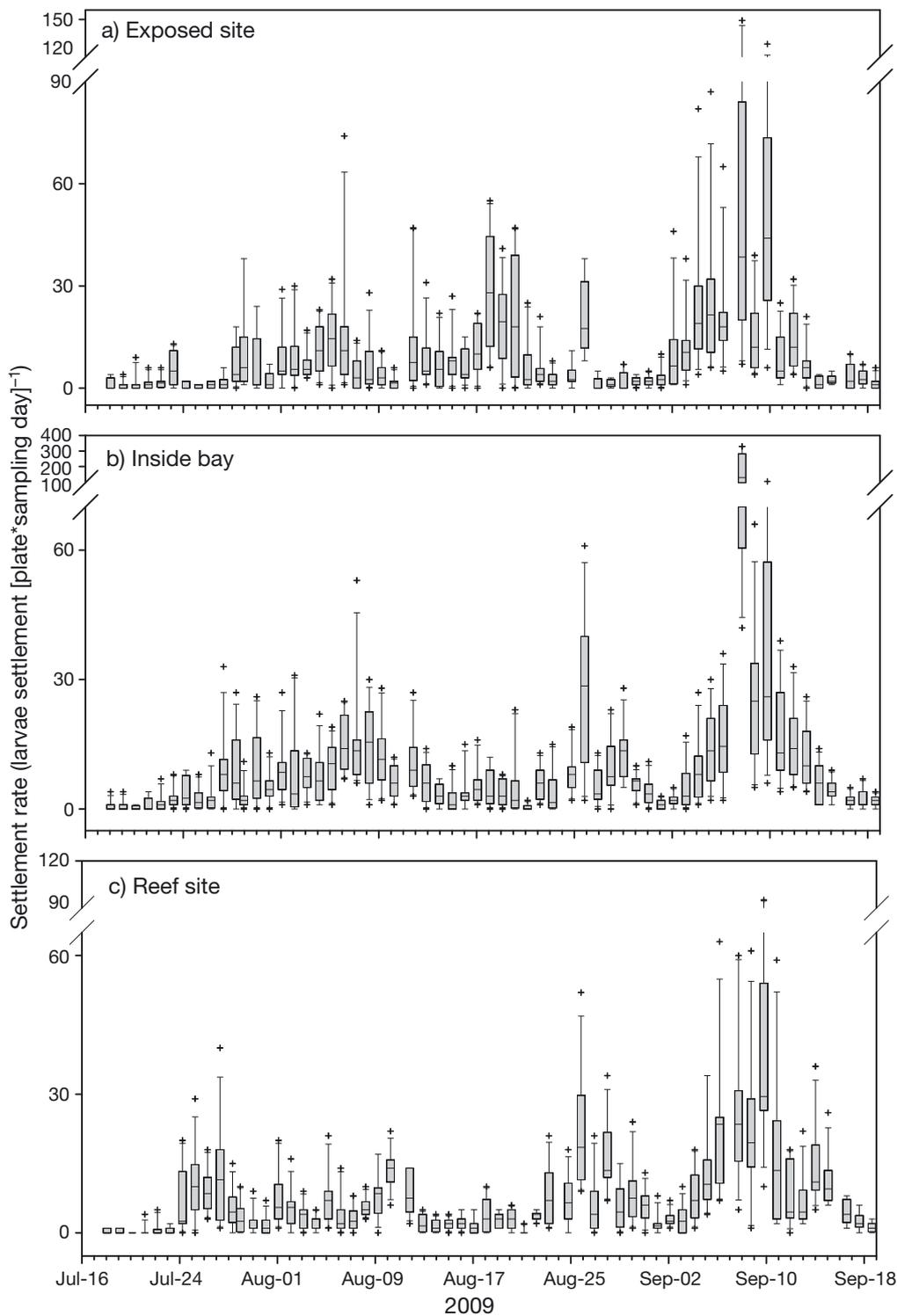


Fig. 2. Raw *Chthamalus* spp. barnacle settlement data for study sites: (a) exposed site, (b) inside bay site, and (c) reef site. The central black line marks the median, the 25th and 75th percentiles encompass the box, the whiskers extend out to the extreme data that were not considered outliers, and the outliers are plotted as plus signs

RESULTS

Settlement occurred throughout the study period with an average of 8 ± 14 individuals settled daily. On occasion, however, settlement rates were much higher and entailed settlement pulses as previously

defined (Fig. 2). During July, no settlement pulses occurred, whereas 10 different periods in August and September qualified as settlement pulses (Fig. 3, Table 1). Settlement was greatest overall on 7 and 9 September, with an average settlement rate of 51 and 41 ind. plate⁻¹ d⁻¹, respectively.

