



Internal wave intensity and angle of propagation modulate small-scale settlement patterns of intertidal barnacles during peak recruitment

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ABSTRACT: The settlement of intertidal barnacles *Chthamalus* spp. was measured for an entire recruitment season at 3 sites separated by 100 m in Baja California, Mexico. During a 10 d pulse that accounted for nearly 30% of yearly settlement, coastal wind speed and direction, nearshore water column temperature, and current velocities were also measured. During this period, strong internal tidal forcing was observed, with short episodes (1–1.5 h) of rapid fluctuations in water column temperature, stratification, and currents. *Chthamalus* spp. settlement was significantly and positively correlated with cumulative high-frequency fluctuations in temperature, thermal stratification, and surface current flows, but not with onshore winds. Furthermore, the spatial pattern in the number of settlers was correlated with the angle of propagation estimated for onshore-moving internal waves, potentially modulated by nearshore bathymetry. This relationship between *Chthamalus* spp. settlement and high-frequency changes in water column temperature was also shown for a site in La Jolla, California, USA, but not for a similar barnacle, *Balanus glandula*, suggesting that interspecific differences in larval behavior and nearshore depth distribution may translate into differences in transport. Our results suggest that both the number of settlers at shore and their spatial pattern can be modulated by the intensity and direction of internal wave events, at least during peak settlement periods. Future research should consider both the intensity and geometry of internal-wave-induced variability in the nearshore, as well the small-scale features of coastal geomorphology and bathymetry.

KEY WORDS: Larval settlement · Small-scale spatial variability · Internal waves · Tidal bores · Barnacle · *Chthamalus* · Baja California

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1. INTRODUCTION

The pelagic larvae of most benthic marine invertebrates, which are a conspicuous component of most coastal ecosystems, require the aid of physical advective processes to return to shore and reach habitats suitable for settlement (Shanks 1983, 1995, Far-

rell et al. 1991, Pineda 1991, 1999, LeFèvre & Bourget 1992, Shanks et al. 2000). These physical phenomena span a range of spatial and temporal scales (Morgan et al. 2018) and include wind-induced upwelling and relaxation (Farrell et al. 1991, Wing et al. 1995a,b, Shanks et al. 2000, Trindade et al. 2016), surface transport generated by wind forcing (Hawkins &

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Hartnoll 1982, Bertness et al. 1996, Tapia et al. 2004), surface waves (Navarrete et al. 2015, Morgan et al. 2018, Weidberg et al. 2018), and internal waves and bores (Shanks & Wright 1987, Pineda 1991, 1994a,b, Ladah et al. 2005, Shanks et al. 2014, Valencia-Gasti & Ladah 2016, Fernández-Aldecoa et al. 2019). These physical processes interact with the availability of competent larvae in the larval pool (Pineda et al. 2010), larval swimming behavior (LeFèvre & Bourget 1992), surf zone dynamics (Rilov et al. 2008, Morgan et al. 2016, Shanks et al. 2017), the availability of suitable substrate (Raimondi 1988, Minchinton & Scheibling 1993, Menge et al. 2010), and early post-settlement mortality (Gosselin & Qian 1997, Hunt & Scheibling 1997, Jarrett 2000, Liévana MacTavish et al. 2016) to eventually determine patterns of recruitment into the adult population.

Many advective processes that contribute to the cross-shelf transport of larvae vary over small scales: temporally due to tides, time of day, and seasons (Pineda 1991, 1995, Jacinto & Cruz 2008), and spatially through their interaction with local hydrodynamics and bathymetry (Porri et al. 2006, Tapia & Navarrete 2010, Filonov et al. 2014). For instance, the daily sea breeze, which can drive the onshore transport of surface material (Tapia et al. 2004), may interact with solar heating to cause local changes in nearshore stratification (Kaplan et al. 2003). Furthermore, changes in nearshore stratification are closely linked to local bathymetry and the generation and strength of nonlinear internal waves (Pineda 1995), which can vary significantly over small distances and time-scales (Ladah et al. 2012, Bonicelli et al. 2014, Filonov et al. 2014).

Although physical processes mediating the onshore transport of planktonic invertebrate larvae are among the primary drivers of settlement (e.g. Pineda 1999, Queiroga & Blanton 2005, Narváez et al. 2006), other physical and biological factors may also shape the resulting patterns (Gaines et al. 1985, Tapia & Navarrete 2010, Pfaff et al. 2015), often inducing small-scale spatial heterogeneity (Ladah et al. 2005, Valencia-Gasti & Ladah 2016, Shanks et al. 2017). For instance, spatial patterns may result from variability in the nearshore pool of larvae (Pineda et al. 2010), which can depend on the timing and intensity of adult reproduction (Macho et al. 2005), the interaction of behavior and nearshore hydrodynamics (Butman 1987, Helfrich & Pineda 2003, Scotti & Pineda 2007, Shanks et al. 2017), and factors affecting the survival of larvae in the plankton such as predation (Rumrill 1990, Morgan 1995) and food availability (Boidron-Métairon 1995, Giménez et al. 2017).

For barnacle larvae, both their distribution in the water column and their behavior can modulate settlement patterns (Grosberg 1982, LeFèvre & Bourget 1992). The ability of larvae to maintain or adjust their vertical position when confronted with rapidly changing vertical and horizontal flows appears to be critical for transport leading to settlement, as shown both from theory and from simulations (Franks 1992, Scotti & Pineda 2007, Garwood et al. 2021). For example, differing vertical patterns of settlement in *Balanus glandula* and *B. crenatus* correspond with the vertical distribution of cyprids in the plankton (Grosberg 1982). Cyprids of *Chthamalus* spp. are typically found close to the bottom in cold or sub-thermocline waters off Southern California (Pineda 1991, Tapia et al. 2010) and in Baja California, Mexico (Liévana MacTavish et al. 2016), but can be found near the surface when internal perturbations cause the thermocline to tilt upwards, aiding in their onshore transport in surface currents (Pineda 1999). Balanid cyprids, on the other hand, are found closer to the surface when sampled in nearshore waters (e.g. Grosberg 1982, Bonicelli et al. 2016), and their ability to maintain their position near the surface increases accumulation in onshore-moving currents (Shanks 1986, Pineda 1999).

