



Onshore transport of plankton by internal tides and upwelling-relaxation events

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ABSTRACT: Identifying biophysical mechanisms of larval transport is essential to understanding the delivery of larvae to adult habitats. In addition, harmful algal blooms (HABs) can be transported onshore from populations that form offshore. In summer 2011, we measured sea surface and bottom temperatures and daily phytoplankton abundance and intertidal cyprid (barnacle post larvae) settlement at Carmel River State Beach, California, USA. Using time-series analysis, we compared the abundance of *Pseudo-nitzschia* spp. and daily cyprid settlement to physical forcing mechanisms (e.g. internal tides and upwelling-relaxation events) that could generate onshore delivery. Minimum bottom water temperature was significantly cross-correlated with the spring–neap tidal cycle; minimum temperatures occurred between neap and spring tides, and maximum temperatures were recorded around neap tides. When the temperature data were transformed to remove the relationship between tides and temperature, we found significantly higher maximum sea surface temperatures during upwelling-relaxation events. We observed 4 pulses in *Pseudo-nitzschia* spp. abundance. *Pseudo-nitzschia* spp. chains were longest at the start of pulses and then decreased, suggesting that they had been transported to shore from a more productive site offshore, likely the upwelling front. Pulses occurred during periods of maximum sea surface temperature associated with upwelling-relaxation events. In contrast, cyprid settlement was significantly cross-correlated with the spring–neap tidal cycle, with settlement peaks occurring during fortnightly periods of cold bottom temperatures; onshore transport of cyprids appears to have been due to the internal tides.

KEY WORDS: Internal waves · Recruitment · Harmful algal bloom · HAB · *Pseudo-nitzschia* · Cyprid · Settlement

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INTRODUCTION

As part of a study of the effect of surf zone hydrodynamics on the delivery of larvae to the shore, we made daily measurements of the concentration of phytoplankton in the nearshore ocean and the surf zone and followed barnacle settlement at 2 sites. Concurrent with this sampling, we collected physical

oceanographic data. These data are being used to investigate surf zone hydrodynamics and the delivery of larvae to the shore, but they also allowed us to investigate at the same place and time the mechanisms of cross-shelf transport of barnacle post larvae (cyprids) and phytoplankton including the harmful algal bloom (HAB) species *Pseudo-nitzschia* spp.; the cyprids appear to have been transported by the inter-

nal tides, whereas phytoplankton transport appears to have been due to upwelling-relaxation events.

Larval settlement is a key determinant of the dynamics and structure of marine populations and communities. Due to the effect of changing ocean conditions on larval production, survival, and transport, settlement is highly variable in space and time (Morgan 1995, Underwood & Keough 2001, Shanks et al. 2010). Identifying the biophysical mechanisms that govern larval transport is essential to understanding how variation in ocean conditions affects recruitment to adult habitats and, ultimately, community structure. For example, if larvae are transported to shore by upwelling-relaxation events, then, in space, settlement may be higher in areas with less persistent upwelling and, in time, settlement would be highest during upwelling-relaxation events (Connolly et al. 2001). Determining the multiple processes returning larvae to adult populations is especially important in recruitment-limited regions where larval supply more strongly influences the distribution and abundance of adults than in regions of high settlement where density-dependent effects on post-settlement mortality play a more important role in structuring adult populations (Morgan 2001, Underwood & Keough 2001).

In upwelling regions, blooms of phytoplankton, including harmful algal species, often form offshore (Gentien et al. 2005, Adams et al. 2006). HABs that remain offshore can pose a threat to sea birds and marine mammals (Fryxell et al. 1997) but pose little threat to humans. However, if blooms are transported to shore, they can pose serious health risks for humans by contaminating shellfish (Tilstone et al. 1994, Adams et al. 2006). A capacity to predict when blooms might be transported to shore could assist management of coastal shellfish resources and minimize the health threat posed by HABs.

Larvae and phytoplankton can be transported shoreward by a variety of mechanisms (Queiroga et al. 2007). Comparisons of the biological and hydrographic time series collected for this paper identified 2 dominant transport mechanisms: transport during upwelling-relaxation events and transport by internal tides.

In regions of strong wind-driven coastal upwelling, Equatorward winds combined with the Coriolis force push surface waters toward the Equator and offshore (Ekman transport) while cold, nutrient-rich bottom waters upwell along the shore, generating high productivity. The cold upwelled waters push the warmer, less dense surface waters offshore, generating an upwelling front (Bowman & Esaias 1978). Phytoplankton blooms, including HABs, tend to form

around the front where upwelling provides a steady supply of nutrients and the upwelling front provides a stable shallow mixed layer (Tweddle et al. 2010). In addition, it has been hypothesized that zooplankton (holo- and meroplankton) in surface waters may be advected offshore by upwelling and accumulate at the upwelling (Parrish et al. 1981, Roughgarden et al. 1988, Shanks 1995). When upwelling winds weaken (relax) or reverse, the upwelling front moves shoreward and can transport larvae (Shanks et al. 2000, Narváez et al. 2006) as well as phytoplankton (Tilstone et al. 1994, Adams et al. 2006) associated with the front shoreward. Thus, episodic settlement of invertebrates and the arrival of HABs at the coast have been hypothesized to be due to onshore transport during upwelling-relaxation events (Yoshioka 1982, Roughgarden et al. 1988, Farrell et al. 1991).

As the tide ebbs off the continental shelf, large internal waves are generated at the shelf break (Osborne & Burch 1980). When the tide changes to flood, these internal waves propagate toward shore as the internal tide (Haury et al. 1979, Shearman & Lentz 2004). The internal tide takes the form of large internal waves and bores, which are common along all continental shelves (Chereskin 1983). The amplitude of these internal waves varies directly with the amplitude of the surface tides; larger surface tides generate larger internal waves (Winant 1974, Holloway et al. 1997, Trevorrow 1998). The internal tides can transport both larvae (Shanks 1983, 1988, Kingsford & Choat 1986, Pineda 1991, 1994, Leichter et al. 1998) and phytoplankton shoreward (Omand et al. 2011). Shanks & McCulloch (2003) found that peaks in abundance of *Pseudo-nitzschia* spp. at the shore were cross-correlated with warm water events associated with the internal tides; warm, offshore water and associated phytoplankton were transported onshore by the internal tides. Ryan et al. (2005) described the concentration of a dinoflagellate bloom by the passage of large internal waves in Monterey Bay, California (USA); the very high concentration of phytoplankton in the internal waves suggested that transport of phytoplankton occurred. Omand et al. (2011) presented a detailed description of the transport of a dinoflagellate bloom to the shore by internal waves.