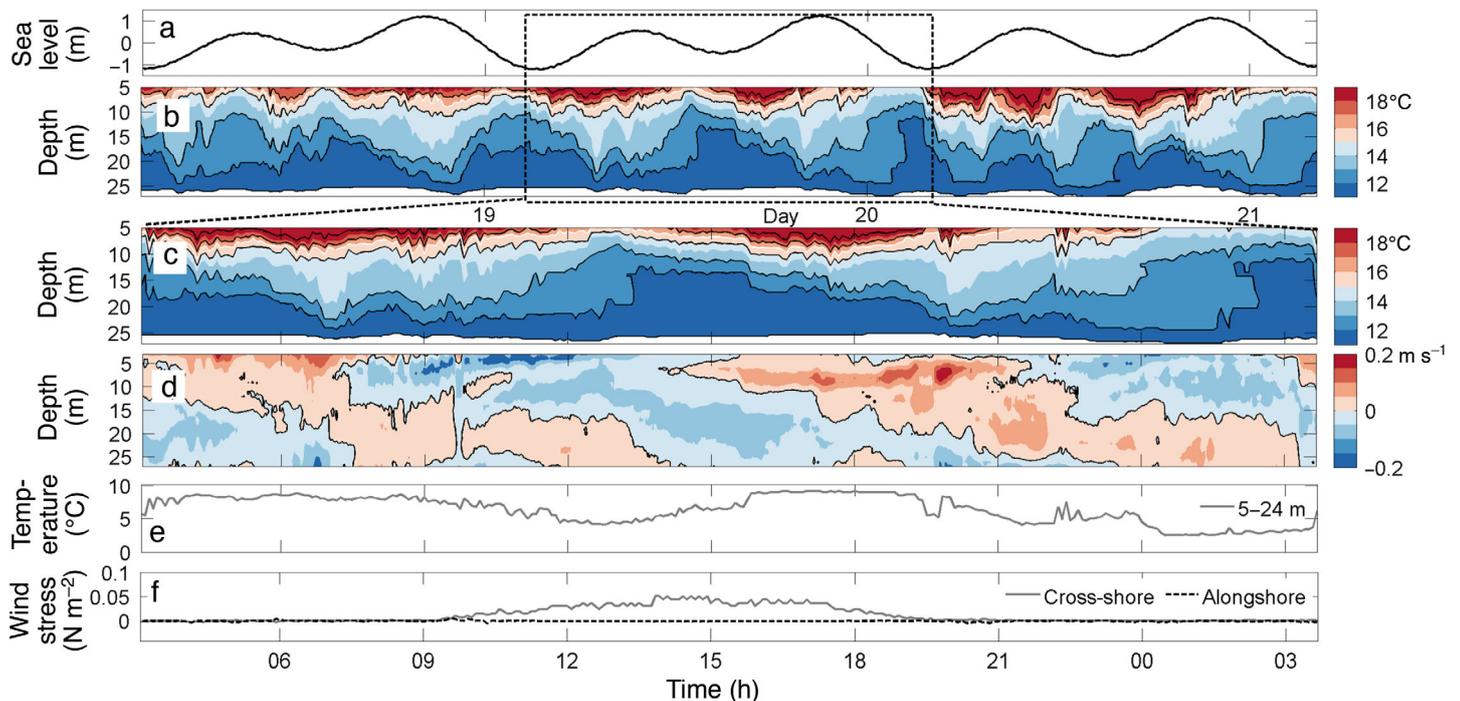


Fig. 4. (a) Sea level and (b) vertical distribution of temperature from 18 August (02:30 h) to 21 August (4:14 h) 2009. A zoomed view (black dashed box) during an individual *Chthamalus* spp. barnacle settlement event from 19 August (3:05 h) to 20 August (3:40 h) shows (c) the temperature profile, (d) the vertical distribution of currents perpendicular to the coast during this settlement pulse, and (e) the temperature difference between the 5 and 24 m depths (gray line). (f) Wind stress components for the zoomed period, in the onshore–offshore direction (gray line) and alongshore (dashed black line). The contour interval for currents (temperature) is 0.05 m s^{-1} (1°C); positive velocities indicate onshore currents. Zero current is indicated by the black contour

The temporal occurrence of settlement was significantly correlated between sites, viz. the bay and reef sites (Spearman's rank correlation [r_s] = 0.56, $p < 0.001$, $n = 165$), the exposed and bay sites ($r_s = 0.39$, $p < 0.001$, $n = 165$), and the exposed and reef sites ($r_s = 0.23$, $p = 0.003$, $n = 165$), suggesting that settlement occurred in synchrony at all 3 sites.