Internal-wave mediated transport of planktonic larvae to settlement sites involves a complex suite of processes in the nearshore ocean that interacts with both the vertical distribution of larvae and their behavior. Internal waves are generated by perturbations, often induced by the wind or tide, interacting with abrupt bathymetry and a stratified water column. More intense internal wave formation results from increased stratification and stronger perturbations at the site of origin. Internal waves then propagate away from this site as gravity waves along the thermocline, resulting in its successive shoaling and sinking, with crests and troughs visible as oscillating water-column temperatures and rapidly changing vertical and horizontal currents. At the surface, convergence zones form above internal wave troughs and are often visible as smooth areas or slicks, which have been shown to accumulate and transport plankton with depth-keeping behavior (Shanks 1983, 2006, Lamb 1997, Lennert-Cody & Franks 2002, Helfrich & Pineda 2003, Weidberg et al. 2014, Fernández-Aldecoa et al. 2019, Garwood et al. 2020). Because internal waves often induce contrasting horizontal currents above and below the thermocline (referred to as mode-1 internal waves), changes in the vertical distribution of larvae can ultimately determine flow entrainment (Pineda 1999).

In shallower waters, internal waves become highly non-linear, and as internal waves break, they form bores. Internal tidal bores are breaking internal waves and are often manifested as strong onshore currents of first cold and then warm surface waters, at times encompassing the entire water column (Winant 1974, Pineda 1994b, 1999). The more non-linear the process is, the greater the potential for transport of particles and scalars entrained in the wave. Once internal waves enter very shallow water, they interact with winds, Stokes drift, and benthic streaming to transport larvae, depending on their ability to float or sink, across the final barrier of the surf zone, with its width modulated by bathymetry ranging from reflective shores with abrupt depth changes to gently sloping dissipative shores (Rilov et al. 2008, Shanks et al. 2014, 2015, Navarrete et al. 2015, Morgan et al. 2018, Fernández-Aldecoa et al. 2019).

In this study, we focus on the short-term variability of barnacle settlement over small spatio-temporal scales in Baja California, Mexico, and explore its connection with nearshore physical processes that may deliver larvae to shore. We monitored the settlement of *Chthamalus* spp. cyprids at 3 sites separated by 100 m each during a 10 d settlement peak, which accounted for almost 30% of total *Chthamalus* spp. settlement recorded during the year at this site (4290 settlers out of 15 914 total). In a previous contribution (Ladah et al. 2005), we showed that the timing of settlement was correlated with short-term perturbations

in nearshore stratification over the year. Here we used more intensive physical observations during the largest settlement peak of the year to test whether the intensity of internal motions could be driving small-scale patterns in the number of settlers arriving at intertidal habitats. We then applied the same analysis to a peak of settlement data for a site further north, in La Jolla, California, USA.

2. MATERIALS AND METHODS

2.1. Study site

Playa de San Miguel (31° 54' N, 116° 44' W) is a wave-exposed, south-facing rocky shore, composed principally of weathered volcanic basalt boulders, located in the Bay of Todos Santos on the Pacific coast of Baja California, Mexico (Fig. 1). Local oceanographic conditions in this area are dominated by wind-driven upwelling in spring, with solar heating of surface waters, an energetic internal tide (Filonov et al. 2014) and a strong sea breeze in summer (Tapia et al. 2004), and strong surface wave activity in the fall and winter months (see Ladah et al. 2005 for a more detailed site description). A gradient in wave exposure and bathymetry exists along this shore, adding complexity to nearshore hydrodynamics. Also, a strong alongshore current into the Bay of Todos Santos occurs during large northern swells in

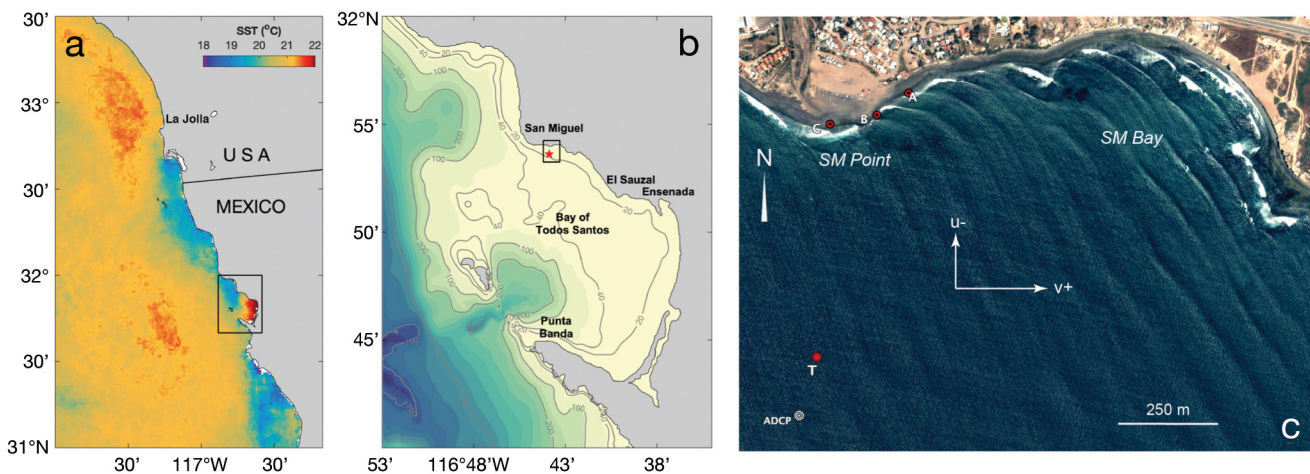


Fig. 1. (a) Bay of Todos Santos (Mexico) and La Jolla (California, USA), relative to the USA–Mexico border, and mean pattern of sea surface temperature (SST) from MODIS-Aqua for August 2005, when the settlement observations were conducted. (b) Study site in the Bay of Todos Santos and bathymetry of the bay; gray contours correspond to the 200 and 50 m isobaths. (c) Layout of the settlement sites (A, B, C) on the shoreline (respective coordinates, 31° 54' 4.60" N, 116° 43' 42.32" W; 31° 54' 2.73" N, 116° 43' 45.51" W; 31° 54' 1.94" N, 116° 43' 50.23" W) and moored instrumentation: acoustic Doppler current profiler (ADCP) and thermistor mooring (T); vectors shown in white indicate the orientation of the primary and secondary axes determined for current velocities (see Section 2 for a detailed description). The v and u axes of rotated currents were positive when pointing eastward (i.e. into the bay) and southward (i.e. offshore), respectively. Image in (c) corresponds to May 2004 (from Google Earth)

winter. The San Miguel point is the most wave-exposed site at the north-western end (Fig. 1b,c), with rapid changes in bathymetry leading to a reflective surf zone with complex offshore topography (Fig. 1b). In contrast, on the south-eastward part of the shore, a bend in the coast where an old boat ramp and jetty used to exist protects a small embayment from northern surf (Fig. 1c), with smaller wave heights where bathymetry changes less drastically with a less reflective surf zone. The La Jolla site in Southern California (Dike Rock) is a more dissipative site, where waves break offshore and gently roll in on a more gently sloping bottom.