Each of these onshore transport mechanisms has a different physical signature and can be detected by establishing the relationship between physical variables and peaks in the abundance of settlers on the shore or phytoplankton at the coast. In the nearshore waters and surf zone, we made daily measurements of the concentration of cyprids and the HAB species *Pseudo-nitzschia* spp., and in addition, we made dai-

ly measurements of barnacle settlement in the intertidal zone. We then inferred mechanisms of onshore transport by statistically comparing the time series of settlers and phytoplankton concentrations to ocean conditions. If cyprids and phytoplankton were directly advected onshore by the wind, then pulses of these organisms should occur during onshore wind events. If they were transported onshore by the internal tides, either at the surface in internal wave convergences, in internal bores, or by upwelling fronts generated by the tides, then we should see a cross-correlation between the maximum daily tidal range and their abundance. The internal tides produce both cold and warm bores (Pineda 1995, Wolanski & Delesalle 1995, Leichter et al. 1996), and hence, the abundance of cyprid settlers or phytoplankton may vary with cold and warm events, which in turn vary with the fortnightly periodicity of the tides. If onshore transport occurs during upwelling-relaxation events, then plankters should arrive in pulses of warm water after upwelling-favorable winds weaken or reverse direction, allowing the warm surface waters that had been pushed offshore by upwelling to move onshore.

MATERIALS AND METHODS

The study was conducted at Carmel River State Beach (CRSB) in central California ($36^{\circ}32'18''\text{N}$, $121^{\circ}55'43''\text{W}$; Fig. 1). CRSB is a pocket beach that is located within Carmel Bay at the mouth of the Carmel River. Rocky outcrops occur at both ends of the beach, and a large kelp bed was situated offshore of the northern end of the beach. Small kelp beds were also present off the southern end of the beach. The Carmel Submarine Canyon, an arm of the Monterey Submarine Canyon, runs the length of Carmel Bay.

From 11 June through 18 July 2012, barnacle settlement was measured on plots (100 cm^2) on rocks at the southern and northern ends of the beach (Fig. 1). Three plots were monitored at each sample site. Plots were cleared with a wire brush before the start of the time series. Counts were made daily using a hand lens ($10\times$ magnification) during daytime low

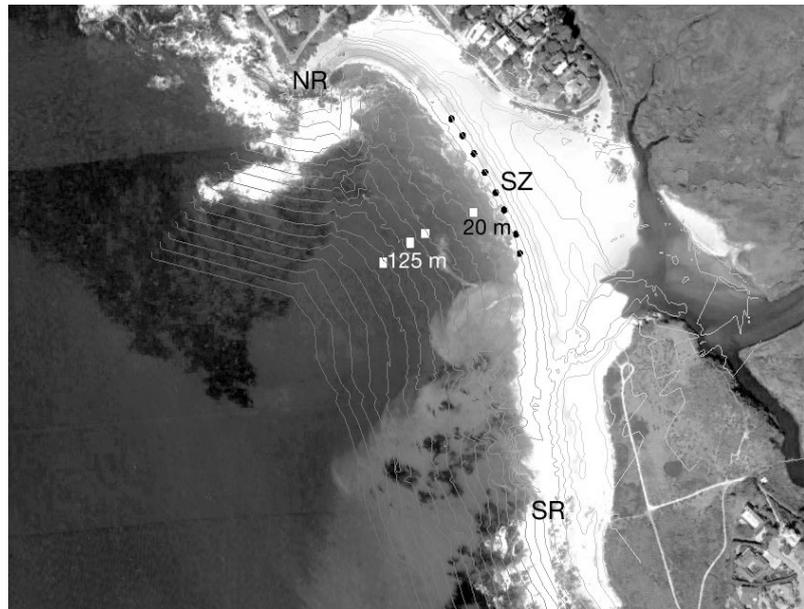


Fig. 1. Study site at Carmel River State Beach, California, USA. Barnacle settlement was measured on the rocks to the north and south of the beach (NR and SR, respectively). Phytoplankton samples were also collected at these sites. Zooplankton and phytoplankton samples were collected with a pump in the surf zone of the beach (SZ) and offshore at the 125 m mooring. Sea surface and near bottom temperatures were measured at the most offshore mooring (white squares). Filled circles along the shore indicate locations of additional sensors, from which data were not used in this study. The darker water seaward of the NR site is a large kelp bed. A smaller bed was present off the SR site. Modified from a Google Earth image

tides, and new settlers were removed with a toothbrush.

From 15 June through 15 July, plankton samples were collected daily inside the surf zone and at a station about 125 m offshore (Fig. 1). Surf zone samples were collected with a pump system. A hose (6 cm diameter) attached to pipes that were jetted into the sand was run through the surf zone from the beach. A gas-powered pump sampled about 240 l of water per min for 10 min resulting in 1.2 m^3 of water being filtered for each of 3 replicate samples collected daily. Samples were collected around high tide, at which time the intake was usually located ca. 1 m seaward of the breaking waves. Samples were filtered through a net ($200\text{ }\mu\text{m}$ mesh) that was suspended in a water-filled box. Three replicate phytoplankton samples (1 l) were collected from the pump system. In the rocky shore surf zone to the north and south of the beach (Fig. 1), 3 replicate phytoplankton samples (1 l) were collected by casting a well sample bailer into the surf. Samples were collected approximately 10 m from shore.

Offshore samples were collected in the morning before the onset of stronger afternoon winds. Zoo-

plankton was collected using a net (200 μm mesh, 0.25 m^2 diameter mouth) equipped with a flow meter. Three replicate zooplankton samples were collected daily by hauling the net from near the bottom to the surface of the water column filtering an average of 2 m^3 of water. Three replicate phytoplankton samples (1 l) were collected from approximately 5 m depth using a well sampling bailer. Zooplankton and phytoplankton samples were preserved in buffered formaldehyde and acid Lugol's solution, respectively.