No significant spatial difference was found between settlement rates at the 3 sites for more than half of the settlement pulses (6 of 10 pulses; Table 1). On occasions when settlement was spatially heterogeneous, the site with greater settlement was not consistent, showing 2 general patterns. For 2 of the spatially heterogeneous pulses (on the pulse from 18–20 August and on the 4 September pulse), the exposed site located farthest to the north showed significantly greater settlement, with the 2 other sites having lower and similar settlement. The 2 other spatially heterogeneous pulses (6 August and 7 September) showed greatest settlement at the site inside the bay, lower settlement at the exposed site, and the lowest settlement at the reef site (see Table 1).

Tidal influence on settlement

Settlement pulses occurred during the transitional periods from the spring tide to the neap tide (Fig. 3), associated with the full moon and the third-quarter moon, and a tidal range of 1.1 to 1.5 m. Average daily settlement and the tidal range (1.0 to 2.6 m) were significantly correlated ($r_s = -0.37$, $p = 0.006$, $n = 55$).

Comparison between the two major settlement periods

Of the 2 settlement periods, the period between 18 and 21 August showed lower settlement than the period between 6 and 10 September, when the maximum settlement rate of $51 \text{ ind. plate}^{-1} \text{ d}^{-1}$ was detected (Fig. 2).

During the settlement period between 18 and 21 August, there were changes in the position of the thermocline and alternating intrusions of colder and warmer waters throughout the water column at semi-diurnal intervals, with temperature changes up to