2.2. Settlement observations

Settlement observations were conducted in the summer of 2005 at 3 sites spanning ca. 200 m of shoreline (Fig. 1c), ranging from near the surf point to the small embayment. Settlement collectors deployed at each site were made of 11 cm long pieces of white PVC pipe (2.54 cm diameter), which were cut in half lengthwise and grooved in 3 areas (see Ladah et al. 2005 for details). Collectors were deployed and replaced after 8–15 h during the low tide. Between 8 and 14 collectors were recovered during each collection, and barnacle cyprids were identified to the genus level and enumerated using a stereomicroscope.

Although we could not identify *Chthamalus* spp. settlers to the species level, which is difficult from a strictly morphological examination (Miller et al. 1989), *C. fissus* is the most abundant species in the study region and the most likely to occur on our settlement collectors. The northern species, *C. dalli*, has been found as far south as San Diego (see Chan et al. 2016 and references therein), and therefore its presence in our study area cannot be ruled out.

2.3. Environmental data

Wind data were gathered at 1 min intervals from a nearby weather station located 2 km south of our study site (El Sauzal, see Fig. 1) and 10 m above sea level. At the scale of our study site, the shoreline has an E–W orientation, and southerly winds blow perpendicular to the shoreline, with most of the variability in summertime coastal wind corresponding to the diurnal cycle of the onshore sea breeze (Tapia et al. 2004). We used the E–W component of wind velocity, which explained 87% of wind variability during our

study, to test for the effects of wind forcing on larval settlement. Wind data were low-pass filtered with a 20-point running mean and converted into an hourly record. Wind stress was then computed as in Large & Pond (1981) and subsequently time-integrated for the duration of each collector deployment.

Subtidal temperatures were measured with a thermistor mooring (see Fig. 1), deployed 1 km offshore at 20 m depth. StowAway TidBit loggers (Onset Computer) were placed at 1, 4, 7, 10, 13, 16, and 19 m above the bottom (mab) and programmed to record temperature every 5 min. Each time series of raw temperature data was linearly detrended and subdivided into non-overlapping segments of 4096 observations (14.2 d) before the computation of average power spectra using the Welch method (Stoica & Moses 1997). For each depth/spectrum we calculated the percentage of total spectral density found within the following frequency bands in cycles per day (cpd): diurnal (0.8–1.2 cpd), semi-diurnal (1.8–2.2 cpd), and high-frequency (>2.2 cpd).

To characterize the variability in water column stratification, we computed the square of the Brunt-Väisälä frequency (N^2) for each one of the 6 pairs of temperature series (i.e. 1–4, 4–7, 7–10 mab, etc.) as:

$$N^2 = \frac{g}{\rho_0} \frac{d\rho}{dz} \quad (1)$$

where g is the gravitational acceleration (9.8 m s^{-2}), ρ_0 is the mean density of the water column, and z is height (mab). A constant salinity of 34 was assumed, as density is principally controlled by temperature in this area (see Filonov et al. 2014).

A bottom-mounted 300 kHz acoustic Doppler current profiler (Sentinel Workhorse ADCP, Teledyne RD Instruments) was deployed near the thermistor mooring (Fig. 1). The instrument recorded average water velocities over 1 min intervals (1 ping s^{-1}) and within depth bins of 1 m. The first bin was at 3.7 mab, whereas the top bin was at 13.7 mab. Since most of the variability in horizontal currents was aligned with the E–W axis, which is consistent with local bathymetry at San Miguel, we rotated the coordinate system to define the alongshore currents (v) and across-shore currents (u) as shown in Fig. 1c.

2.4. Data analysis

Statistical analyses of settlement data were conducted using R (R Core Team 2017), whereas all time-series analyses were implemented in MATLAB version 9.4.0 (The Mathworks).

Correlation analyses for settlement and nearshore physical forcing entailed the formulation of indices for cumulative physical variability during each deployment. As a proxy for wind forcing, the cumulative cross-shore (E–W) surface stress (C , Pa) was computed for each collector deployment i as:

$$C = \sum_{i=1}^t \tau_{wi} \quad (2)$$

where τ_{wi} is wind stress along the E–W axis, t is the number of 20 min time steps spanned by a collector deployment, and positive values of C indicate net onshore wind stress. To devise indices of water column variability indicative of internal motions, we focused on short-term changes in (1) vertical velocities measured by the ADCP, (2) temperature at a fixed mid-water depth (10 mab), and (3) mid-water stratification. The computation of these 3 indices is described below.

When internal waves occurred, there was a clear and characteristic pattern of successive changes in the sign of vertical flows throughout the water column. The random error of vertical velocities measured during our study was estimated for each depth bin as the standard deviation of the difference in vertical velocity estimates made by the 2 pairs of acoustic beams (Gordon 1996). Vertical velocities recorded during each internal wave event were up to twice the magnitude of the largest random error calculated for depth bins 1–11 (0.036 m s^{-1}). Thus, for each deployment of our settlement collectors, we calculated an index for variability in ADCP vertical velocities (W) over t time steps as:

$$W = \sum_{i=1}^t \left(\frac{1}{B} \sum_{j=1}^B w_j^2 \right) \quad (3)$$

where the term in brackets is the mean of the squared vertical velocities w_j over the $B = 11$ depth bins (i.e. 3.7–13.7 mab) at time i , and t is the number of 1 min ADCP data ensembles gathered during the collector deployment. Greater variability in vertical flows should increase the value of W , indicating greater high-frequency internal variability.