Zooplankton was enumerated using dissecting microscopes following the techniques used by Shanks & Shearman (2009). Briefly, we washed the samples free of formalin and then added water to the sample until it reached 200 ml. After agitating the sample, an aliquot was taken with a Stempel pipette. Aliquots were counted serially until about 200 cyprids had been enumerated. This yielded a sample standard deviation of about 10% (Venrick 1978). Cyprids were identified using an identification guide to west coast larval invertebrates (Shanks 2001). *Pseudo-nitzschia* spp. were identified to genus and counted using standard techniques (Sournia 1978).

Measuring chain length of the *Pseudo-nitzschia* spp. provided valuable information. Four pulses of *Pseudo-nitzschia* spp. occurred during the study. During these pulses, the concentration of *Pseudo-nitzschia* spp. increased by a factor of from 3 to 6 times in a day. The increase was too rapid to be accounted for by growth of the local population (Parson et al. 1984), suggesting that these pulses were likely due to the transport of a population into the study area. We present evidence suggesting that phytoplankton was transported to shore during upwelling-relaxation events. If this was the case, then the *Pseudo-nitzschia* spp. may have been transported from a habitat favorable to their growth, viz. the upwelling front, to one less favorable to their growth, i.e. Carmel Bay. Under favorable growing conditions, *Pseudo-nitzschia* spp. produce long chains, but under poor growing conditions, i.e. low nutrient concentrations, chains break up (Fryxell et al. 1997). We measured chain length starting on the first day of each pulse and for 3 d after.

Temperature was recorded every 5 s from 9 June to 19 July 2011 by CTDs moored near the bottom and surface

of the water column. The mooring was located approximately 150 m from shore (Fig. 1). Time series of wind speed and direction were obtained from the NOAA National Data Buoy Center buoy 46042 located seaward of the mouth of Monterey Bay. Using these data and standard equations (Pedlosky 1987), hourly along- and cross-shore wind stresses were calculated and averaged to obtain daily wind stresses. Because a constant drag coefficient was used, values should be considered pseudo-wind stresses. We cross-correlated the time series of minimum daily bottom temperature with the daily along-shore wind stress and the maximum daily tidal range to determine whether wind-driven upwelling and/or the internal tides may have delivered cold water onshore. We also cross-correlated sea surface temperature with the alongshore wind stress and the maximum daily tidal range to determine whether upwelling-relaxation and/or large internal waves may have delivered warm water onshore.

Relationships between physical variables (wind stress, surface maximum daily temperature, bottom minimum daily temperature) and daily cyprid settlement and *Pseudo-nitzschia* spp. concentration were analyzed with cross-correlations, a standard time series technique (Emery & Thomson 1997). Prior to running cross-correlations, settlement densities and *Pseudo-nitzschia* spp. concentrations were log transformed. Because the abundance of *Pseudo-nitzschia* spp. increased over the course of the time series, the

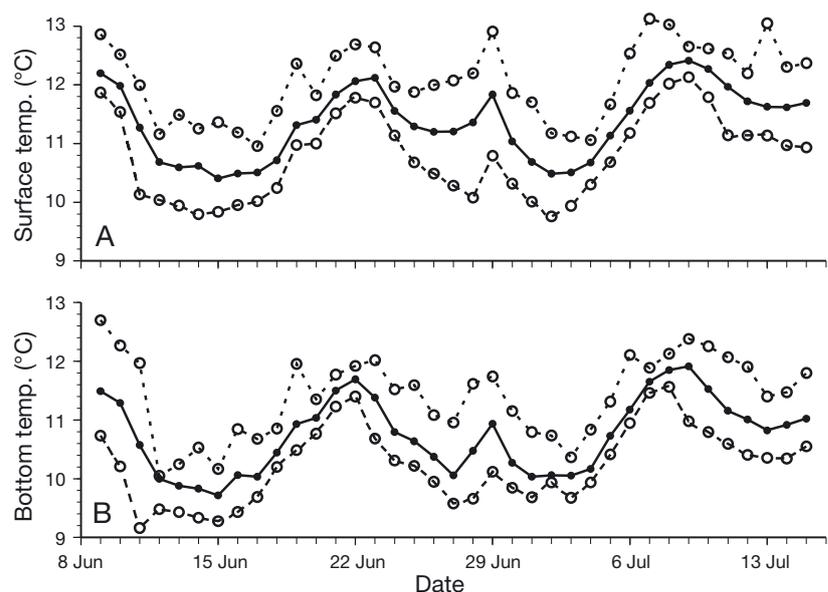


Fig. 2. (A) Sea surface and (B) bottom temperature at a station 150 m offshore from Carmel River Beach in 10 m of water. Plotted in each panel is the average daily temperature at each depth (solid line, closed circles) and the minimum and maximum daily temperature (open circles, dashed lines).