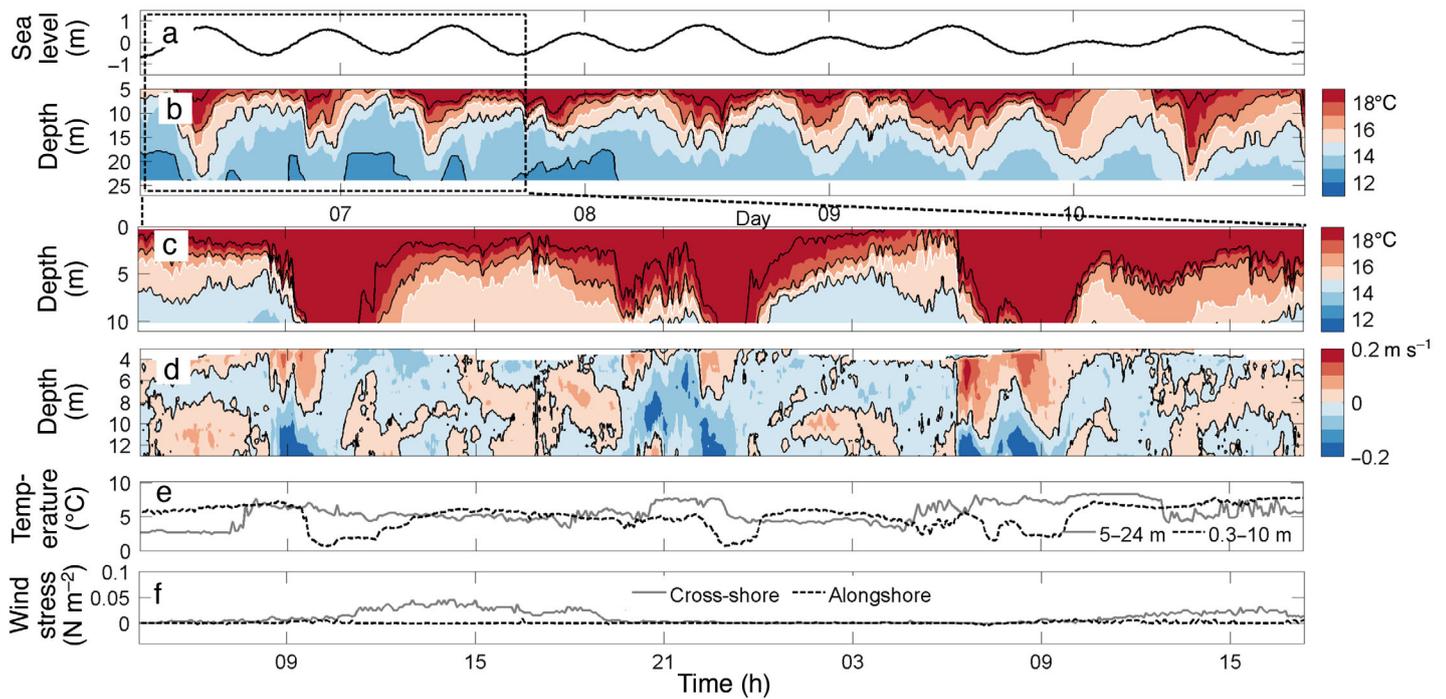


Fig. 5. (a) Sea level and (b) vertical distribution of temperature from 6 September (4:18 h) to 10 September (22:42 h) 2009. Zoomed view (black dashed box) highlights an individual *Chthamalus* spp. barnacle settlement event from 6 September (4:18 h) to 7 September (17:21 h) and shows (c) the temperature profile and (d) the vertical distribution of currents perpendicular to the coast during this settlement pulse observed inshore at R5. (e) The temperature difference between the 5 and 24 m depths (gray line) observed at L05 mooring. We include in this panel a comparison with the temperature difference between surface and 10 m depth (dash-black line) inshore at R5. (f) The wind stress components for the zoomed period, in the onshore-offshore direction (gray line) and alongshore (dash-black line). The contour interval for currents (temperature) is 0.05 m s^{-1} (1°C); positive velocities indicate onshore currents. Zero current is indicated by the black contour

5°C in short periods of time (Fig. 4). Over several minutes, strong asymmetric temperature changes ($>3^\circ\text{C}$) were also observed throughout the water column, with sharp troughs and smooth crests in the isotherms. The temperature at 5 m depth repeatedly cooled and then abruptly warmed as internal tidal bores arrived (i.e. 19 August from 19:45 to 20:00 h and from 22:00 to 23:00 h) associated with near-surface, shoreward-flowing currents reaching 0.2 m s^{-1} (Fig. 4c–e). The temperature difference between 5 and 24 m ($\Delta T \sim 5^\circ\text{C}$) reduced during the arrival of the cold phase of the internal tide, homogenizing the water column and decreasing stratification, due to the movement of cold water towards the surface, followed by a restratification during warm bore arrival (Fig. 4b–d). The wind component perpendicular to the coast (onshore winds) was dominant during this period (Fig. 4f). Positive values in cross-shore winds (i.e. onshore) were observed, indicating the presence of a diurnal sea breeze (between 9:00 and 19:00 h) with intensification at 14:00 h.

A similar pattern of a diurnal sea breeze and alternating intrusions of cold and warmer waters was also

observed during the large settlement peak from 6 to 10 September (Fig. 5). However, during this period, the water column was warmer, with surface isotherms penetrating deeper into the water column (Fig. 5b). The temperature difference between 5 and 24 m depth, averaged for this settlement period, was almost 1°C stronger than that for the previous period ($5.5 \pm 1.6^\circ\text{C}$ vs. $6.4 \pm 2.1^\circ\text{C}$), with a more stratified water column. For several hours during this settlement period, surface temperatures cooled abruptly, nearing values found at 24 m depth, homogenizing and cooling the entire water column, followed by restratification numerous times ($\Delta T > 2.5^\circ\text{C}$; Fig. 5e). The comparison of cross-shore temperatures observed at L05 (offshore) and R5 (located $\sim 1200 \text{ m}$ inshore; Fig. 5b,c), and the differences between surface and bottom temperatures offshore and inshore (Fig. 5e), show progressive internal wave arrival and disintegration events near the coast, where the warm phase of the bore overtakes the entire water column at 10 m depth with strong shoreward currents in the upper half of the water column occurring at semi-diurnal intervals (Fig. 5d). This period coincided with

8 d of very high settlement (>2 SD), which may be due to the strong advection of larvae towards the coast when currents reached 0.2 m s^{-1} shortly before and during bore arrival.

Quantification of the temporal relationship between the abundance of settled larvae and the intensity of physical forcing

In the settlement time series, about a quarter of the variance was due to persistence or autocorrelation

($>24\%$ variance explained, Fig. 6), whereas in the physical time series, autocorrelation increased ($>40\%$ variance explained; see Table S1). This is not surprising, as large physical changes are restricted in nature due to thermodynamics, requiring a lot of energy to change initial conditions, particularly in water temperature. Because physical conditions modulate settlement, a settlement time series can also be autocorrelated due to its dependence on the physical mechanisms that result in settlement, as well as because of the simultaneous timing of reproduction and the duration of the retained larval pool nearshore.