In addition to rapid changes in vertical flows, episodes of high internal variability coincided with an intensification of surface currents and vertical shear, particularly along the E–W axis (see Section 3). We first computed instantaneous eastward surface transport U_t ($\text{m}^2 \text{ s}^{-1}$) by depth-integrating each velocity profile:

$$U_t = \Delta z \sum_{i=b}^{11} u_i \quad (4)$$

where $\Delta z = 1 \text{ m}$ and east velocities u (in m s^{-1}) are integrated from the top bin ($i = 11$) down to a depth $i = b$ where velocities change sign. Total eastward surface transport over each collector deployment (U_d) was then calculated by integrating the series of surface transport estimates U_t over the deployment time:

$$U_d = \Delta t \sum_{t=1}^T U_t \quad (5)$$

where $\Delta t = 60 \text{ s}$ corresponds to the sampling interval of our ADCP measurements, and T is the number of such intervals during the deployment. The same procedure was followed to estimate surface transport on the N–S axis (V_d).

Although temperature data were gathered at a lower frequency than ADCP data (every 5 min vs. every minute), internal wave episodes were visible in our thermistor mooring dataset as well (see Section 3). Furthermore, gap-free temperature data were available for the duration of the study, whereas a 24 h gap in the ADCP dataset (see Fig. 2) reduced the number of settlement observations that could be used in the correlation analysis. We calculated an index for short-term internal variability in temperature as

$$dT = \sum_{i=2}^t |T_i - T_{i-1}| \quad (6)$$

where a series of absolute differences between consecutive temperature measurements at a given depth; in this case, 10 mab; is integrated over each deployment of settlement collectors. The index value is thus proportional to internal variability in temperature at scales of minutes and also represents internal wave intensity. We performed a similar calculation with the series of squared Brunt-Väisälä frequencies (see Eq. 1) computed for the 10–7 mab depth range (i.e. mid-depth), integrating absolute differences in consecutive estimates of mid-water stratification for each deployment.

Correlations between settlement and the above-described cumulative indices of physical forcing, termed internal wave intensity, were assessed through a non-parametric Spearman test, as data lacked normality and homoscedasticity. Since both our physical indices and settlement observations were likely to be non-independent, as most time series observations are auto-correlated, regression analyses were performed on the first-differenced series of settlement and physical indices, i.e. vectors of length n with physical indices and mean settlement rates were converted into vectors of length $n - 1$, corresponding to the $n - 1$ differences between observations at

time $t + 1$ and observations at time t . This procedure has been applied in previous studies to remove auto-correlation from physical-biological time series (e.g. Tapia et al. 2004, Tapia & Navarrete 2010).

ADCP data were utilized to estimate the angle of propagation for each of the internal features (Pineda 1999), based on the assumptions that (1) internal motions behave according to internal mode 1 in this region (which has been documented for this area by Filonov et al. 2014) and that (2) cross-shore forcing during these short periods is dominated by the occurring internal bore. Under these 2 assumptions, vertical variability of horizontal currents should be at a maximum in the direction an internal wave is propagating. Progressive 1-degree rotations of the measured horizontal currents allowed us to find the direction that maximized the vertical standard deviation (i.e. computed across the 11 depth bins) of current speeds averaged within each bin over the duration of each bore event (for more detail see Pineda 1999, Eqs. 3–5). We regarded this direction as an estimate of internal wave propagation and used it to evaluate whether spatial patterns in settlement might be related to the angle of propagation.

To assess the generality of patterns revealed by our data from San Miguel, we used the same procedure outlined above to analyze an 8 d dataset of daily barnacle settlement and temperature variability gathered off La Jolla during a settlement peak in March 2003 (Tapia & Pineda 2007). These data allowed us to compare the patterns observed for *Chthamalus* spp. settlement at San Miguel with those of *Chthamalus* spp. and *Balanus glandula*, the other most abundant species of intertidal barnacle in the region, at a site (Dike Rock) where it settles at rates nearly 10 times higher than in Baja California (Pineda & López 2002).

3. RESULTS

3.1. Physical conditions

As expected for summertime conditions in the study region, the coastal wind signal was dominated by a diurnal increase of E–W velocities, with westerly winds of up to 6 m s^{-1} in the afternoon (Fig. 2a). Zonal winds accounted for 87% of total wind variability during our study, whereas meridional winds were weaker and more variable, generally blowing from the northwest in the afternoon (Fig. 2a).

There was an increase in thermal stratification of the nearshore water column during the second half

of the study, with differences between surface and bottom temperatures reaching approximately 10°C on 7–8 August (Fig. 2b,c). Perturbations in thermal structure forced by internal waves were visible in the moored temperature series (Figs. 2b,c & 3). Intrusions of near-bottom cold water followed by a sudden depression of the thermocline were often observed 1–2 h after the surface tide reached peak heights (Figs. 2b,c & 3).

In addition to their thermal signature, high-frequency internal waves were visible as changes in the vertical structure of nearshore flows (Fig. 3d,e). Rapid fluctuations in the vertical distribution of temperature (Fig. 3b) coincided with strong vertical shear on E–W currents (Fig. 3e) and with the intensification of mean vertical velocities (Fig. 3f). As shown by the spectral analyses of the temperature series, thermal variability below 10 mab was dominated by high-frequency oscillations, whereas near the surface, it was dominated by diurnal heating and cooling (Fig. 4).

3.2. Settlement relationship with physical conditions

The mean (\pm SE) settlement rate across sites was greatest on 9 August for the evening collection (6.4 ± 2.2 settlers h^{-1}) (Fig. 2f), and the deployment period preceding this collection coincided with significant warming of surface waters, with a ca. 6°C difference between surface and bottom temperatures and strong vertical shear on E–W currents after the noon high tide (Fig. 3e). The settlement numbers for *Chthamalus* spp. were positively and significantly correlated with the intensity of eastward surface flows (Fig. 5a), with short-term variability of mid-depth temperature (Fig. 5b) and with stratification (Fig. 5c). No relationship was observed between settlement and northward surface flows (Fig. 5d), cross-shore winds (Fig. 5d), or vertical velocities (Fig. 5e).

The dataset from La Jolla revealed a settlement pattern that was similar to that found at Todos Santos Bay for *Chthamalus* spp., with settlement rates significantly correlated with high-frequency temperature changes. However, the settlement of *Balanus glandula*, another common intertidal barnacle in La Jolla, was not correlated with nearshore temperature variability (Fig. 6).