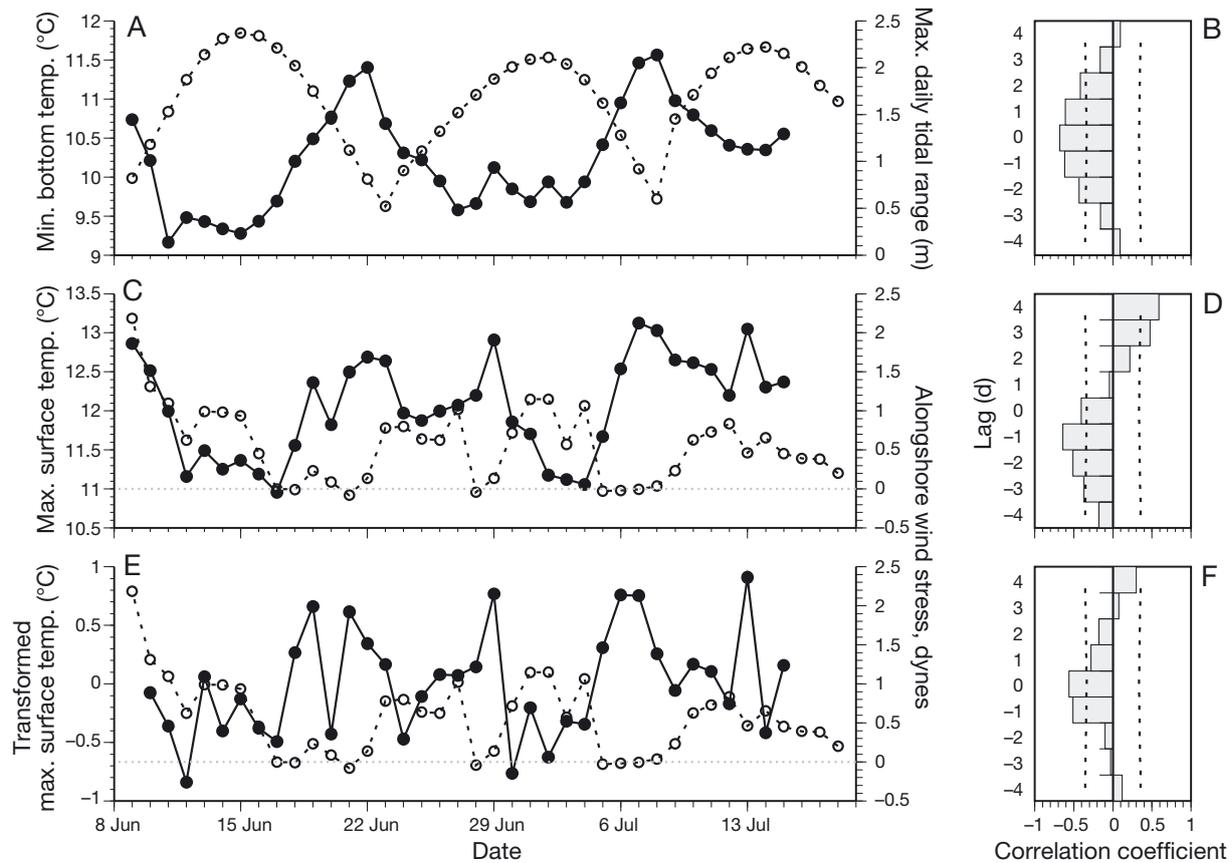


Fig. 3. (A) Minimum daily bottom temperature (solid line, closed circles) plotted with the maximum daily tidal range (dashed line, open circles). (B) Results of a cross-correlation between the maximum daily tidal range and the minimum bottom temperature. (C) Maximum daily sea surface temperature (solid line, closed circles) plotted with the alongshore wind stress (dashed line, open circles). (D) Results of a cross-correlation between the alongshore wind stress and the maximum sea surface temperature. (E) Transformed (see 'Materials and methods') maximum daily surface temperature (autocorrelation due to the effect of the tidal range on temperature was removed) (solid line, closed circles), plotted with the average daily alongshore wind stress (dashed line, open circles). (F) Results of a cross-correlation between the alongshore wind stress and the transformed (see 'Materials and methods') maximum bottom temperature. Positive values of alongshore wind stress, values above the horizontal dashed line, indicate upwelling-favorable winds, and wind stress near 0 or negative indicates upwelling-relaxation events. In (B), (D), and (F) the vertical dashed lines represent the 95% confidence interval. Bars that extend beyond these lines indicate significant ($p < 0.05$) correlation coefficients

data were also detrended. Because maximum daily sea surface temperature co-varied with the tidal amplitude cycle, the fortnightly periodicity was removed from the temperature time series by removing the autocorrelation in the data set. The biological and physical data were cross-correlated by holding the physical time series stationary while the biological data were lagged.

RESULTS

Physical data

At both the surface and bottom, water temperature varied in a regular pattern (Fig. 2). Temperatures were high at the start of the time series and around 22

June and 9 July and they were low around 12 June and 2 July. If internal tidal bores (cold or warm bores) were present during the study, they should appear as cold or warm water events cross-correlated with the fortnightly spring–neap tidal cycle. Cold events should be most apparent at the bottom thermistor. Indeed, the minimum daily bottom temperature varied with the spring–neap tidal cycle (Fig. 3A). Between the neap and spring tides, temperatures dropped such that minimum temperatures tended to occur around spring tides. At or shortly after spring tides, minimum bottom temperature rose, with the warmest water present around neap tides. This relationship was supported by significant negative cross-correlations between the maximum daily tidal range and the minimum bottom temperature (Fig. 3B). A similar pattern was apparent in the surface temperature data (Fig. 2).

Maximum sea surface temperature appeared to be influenced by both the internal tides and upwelling-relaxation events (cf. Fig. 3A,C). Significant cross-correlations were found between the maximum daily tidal range and maximum sea surface temperature ($r = -0.419$ to -0.555 , $p < 0.05$, at lags of 0 to -2 d, graph not presented), with peak sea surface temperatures occurring around neap tides. In addition, alongshore wind stress and the maximum daily sea surface temperature were significantly cross-correlated (Fig. 3D), with higher sea surface temperatures occurring at and several days after upwelling-relaxation events (negative cross-correlations) and lower sea surface temperatures occurring several days after upwelling-favorable winds (positive cross-correlations). We found significant negative cross-correlations at lags of -1 and 0 d; warm water events

occurred during or just after upwelling-relaxation events.

Barnacle settlement

During the entire 39 d sampling period, we observed only 1 barnacle cyprid settle at the North rocks site (Fig. 4A); this 1 settler was observed during a pulse in barnacle settlement at the South rocks site. At the South rocks site, barnacle settlement was low but consistent (Fig. 4A). Settlement at this site was not correlated with the abundance of cyprids 125 m offshore of the study site or the abundance of cyprids in the pump samples from the surf zone ($r = 0.08$, $p > 0.10$, $n = 28$; $r = 0.245$, $p > 0.10$, $n = 28$, respectively). Settlement was also not significantly cross-correlated