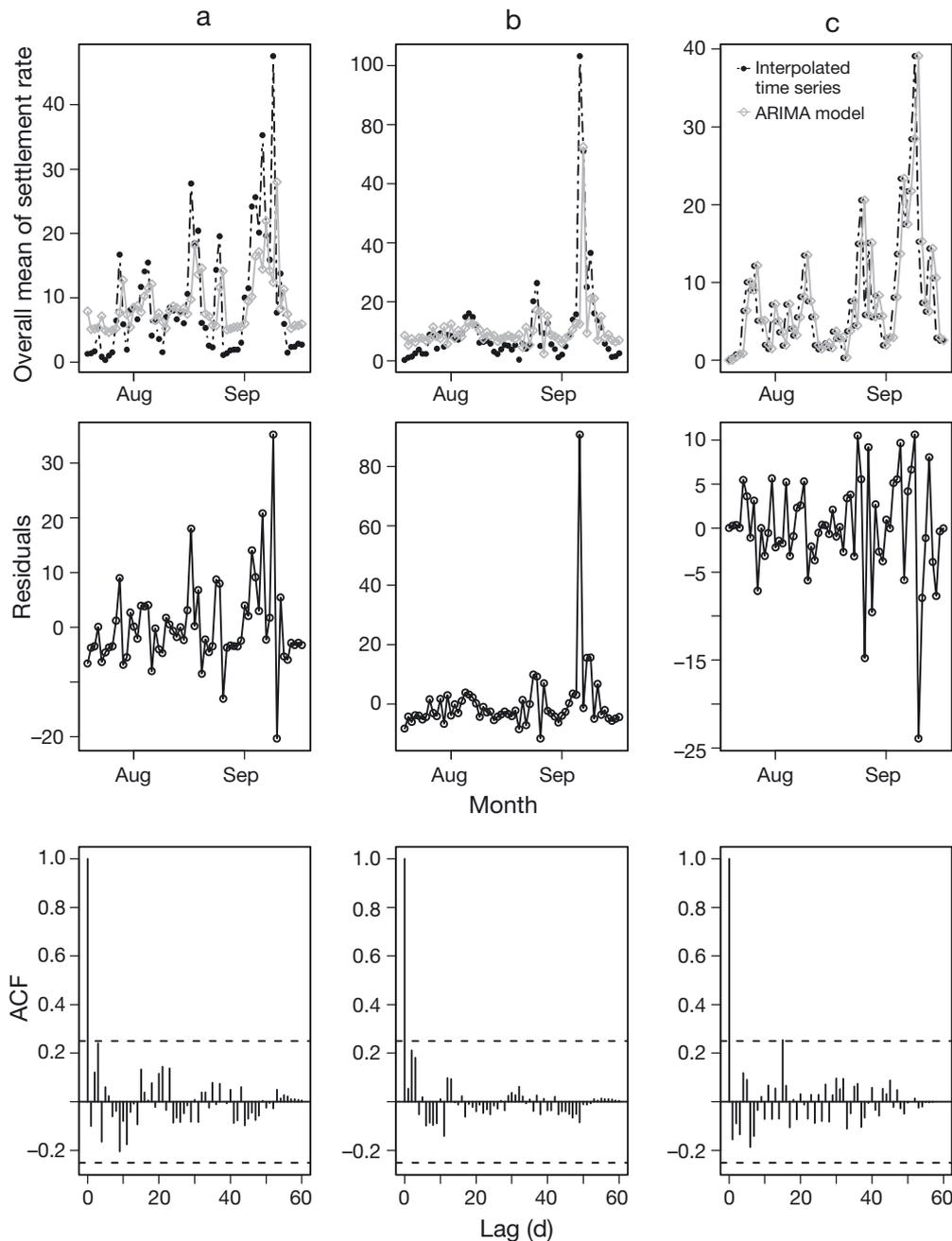


Fig. 6. Non-seasonal autoregressive integrated moving average (ARIMA) models fit to the interpolated *Chthamalus* spp. barnacle settlement time series for (a) the exposed, (b) inside bay, and (c) reef sites. Top panels show a comparison between interpolated time series for settlement (black dashed and dotted line + circles) and the ARIMA model (gray line + diamonds). Center panels show the residuals obtained from the ARIMA models. For all sites, the autocorrelation function (ACF) in the bottom panels shows that the autocorrelation has been removed

The residual-interpolated data were used to define 3 independent modes of variability in the environmental patterns by the PCA (Table 2). For all sites, the PCA displayed 3 components (eigenvalues > 1) which explained about 60% of the cumulative total variability, lending themselves to consistent physical interpretations. Settlement at the reef site and the bay site were significantly related to the tidal forcing PCA modes of variability (maximum tidal range and isopycnal vertical displacements, PC2 and PC3), whereas the exposed site was associated only with the wind-forcing mode (PC1). The concomitant variables explained by the uncorrelated PC2 (maximum tidal range) and PC3 (isopycnal vertical displacements) in the more southern sites (reef and bay) may suggest delivery of larvae related to tidally forced internal waves.