All 11 internal wave events for which angles of propagation were estimated (Table 1) appeared to move towards the northeast, with directions of propagation ranging between 13 and 66° from true North (Fig. 7), in agreement with internal wave field char-

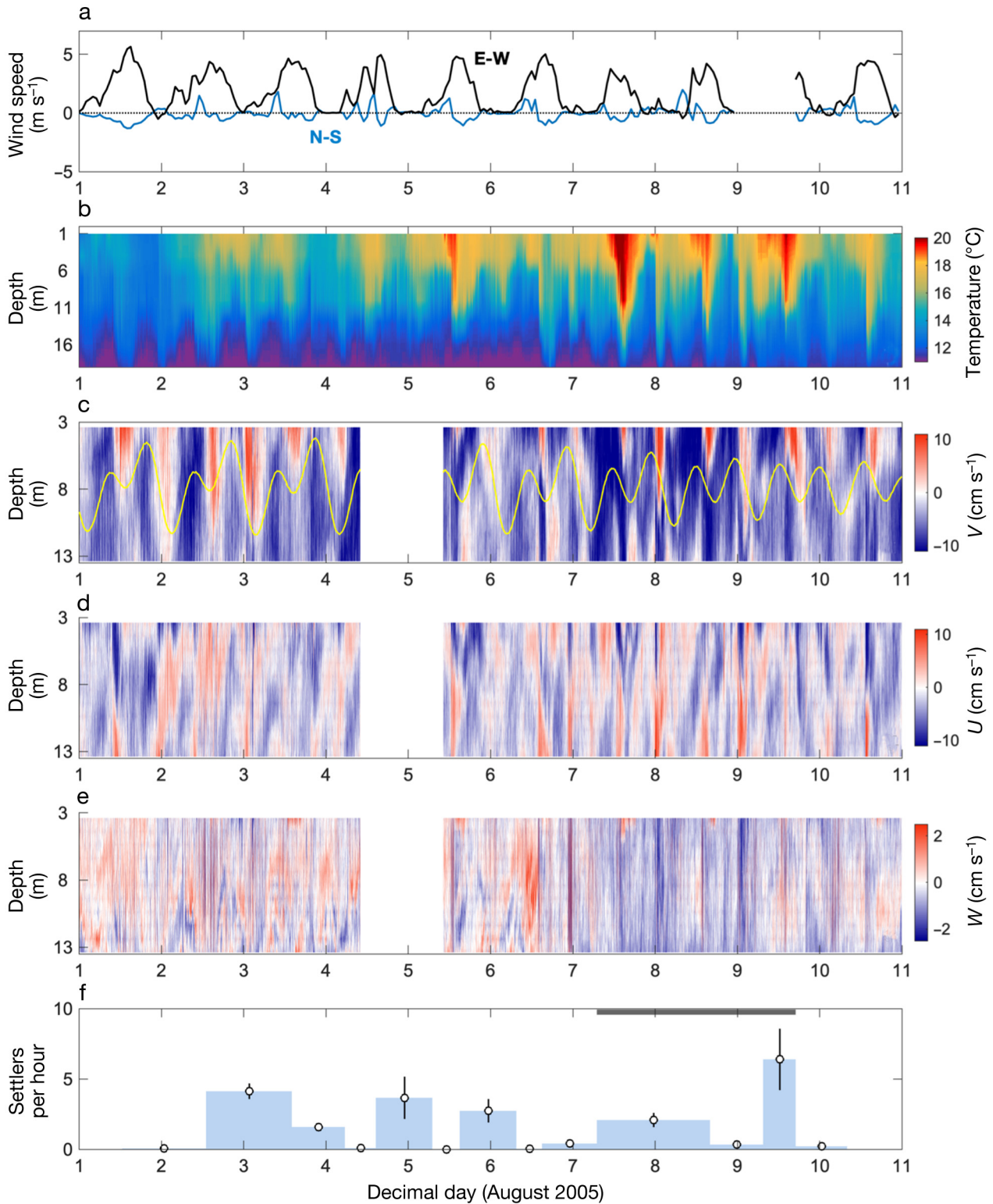


Fig. 2. Temporal variability of physical conditions and *Chthamalus* spp. settlement during the study in San Miguel, Baja California. (a) Wind components correspond to a record from El Sauzal (see Fig. 1b). N-S: north-south; E-W: east-west. (b) Water temperature profiles correspond to data collected every 5 min at the thermistor mooring shown in Fig. 1c. Velocities in the (c) along-shore, (d) across-shore, and (e) upward directions, together with water depth (yellow line in c), were recorded at 1 min intervals with a 300 kHz ADCP. Note the change in scale for upward velocities in (e). (f) Larval settlement is shown as the number of settlers per hour of deployment, with error bars showing standard errors. The gray horizontal bar in (f) indicates the period shown in detail in Fig. 3