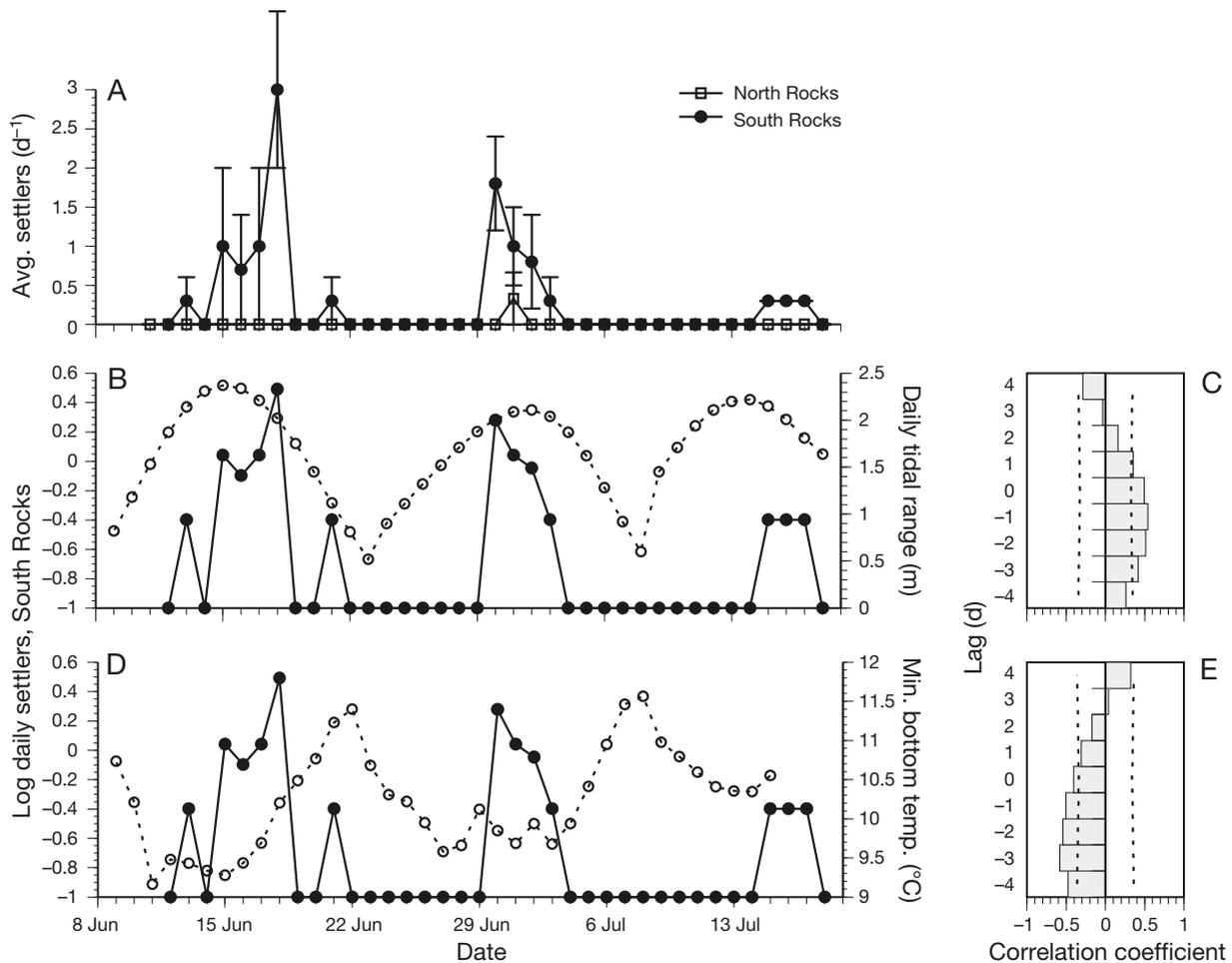


Fig. 4. (A) Average daily barnacle settlement ($\pm 95\%$ confidence interval) on the North (open squares) and South (closed circles) rocks. (B) Log of the daily barnacle settlement on the South rocks (solid line, closed circles) plotted with the maximum daily tidal range (dashed line, open circles). (C) Results of a cross-correlation between the maximum daily tidal range and the log of the daily settlement on the South rocks. (D) Log of the daily barnacle settlement on the South rocks (solid line, closed circles) plotted with the minimum daily bottom temperature (dashed line, open circles). (E) Results of a cross-correlation between the minimum daily bottom temperature and the log of the daily settlement on the South rocks. In (C) and (E), the dashed lines represent the 95% confidence interval. Bars that extend beyond these lines indicate significant ($p < 0.05$) correlation coefficients

with the average daily wave height ($r = 0.288$, $p > 0.05$, $n = 39$). Settlement varied with the tidal amplitude cycle (see below), which may obscure the relationship between settlement and wave height. We, therefore, removed the fortnightly signal in settlement by removing the autocorrelation in these data, but settlement still was not significantly correlated with wave height ($r = 0.079$, $p > 0.10$, $n = 39$). We observed 3 pulses in settlement (Fig 4B) that occurred 0 to 3 d after spring tides; settlement was significantly cross-correlated with tidal amplitude (Fig. 4C). Settlement peaked as minimum bottom temperatures were beginning to rise (Fig. 4D), as evidenced by negative cross-correlations at lags of 0 to -4 d (Fig. 4E).

Pseudo-nitzschia spp. abundance

The concentration of *Pseudo-nitzschia* spp. at the offshore station was positively correlated ($p < 0.001$) with the concentrations of all other enumerated phytoplankton genera including *Chaetoceros*, *Thalassionema*, *Skeletonema*, *Thalassiosira*, and *Rhizosolenia*. Thus *Pseudo-nitzschia* spp. are representative of the phytoplankton community, the members of which appeared to be responding in a similar way to the changing ocean conditions.

The concentration of *Pseudo-nitzschia* spp. increased steadily during the study period, and superimposed on this increase were 4 pulses in the