Settlement at the reef site was related to increased amplitude in isopycnal vertical displacements (PC3). These displacements occur during internal tidal bores. In the temperature time series, a strong decrease in water column temperature (cold phase) caused by bottom isotherms reaching the surface at semidiurnal frequencies is notable (see Fig. S3b,c). On the other hand, settlement at the exposed site was associated with PC1, with the highest correlation coefficients obtained for this component. This mode was directly related to winds blowing onshore.

DISCUSSION

Chthamalus larvae settled synchronously at the small spatial scales of this study, with settlement peaks occurring during periods of strong stratification and internal tidal forcing, as expected. For 2 of the studied sites, greater settlement was associated with strong internal wave forcing and a larger tidal range. However, surprisingly, at the third, exposed site, which is the site with the greatest semidiurnal internal wave

Table 2. Principal component analysis for *Chthamalus* spp. barnacle settlement sites in Todos Santos Bay, Baja California, Mexico. For each site, results of the eigenanalysis and Pearson correlation coefficients are shown. The analysis displayed the most significant components (Comp. with eigenvalues > 1). The most significant correlation coefficients are shown in **bold** (alpha 5%, critical value $r = 0.254$). The analysis used the residuals obtained with the autoregressive integrated moving average (ARIMA) models for the settlement data

Exposed site parameter	PC1	PC2	PC3
Eigenvalue	1.7	1.5	1.1
Proportion of the total variability explained by each principal component (PC)	0.2	0.2	0.2
Cumulative total variability explained by cumulative PC	0.2	0.5	0.6
Parameter	Comp. 1	Comp. 2	Comp. 3
Settlement rate anomalies	0.3	-0.2	0.3
Percent of lunar illumination	0.0	0.3	0.6
Isopycnal vertical displacements	-0.1	0.6	-0.5
Maximum tidal range	-0.1	0.6	0.5
Thermal stratification in water column	-0.4	-0.7	0.3
Integrated onshore winds	0.8	-0.2	-0.1
Integrated alongshore winds	-0.9	-0.1	-0.1
Inside bay parameter	PC1	PC2	PC3
Eigenvalue	1.7	1.5	1.2
Proportion of the total variability explained by each PC	0.2	0.2	0.2
Cumulative total variability explained by cumulative PC	0.2	0.5	0.6
Parameter	Comp. 1	Comp. 2	Comp. 3
Settlement rate anomalies	0.4	-0.4	0.5
Percent of lunar illumination	0.0	0.2	0.5
Isopycnal vertical displacements	-0.3	0.7	-0.2
Maximum tidal range	0.0	0.3	0.8
Thermal stratification in water column	-0.3	-0.8	0.0
Integrated onshore winds	0.8	-0.1	-0.2
Integrated alongshore winds	-0.8	-0.2	0.1
Reef site parameter	PC1	PC2	PC3
Eigenvalue	1.7	1.5	1.2
Proportion of the total variability explained by each PC	0.2	0.2	0.2
Cumulative total variability explained by cumulative PC	0.2	0.5	0.6
Parameter	Comp. 1	Comp. 2	Comp. 3
Settlement rate anomalies	0.2	0.5	-0.5
Percent of lunar illumination	0.0	-0.4	0.3
Isopycnal vertical displacements	-0.1	-0.5	-0.7
Maximum tidal range	-0.1	-0.7	0.4
Thermal stratification in water column	-0.4	0.6	0.4
Integrated onshore winds	0.8	0.1	0.2
Integrated alongshore winds	-0.9	0.1	-0.1

activity in this bay (Filonov et al. 2014), and the site where winds were previously discarded as a forcing factor in a spring settlement study (Ladah et al. 2005), a significant relationship was detected between set-

tlement and onshore winds, with no relationship to any of the tidal forcing modes, including the internal tide. Our results highlight the fact that at very nearby sites, transport across the inshore platform and surf zone, and eventual settlement at the shore, may actually be the result of different physical mechanisms which may act in concert, and appear to vary temporally and spatially in their dominance and site-specific relevance due to bathymetry or geomorphology.

The synchronization and general homogeneity of settlement between sites, and the fortnightly signal detected in the autocorrelation functions of settlement for all sites, suggest that (1) the larval pool was fairly homogeneous across the spatial scales of this study, (2) a physical process with a lunar periodicity influences the spatial scales of the study area (>1 km along the coastline), and/or (3) reproduction and larval availability are timed to occur every 2 wk. Thermal vertical displacements showing high frequency changes of nearshore seawater temperature and stratification, which are most likely associated with internal wave activity (Shanks & Wright 1987, Pineda 1995, 1999, Filonov 2011, Filonov et al. 2014), were greatest at the offshore mooring on days when settlement pulses occurred. A considerable part of the variance in settlement at the reef site was positively correlated with the shoaling of bottom isotherms, suggesting that internal waves play an important role in transport, as has been found previously (Shanks & Wright 1987, Pineda 1999, Pineda & López 2002, Ladah et al. 2005). However, the results of our study also suggest that internal waves do not always explain settlement, even at sites that have a very strong semidiurnal internal wave signal, such as the exposed site at San Miguel.