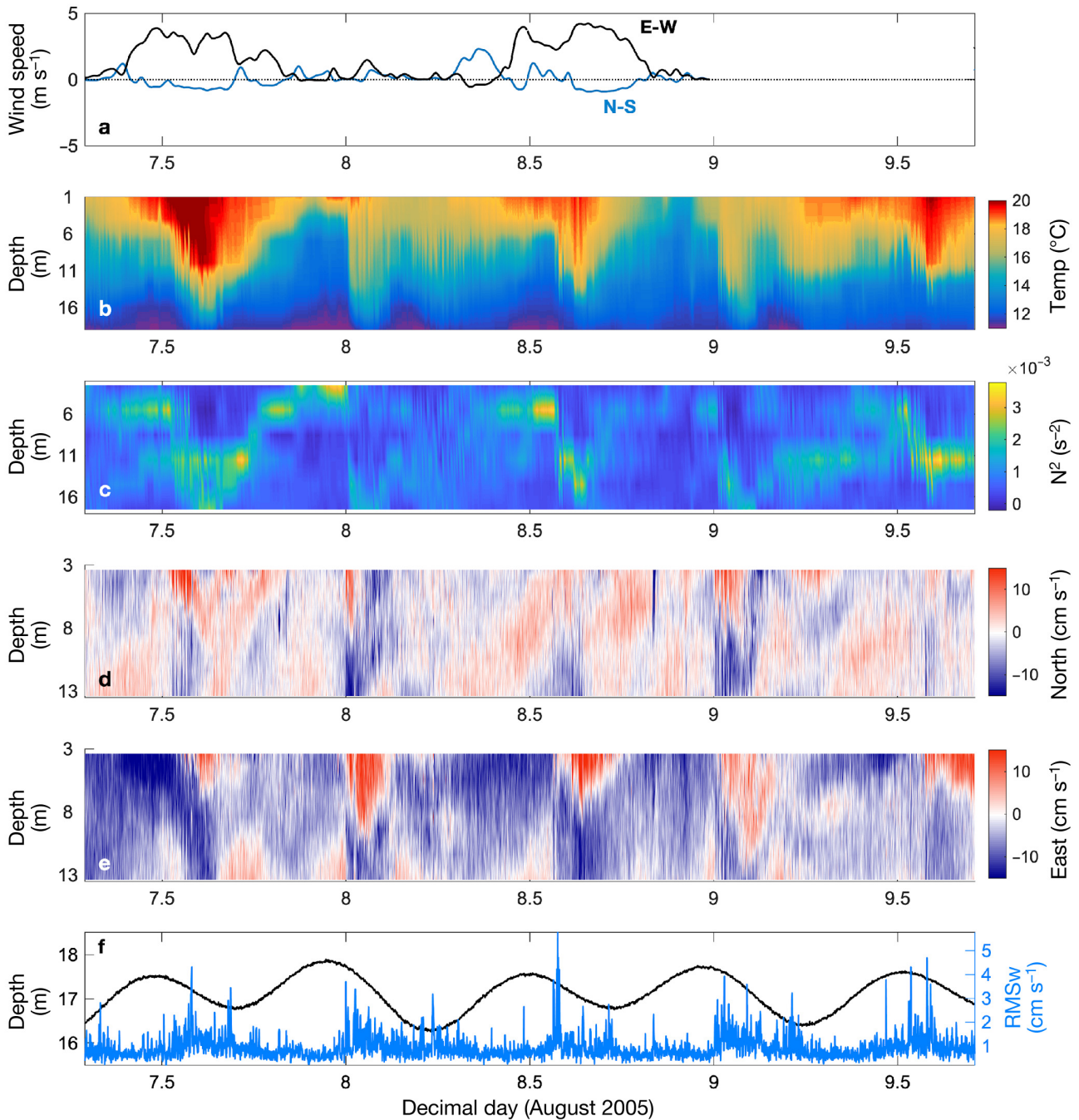


Fig. 3. Detail of temporal variability of (a) winds, (b) water temperature, and (c) thermal stratification at the thermistor mooring; ADCP velocities along the (d) cross-shore and (e) along-shore axes; as well as (f) water depth (black line) and depth-averaged vertical velocities recorded between 7 August at 07:00 h and 9 August at 17:00 h Pacific Daylight Time. Three deployments of settlement collectors took place within this period (see Fig. 2)

acterizations for this site (Filonov et al. 2014). Settlement observations were available for 7 out of the 9 internal wave events characterized during this study, as 3 of the events occurred within the same settlement collector deployment period (Table 1). Settlement rates at sites A and B (see Fig. 1c) showed sig-

nificant linear relationships with the angle of internal wave propagation (site A, $r = 0.77$, $p = 0.041$; site B, $r = 0.80$, $p = 0.029$), whereas settlement at site C appeared to be decoupled from the direction of propagation ($r = 0.56$, $p = 0.19$). Beyond the apparent relationship between the angle of bore propagation and

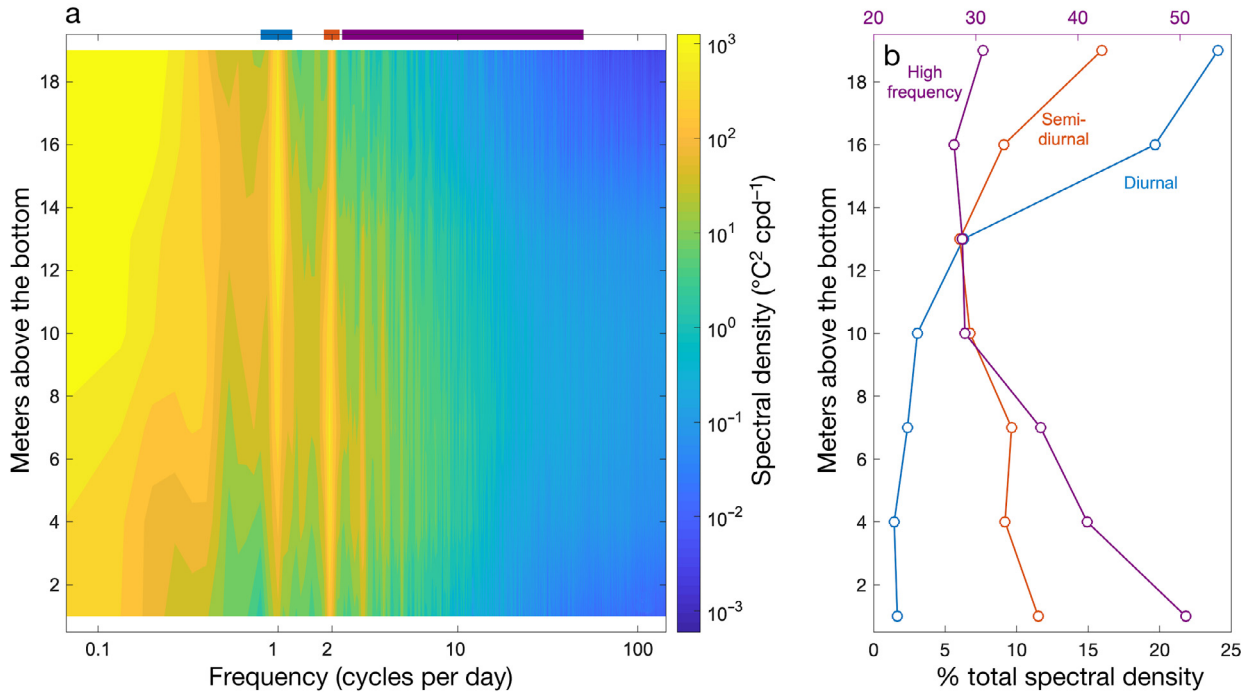


Fig. 4. (a) Vertical structure of power spectra computed for the time series of water temperatures collected from 7 depths at the thermistor mooring between May and October 2005. (b) Vertical change in percentages of total spectral density that corresponded to diurnal (0.8–1.2 cycles per day, cpd), semi-diurnal (1.8–2.2 cpd), and high-frequency (2.2–50 cpd) bands. Colored horizontal bars on the top axis of (a) indicate the frequency bands used to compute percentages shown in (b)