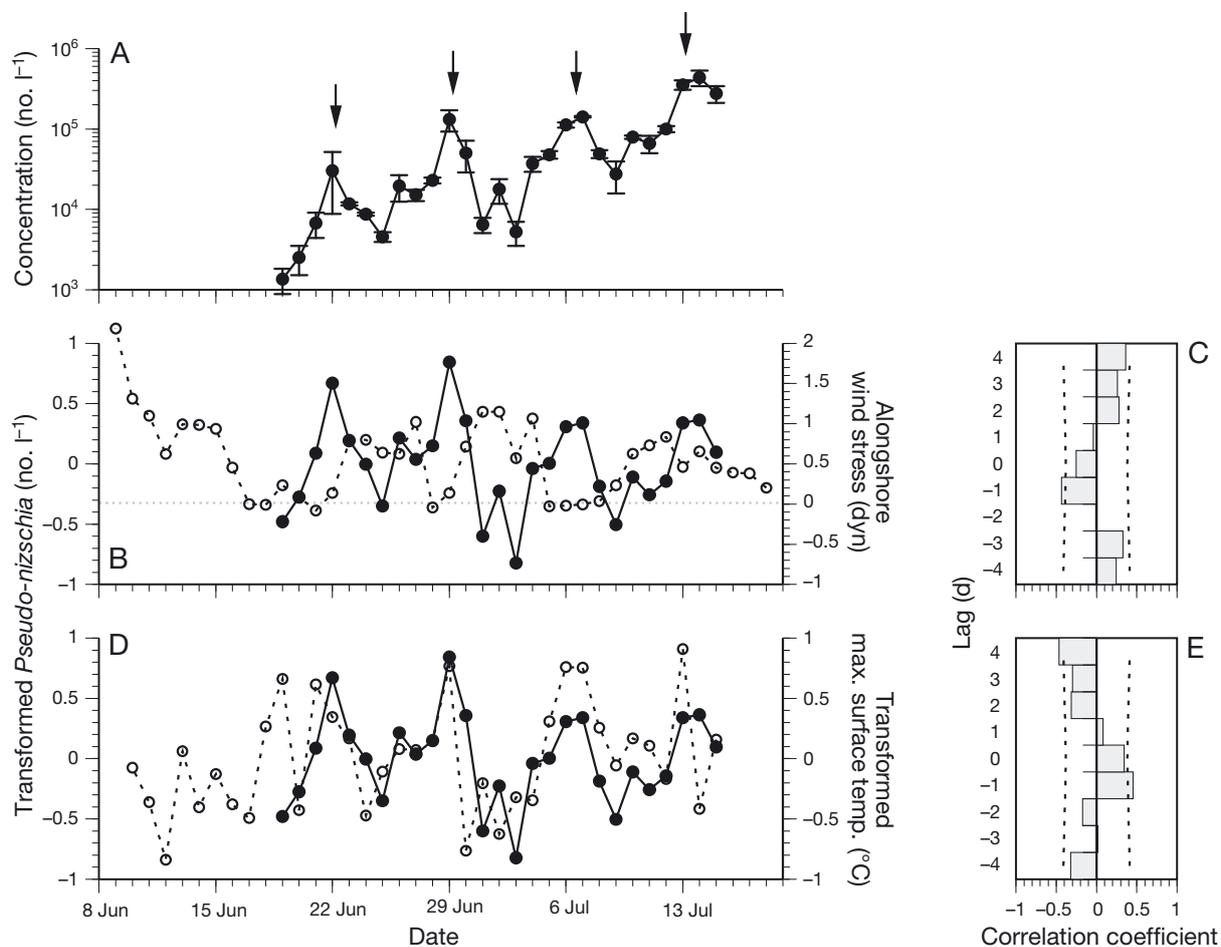


Fig. 5. *Pseudo-nitzschia* spp. (A) Average nearshore daily concentration ($\pm 95\%$ confidence interval). Arrows indicate pulses in the abundance of *Pseudo-nitzschia* spp. when the increase in abundance was larger than could be due to growth of the population, suggesting that advection had carried cells to the site. (B) Log-transformed and detrended concentration (solid line, closed circles) plotted with the average daily alongshore wind stress (dashed line, open circles). Positive values of alongshore wind stress, values above the horizontal dashed line, indicate upwelling-favorable winds, and wind stress near 0 or negative indicates upwelling-relaxation events. (C) Results of a cross-correlation between the alongshore wind stress and the log-transformed and detrended *Pseudo-nitzschia* spp. concentration. (D) Log-transformed and detrended concentration (solid line, closed circles) plotted with the transformed maximum daily surface temperature (the autocorrelation due to the effect of the tidal range on temperature was removed) (dashed line, open circles). (E) Results of a cross-correlation between the transformed maximum daily surface temperature and the log-transformed and detrended *Pseudo-nitzschia* spp. concentration. In (C) and (E), the dashed lines represent the 95% confidence interval. Bars that extend beyond these lines indicate significant ($p < 0.05$) correlation coefficients

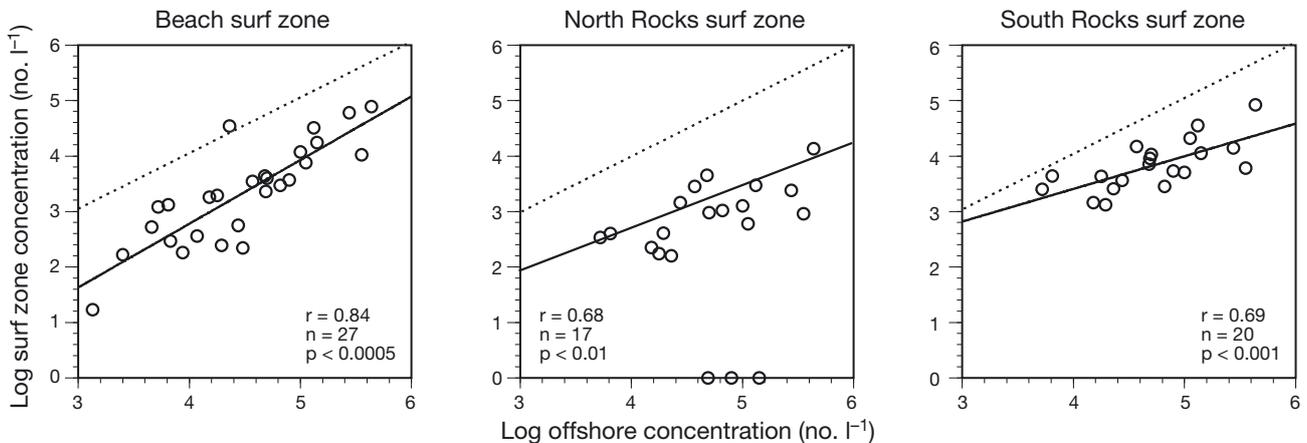


Fig. 6. Log of the concentration of *Pseudo-nitzschia* spp. in samples collected 125 m offshore plotted against the log of their concentration in the surf zones. Dotted line represents a one to one relationship between the variables; note that nearly all data points fall well below this line. Results from a correlation analysis are represented by the solid line and statistical results. The correlation between offshore phytoplankton concentration and that in the North rocks surf zone was done without the 3 outlying data points when the surf zone concentration was 0. If all the data are used, the correlation is not significant

abundance of *Pseudo-nitzschia* spp. (Fig. 5A). The increase in concentration during each of the pulses was too rapid (populations increased by a factor of 3 to 6 times in a day) to have been caused by population growth; the population increases were likely due to transport of phytoplankton into the area. The concentration of *Pseudo-nitzschia* spp. at each of the surf zone sample sites was much lower than offshore (Fig. 6), usually only a small percentage of that seen offshore. Despite the much lower concentrations, the same pulses in phytoplankton abundance were apparent at these surf zone sites as indicated by the significant correlations between concentrations offshore and in the surf zones (Fig. 6).