Greater settlement also occurred during the full and third-quarter moon, which would have great relevance in an area of strong tidally-forced internal waves, and which has been found previously (Pineda 1995). Internal waves generated during spring tides (which are of greater amplitude than those which originate during neap tides at this site; Ladah et al. 2005) or generated at sites where internal wave activity is quite strong (such as the exposed site at San Miguel, see Filonov et al. 2014) may break and dissipate energy offshore, away from inshore settlement sites, due to their greater amplitude, and therefore may not transport larvae all the way to the coast (Pineda 1995). On the other hand, internal waves generated during the neap tide (of lesser amplitude), or at sites with weaker internal wave energy (those farther inside the bay, such as the bay and reef sites),

may actually reach the coast, allowing the internal waves to propagate closer to shore before breaking (Moum et al. 2008), thereby resulting in more settlement. At sites or at times when internal waves break farther offshore, such as in the former case, other transport mechanisms such as wind forcing (found to be relevant to settlement at the exposed site) may be necessary to bring larvae all the way to shore. In the latter case, this would not be necessary, as internal waves that propagate all the way to shore may be sufficient for transport. Obviously the presence in the water of viable cyprids which are ready to settle during these periods of the lunar cycle would also be a requirement for settlement at the coast. However, studies in the area do suggest the continuous presence of cyprid larvae during the months of March through September (Pineda & López 2002, Ladah et al. 2005, Tapia & Pineda 2007).

Settlement was generally homogeneous at all sites for the majority of the study, which was unexpected and different from what was found previously where settlement was not homogeneous between sites (Ladah et al. 2005), suggesting year to year or seasonal variability. The generally homogeneous settlement found among sites may suggest some spatial coherence both in the larval pool and in the transport mechanism across sites, regardless of the varied coastline topography or bathymetry. Occasionally in this study, however, spatial heterogeneity in settlement was detected, which could have resulted from a heterogeneous larval pool in the nearshore water column at those times (Tapia & Pineda 2007, Tapia et al. 2010). Shanks & Shearman (2009) suggested that throughout planktonic larval development, barnacles can change their vertical position by swimming faster than the vertical flow, facilitating onshore retention in combination with coastline topography (headlands). If the transport mechanism acting in the nearshore environment is consistent along the coast, but the larval pool is patchy, resultant settlement at the coast would be heterogeneous. The development of larvae during the life cycle (Jenkins & King 2006, Sponaugle et al. 2006) and the predation of larvae within kelp forests (for example by juvenile rockfish *Sebastes* spp.) may also affect population density (Gaines & Roughgarden 1987), further leading to a patchy larval pool. Larvae may also be transported and sheared into layers by advection due to differential alongshore currents, or due to wave action and other large-scale processes present along the coastline (Pineda & López 2002, Mateos et al. 2009). These factors may interact with others and result in the heterogeneity of the larval pool along the coastline.

Many of these complicating factors have not been studied in the field to date and may help explain the heterogeneity between sites found on occasion in this study.

When spatial heterogeneity in settlement was found, at times greater settlement occurred at the exposed site. In a springtime study, Ladah et al. (2005) also found greater concentrations of larvae settled at sites directly exposed to wave action in comparison to more protected sites, which may be due to high flow velocities resulting in hydrodynamic settlement cues. Sites with a greater rate of water exchange, such as zones with strong wave action, show greater settlement (Shanks et al. 2010) and generate greater mixing and transport due to the irregular topography (as in Moum & Nash 2008). Additionally, Schiel (2004) suggested that filter-feeding benthic invertebrates are more abundant (up to an order of magnitude) in exposed areas than in more protected areas, due to the generation of turbulence in the water column which increases the likelihood of food availability. However, at 2 experimental sites (separated by 130 m) with different ambient flow regimes, Todd (1998) found that almost twice the number of larvae settled in a site with low fluxes, suggesting a velocity window suitable for settlement at $<0.15 \text{ m s}^{-1}$. Future studies require that sites be evaluated with respect to their physical and geomorphological attributes (e.g. flow, tidal amplitude, rugosity, and orientation), as well as an *in situ* quantification of larval supply and concentration in the nearshore larval pool (Fujimura et al. 2014, Shanks et al. 2014, 2015). For example, breaking waves generate an onshore current near the bottom that might transport seabed material accumulated in the outer surf zone (Fujimura et al. 2014). The surf zone varies with beach morphology, with greater exchange of water and material on dissipative shores versus reflective beaches (Shanks et al. 2014). Finally, the larval pool can show contrasting horizontal patterns in the water column, which may result in variable settlement dependent on the depth at which the transport mechanism acts (Shanks et al. 2015).