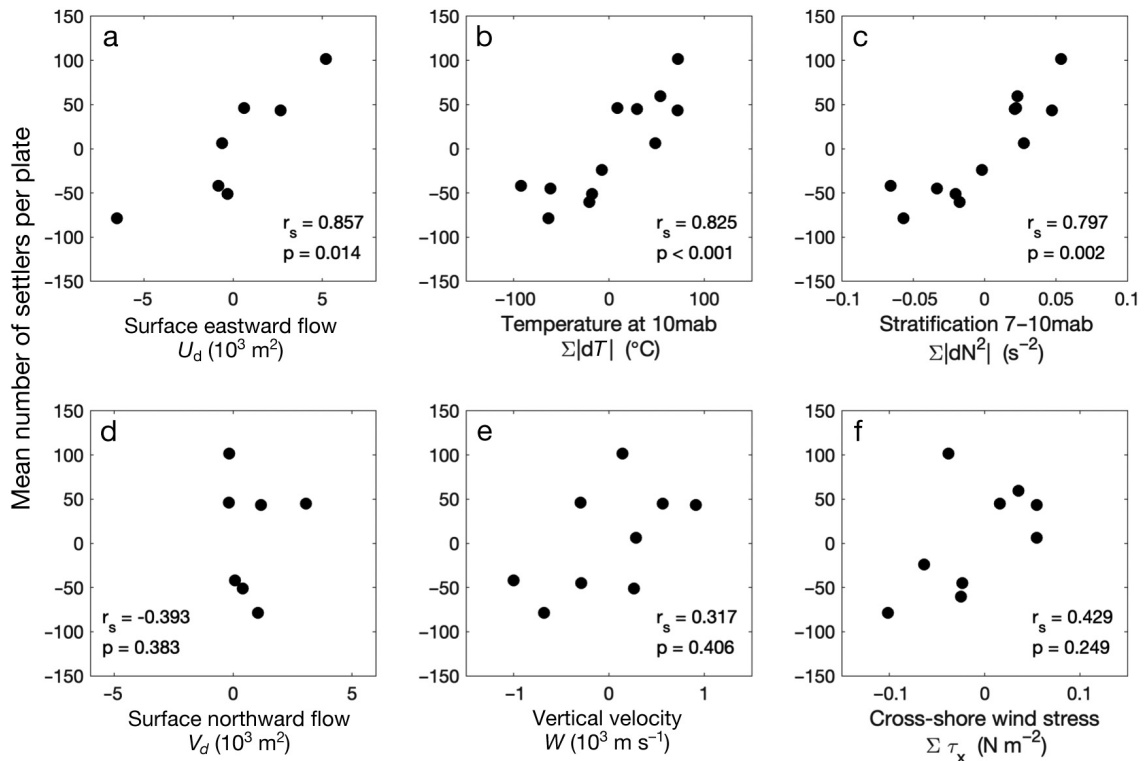


Fig. 5. Correlation between the settlement of *Chthamalus* spp. and (a,d) horizontal surface flows, (b) short-term changes in mid-water temperature (mab: meters above bottom), (c) stratification, (e) and vertical velocities, as well as (f) cumulative onshore wind stress. All physical indices were time-integrated for each deployment (see Section 2)

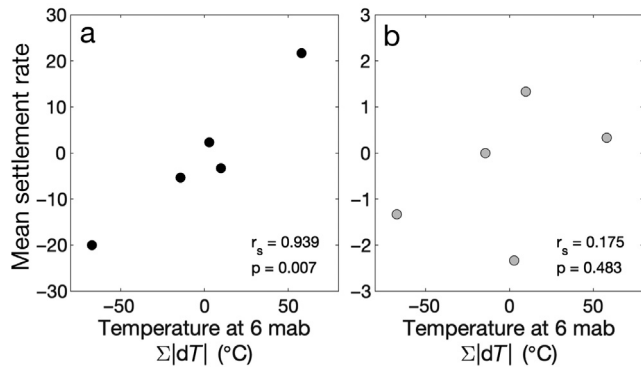


Fig. 6. Correlation between daily changes in larval settlement rates (ind. plate⁻¹ d⁻¹) and cumulative temperature variability in the nearshore water column for (a) *Chthamalus* spp. and (b) *Balanus glandula* in La Jolla, Southern California. Settlement was observed daily in March 2003. See Tapia & Pineda (2007) for more details; mab: meters above bottom

Table 1. Angles of onshore propagation (θ_{prop} ; clockwise from true north, TN) estimated for internal wave events detected in the nearshore water column. Estimates for propagation angle were obtained from high-frequency (1 min) water velocities measured with a moored upward-looking 300 kHz ADCP

| Start date | Local time | Duration (min) | θ_{prop} . (°TN) |
|------------|------------|----------------|-------------------------|
| 1 Aug | 22:48 | 108 | 13 |
| 3 Aug | 00:14 | 58 | 52 |
| 6 Aug | 22:34 | 79 | 21 |
| 7 Aug | 12:29 | 101 | 61 |
| 8 Aug | 00:00 | 29 | 37 |
| 8 Aug | 13:26 | 79 | 34 |
| 9 Aug | 00:00 | 101 | 29 |
| 9 Aug | 13:41 | 58 | 66 |
| 10 Aug | 01:41 | 79 | 50 |

the rate of *Chthamalus* spp. settlement at sites A and B (Fig. 7a), a change in the direction of bore arrival to the shore appeared to shape the spatial pattern of settlement across the study sites. The fraction of empty plates collected after each event increased when the angle of bore propagation was <30° and dropped to zero, i.e. all plates had settlers at the time of recovery, for angles of incidence >50° (Fig. 7b). Consistently with the previous result, the coefficient of variation computed across all plates tended to decrease as the angle of bore propagation increased (Fig. 7c).