Peaks in *Pseudo-nitzschia* spp. abundance tended to occur during upwelling-relaxation events when upwelling-favorable winds were weak (Fig. 5B), and this is supported by a significant negative cross-correlation at a lag of -1 d (Fig. 5C). The transformed *Pseudo-nitzschia* spp. time series was then cross-correlated with the transformed maximum surface temperature time series. Peaks in *Pseudo-nitzschia* spp. abundance tended to occur during periods of higher sea surface temperature (Fig. 5D), and this was supported by a significant positive cross-correlation at a lag of -1 d (Fig. 5E).

Chain length was measured at the peak of each pulse event and on 3 d following the peak (Fig. 7). In 3 out of the 4 cases, the percentage of chains >2 cells long was higher at the peak than on the subsequent days, and the percentage of chains only 1 cell long was lowest at the peak and increased over time.

DISCUSSION

Potential transport mechanisms

Variations in ocean temperature at our study sites were correlated with both the tidal amplitude cycle and alongshore winds; both the tides and winds produce potential mechanisms for transporting water as well as zoo- and phytoplankton onshore. Internal tidal waves are trapped and intensified in Monterey Canyon as they propagate toward the canyon head (Kunze et al. 2002, Hall & Carter 2011), which can result in very large internal waves as has been reported for other submarine canyons (Gordon & Marshall 1976). Internal waves propagating up the Carmel Canyon should behave similarly, and the waves could transport water into the study area; this likely generated the fortnightly variation in temperature at our mooring. Pineda (1995) described fortnightly cycles in tidally driven upwelling at a number of sites along the west coast of North America, including Pacific Grove, which is located just north of Carmel Bay and adjacent to the Monterey Submarine Canyon. The summer cycle in temperature at Pacific Grove is nearly identical to that observed in Carmel Bay. At both sites, seawater temperatures reach a minimum around spring tides and a maximum around neap tides.

Our thermistors were in shallow water (10 m depth) where the signature from the internal tides is likely highly modified by interaction with the bottom, making interpretation of the data more difficult. More importantly, we had a chain of only 2 thermistors, and this did not provide enough vertical resolution to de-

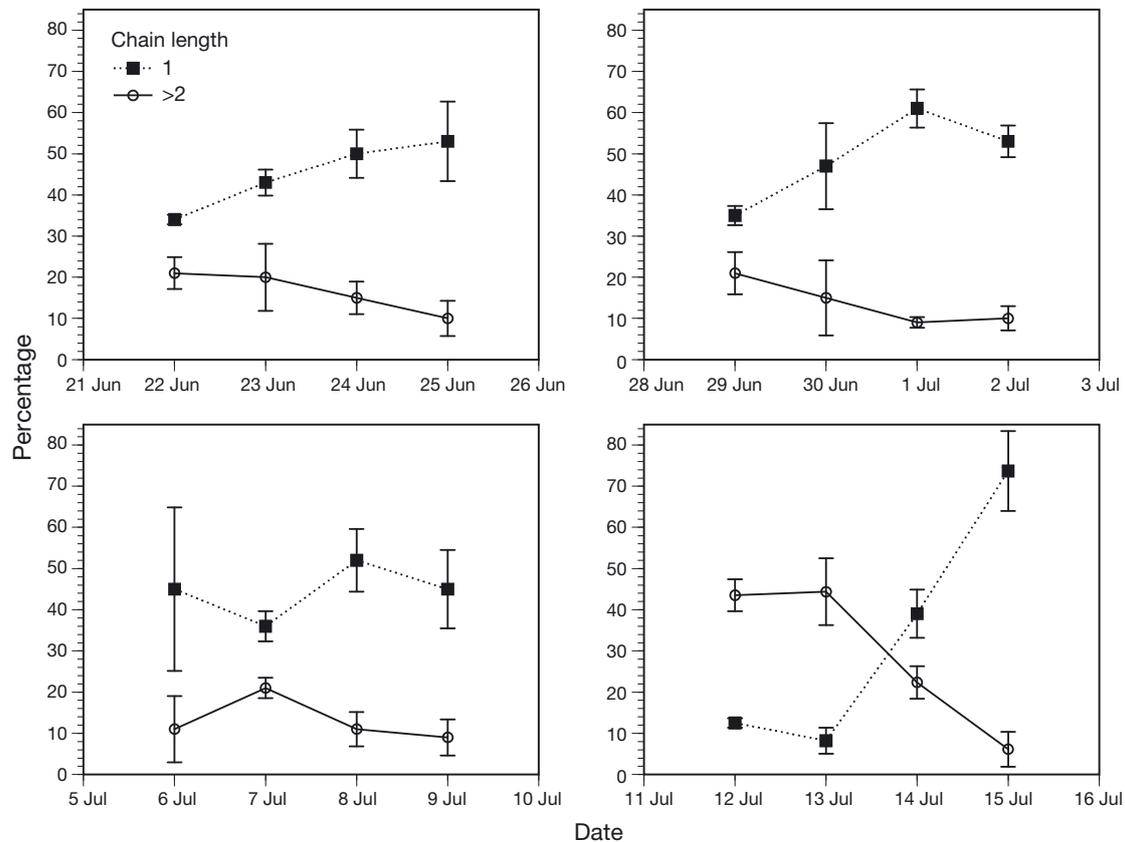


Fig. 7. *Pseudo-nitzschia* spp. Change in chain length following each of the 4 pulses in their abundance. Each data set starts with the first day of the pulse. Values are the average of 3 replicates \pm 95% confidence intervals

fine the shape of internal waves or bores passing the mooring. Given what has been observed at other locations (Pineda 1995, Kunze et al. 2002, Hall & Carter 2011), we hypothesize that during the period of falling temperatures, temperature was driven down by cold internal tidal bores propagating up the canyon and onto the shelf. As tidal energy decreased following the spring tide, the internal waves likely became smaller, causing less disruption of the thermocline until the thermocline reformed near neap tide (Cairns & LaFond 1966, Kropfli et al. 1999), whereupon the internal waves were evident as waves of depression on the thermocline (Lee 1961). We hypothesize that these waves transported warm water up the canyon and onto the shelf, generating the warm periods in the fortnightly temperature cycle.