Forcing mechanisms may also be amplified or modified by bathymetry, currents, circulation, or in the case of the northern part of the bay, by morphology of the beach. It is unclear how the turbulence generated in the highly dynamic surf zone may interact with internal waves very near the shore. It has been suggested that in the surf zone, there may be a barrier to settlement when there is lower exchange of water and that wave action may help overcome this final part of the journey back to shore (Rilov et al. 2008,

Shanks et al. 2010). The most exposed site in this study is also the site with the strongest semidiurnal internal tide in the area (Filonov et al. 2014), making it difficult to tease apart the possible forcing mechanisms. Regardless, the PCA did not implicate either of these factors in settlement at this site, but surprisingly suggested that larval settlement relates to onshore winds, which had been previously ruled out for this site in a spring study (Ladah et al. 2005). Internal waves may still transport larvae to nearshore waters, but the final journey may require onshore winds to ultimately result in settlement. This will be further explored with drifters in the future.

For 2 of the 3 sites studied (the bay and reef sites), tidal forcing mechanisms were implicated in settlement. Settlement at the bay site was directly related to the lunar forcing phase and the maximum tidal range. We speculate that settlement at this site may be modulated by larval capacity to attach to the substrate during very high tides. Because this is a dissipative beach, the extreme high tides may have been necessary to move larvae all the way onto the shore. At the reef site, however, settlement was related to greater isopycnal vertical displacements (wave amplitude), most likely related to non-linear internal wave deformation and disintegration (Filonov 2011).

For the first time in this area, at one of the study sites (the exposed site), a significant relationship was found between the rate of settlement in summer and winds blowing onshore, suggesting that wind forcing is important in summer. Enhanced barnacle larval settlement has been shown to occur with increased onshore winds (Bertness et al. 1996), and variability in settlement has been related to variability in wind conditions (Hawkins & Hartnoll 1982). If internal waves carry larvae to the exposed site, but the internal waves break farther offshore due to the fact that they have their strongest signal just offshore of this site (Filonov et al. 2014), the larvae may need a little extra help from the wind to cross the narrow dynamic surf zone of this reflective beach. Alternatively, larvae may accumulate at this site due to the winds, and internal waves may then transport them to shore. Regardless of which mechanism acts first, wind forcing can result in surface currents with velocities of approximately 10 cm s^{-1} , with a spatial influence of 2 km from the coast on a diurnal cycle, and may explain settlement over time as has been found in other studies (Kaplan et al. 2003, Tapia et al. 2004).

The relationship between internal wave forcing detected in thermistor chains and settlement at the reef and bay sites, and the relationship between wind forcing and settlement only at the exposed site, highlights

the complicated suite of factors that may interact at the small spatial scales of this study, still preventing us from teasing apart wind forcing and internal tidal forcing in settlement processes at smaller spatial scale. Complicating the issue is that both factors may play a role. However, our results highlight the potential interaction of these factors, which may be the reason why the literature is mixed in attributing settlement to winds versus to tidally forced internal waves.

In conclusion, the frequency of this daily sampling over a period of 2 mo allowed for the study of settlement variability for *Chthamalus* spp. barnacles at small spatial scales (~1 km) for the first time in summer, when settlement and internal wave activity are at their greatest. The synchronized settlement at the 3 closely spaced sites may indicate the homogeneity of the larval pool and a consistent physical transport mechanism on a scale of at least 1 km for a majority of the study period. Settlement at 2 of the study sites was related to changing stratification during the period of internal wave or bore arrival, suggesting that internal motions were the principal transport mechanism during this study. However, at 1 of the 3 sites (exposed site), settlement was related to winds for the first time, suggesting that in summer this site may be more affected by onshore wind-driven near-surface currents than previously thought (Ladah et al. 2005). The effect of wave action, bathymetry, and coastline geomorphology modifies the wind and the internal tide forcing along the coast (Filonov et al. 2014), and/or may modify the concentration of the larval pool. Our results suggest that (1) the offshore larval pool does not vary greatly at the small spatial scales (~1 km) of this study, resulting in generally homogeneous, synchronous settlement, (2) a complex suite of factors may interact to result in settlement at the same site, and (3) settlement may be forced by different factors at sites in very close proximity due to differences in geomorphology and/or bathymetry resulting in alongshore variability in transport mechanisms, and may also explain the occasional spatial heterogeneity in settlement detected.

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