4. DISCUSSION

In this study, we show that during the largest chthamalid barnacle settlement pulse of the year at a site in Baja California, Mexico, changes in the number of settlers in the intertidal were correlated with changes in the time-integrated high-frequency internal variability, which we term intensity, of the nearshore water column. Positive and significant correlations between the number of settlers and the short-term, high-frequency variability in mid-depth temperature, stratification, and surface flows suggest that internal waves can affect not only the timing of settlement, as has been shown previously, but also the number of larvae arriving at intertidal habitats.

The internal wave field for Todos Santos Bay in Baja California, Mexico, has been well characterized as strong and spatially variable over small scales in summer, with internal waves generally propagating from S-SW to N-NE (Filonov et al. 2014), similar to what we show herein. Internal waves have often

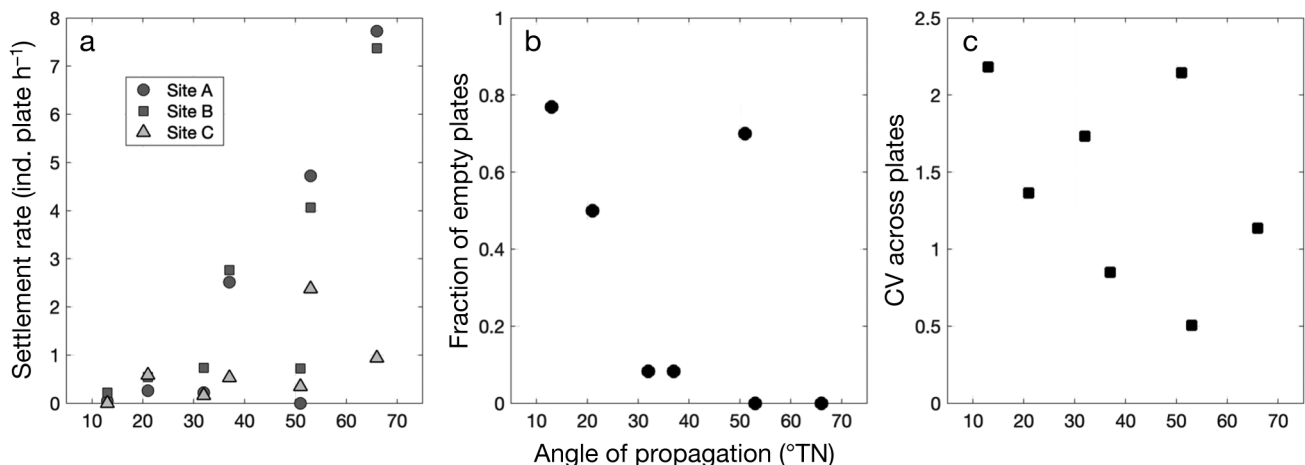


Fig. 7. Changes in the spatial pattern of *Chthamalus* spp. settlement as a function of the angle of propagation estimated for each internal tidal bore event detected in the nearshore during this study. (a) Mean settlement rates of *Chthamalus* spp. larvae at each site, (b) change in the fraction of empty plates recovered from all 3 sites after each event, and (c) coefficient of variation in settlement across all plates as a function of the angle of propagation of the tidal bore

been invoked to explain the onshore transport of larvae (e.g. Shanks 1995, Lamb 1997, Pineda 1999), and studies conducted in this region have documented a correlation between the timing of barnacle settlement and the occurrence of internal motions in the nearshore (Pineda & López 2002, Ladah et al. 2005, Valencia-Gasti & Ladah 2016). However, a significant relationship between the number of larvae that settle and the cumulative high-frequency fluctuations in the water column at daily scales was an unexpected and, to our knowledge, entirely novel result.

We have only presented data on the settlement of *Chthamalus* spp. at the Baja California site, as settlement of other intertidal barnacles found in the area occurred in numbers that were too low for analysis. However, at the site further north (La Jolla, Southern California), where barnacles settle at much greater rates than in Baja California (Pineda & López 2002), *Chthamalus* spp. settlement was also highly correlated with cumulative mid-water internal variability, whereas no such correlation was found for *Balanus glandula*, even though the larvae of both species had very similar horizontal distributions in the inner shelf at that time (Tapia & Pineda 2007). Differences in the way behavior and nearshore physics interact to determine settlement patterns in chthamalid versus balanid barnacles may explain these results and have been previously suggested by studies conducted at similar latitudes on the Chilean coast (Lagos et al. 2005, Bonicelli et al. 2016).

The correlation found between settlement rates at sites A and B and the angle of propagation estimated for internal wave events is intriguing. It suggests that not only intensity but also the spatial pattern of physical forcing may shape the spatio-temporal pattern of larval delivery to shore. Events that propagated at an angle closer to the E–W axis were associated with higher settlement rates. In contrast, those that came from the S–SW and approached the shore at angles <30° (relative to geographic North), coincided with lower settlement rates at sites A and B and greater spatial heterogeneity in settlement across sites. Sites A and B are located within a small, more gently sloping embayment, where retention of surface material is often observed (our pers. obs.) and where surface wave heights are generally reduced, whereas site C corresponds to a point where surface waves are generally much larger, and where depth increases more abruptly offshore. The relationship between settlement patterns and the directionality of physical forcing by internal motions, and how these factors interact with other complex, small-scale nearshore hydrodynamics such as surf zone width, nearshore

topographic features, alongshore flow, and surface wave height at these smaller spatial scales, certainly merits further study.

In summary, during a 10 d settlement peak consisting of almost a third of yearly settlement at a study site in Baja California, Mexico, the rate of *Chthamalus* spp. settlement was correlated with the amount of high-frequency variability in nearshore stratification and mid-depth temperature here termed internal wave intensity. This pattern held for the same barnacle species at a site further north in California, but not for a similar species with different behavior. Our findings support the idea that internal motions not only set the timing of larval arrival at the shoreline, which has long been established, but also suggest that their intensity might determine the number of settlers delivered to intertidal habitats for some species. This hypothesis merits further exploration. A more quantitative understanding of the relationship between physical conditions and larval availability over the area where internal wave accumulation and transport might occur, and their connection with small-scale patterns in larval distribution, behavior, delivery to the shore, competency to settle, and actual settlement, will improve our ability to monitor and manage many important coastal marine populations in the future.

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