Carmel Bay is oriented roughly perpendicular to prevailing northwesterly winds of spring and summer. These winds produce upwelling along the open coast and at the mouth of the bay but do not cause upwelling within the bay. Because the study site was located close to the head of Carmel Bay, it is unlikely that the pulses of cyprids and phytoplankton were due to alongshore transport; alongshore flow should

tend to move across the mouth of the bay rather than penetrate deeply into the bay. The temperature signal characteristic of upwelling and relaxation events was more subtle than that generated by the tides, making it necessary to remove the tidal signal to more clearly detect the effect of the wind on seawater temperature. Following this transformation, there was a clearer signal of pulses of higher temperatures occurring during upwelling-relaxation events. During relaxation events, the upwelling front and warm water seaward of the front propagate toward shore as gravity currents (Shanks et al. 2000). When this front propagates all the way to shore, the shore is bathed with warm water. Depending on the winds, relaxation events may be brief or last days. None of the events that we witnessed appeared to last longer than 2 d (Fig. 2).

Barnacle settlement

Both the North and South rocks sites are reflective surf zones, and settlement was orders of magnitude lower than has been observed on rocks at dissipative

beaches (Shanks et al. 2010). Our research (unpubl. data) suggests that the exchange of surfzone water with offshore water, which would enable competent larvae to cross the surf zone, is more efficient in dissipative than reflective surf zones. At dissipative beaches, the exchange of surfzone water with offshore water is highest during large wave events, resulting in greater barnacle settlement on rocks following these events (Shanks et al. 2010). In contrast, barnacle settlement was not related to wave height at the South rocks, a reflective shore. Lower cyprid settlement at reflective shores appears to be due to weaker onshore transport through the surf zone; the surf zone appears to impede the onshore transport of competent larvae.

Internal tides, rather than upwelling-relaxation events, appeared to have transported cyprids onshore. Seawater temperature at the study site varied with both the tidal amplitude and upwelling-relaxation cycles, indicating that either internal waves and bores or relaxation events could transport cyprids onshore. Relaxation events, however, did not appear to transport cyprids onshore because settlement was not correlated with either alongshore winds or pulses of warm seawater, both indicators of upwelling-relaxation events. In contrast, settlement was significantly cross-correlated with the spring-neap tidal cycle and with low surface and bottom seawater temperatures, both of which also varied with the spring-neap tidal cycle. We conclude that variation in barnacle settlement was not driven by shoreward transport of cyprids by upwelling-relaxation events, but rather was driven by their shoreward transport by the internal tides.

Although larvae can be transported shoreward either in an internal tidal bore (Pineda 1991, Leichter et al. 1998) or in the convergence over tidally generated internal waves (Shanks 1983, 1988), we do not have the data needed to differentiate between these 2 transport mechanisms. Large internal waves are usually associated with internal tidal bores, but we could not describe the shape of the waves or bores that passed our mooring, which only had thermistors near the surface and bottom of the water column. Settlement, however, clearly peaked following minimum temperatures during the spring tide as temperatures were beginning to rise. Thus, internal tides take a form that is conducive to the shoreward transport of cyprids soon after spring tides, as has been observed elsewhere along the west coast of North America (Shanks 1983, 1986, 2009, Pineda 1991, Lada et al. 2005).

We did not find a relationship between settlement and the abundance of cyprids sampled offshore

(125 m from shore) or in the adjacent sandy beach surf zone (about 100 m north). This is somewhat surprising, as others have noted a relationship between water column larval abundance and settlement rate (Bertness et al. 1996). The lack of a relationship in our data is likely due to the way in which we measured cyprid abundance and the mechanism of delivery of the cyprids to the shore (Pineda 2000). We measured water column cyprid abundance once per day from zooplankton samples collected offshore with a zooplankton net and in the surf zone from pump samples. In contrast, studies that have found a relationship between larval abundance and settlement rate have used sample methods that integrate larval abundance over all or much of a day (e.g. larval tube traps or intertidal larval traps; Bertness et al. 1996, Castilla & Varas 1998). The likely delivery mechanism active at our study site, i.e. internal waves or bores, would deliver pulses of larvae to the shore over brief intervals; the odds of our sampling zooplankton during these brief events is minimal, but a sampling mechanism that integrated larval abundance over much of the day would capture this signal and, if we had used an integrative sampling system, we may have found significant correlations between larval abundance and settlement.

Phytoplankton pulses

A phytoplankton bloom often forms around the upwelling front where cold upwelled water contacts the displaced warm surface waters. During downwelling or upwelling-relaxation conditions, cold upwelled water sinks and the warm surface water flows back toward shore as a gravity current (Simpson 1997). Shoreward transport of a phytoplankton bloom associated with the upwelling front during relaxation or downwelling events is likely one of the primary mechanisms for HABs in offshore waters to reach the coast. For example, work on the Washington coast indicates that HABs formed in the Juan de Fuca eddy were carried to the coast during downwelling events, during which they entered the surf zone and contaminated razor clams leading to closure of that fishery (Adams et al. 2006). A similar pattern of shoreward transport of an offshore bloom was observed in Spain (Tilstone et al. 1994).

At the coast, the arrival of an offshore bloom due to an upwelling-relaxation event would appear as an abrupt increase in phytoplankton concentration associated with warmer water, which is exactly what we saw. Peaks in abundance of *Pseudo-nitzschia* spp.

tended to occur during or a day after winds that would favor downwelling-relaxation events and during peaks in sea surface temperature that were likely the indication of the arrival of the upwelling front at the shore. When this occurs, phytoplankters are transported from ideal growing conditions at the front to less favorable conditions at the shore. At the front, chain-forming species should produce long chains as a result of vigorous growth. After they arrive at the shore, due to less favorable growing conditions, chain length may decrease. If this scenario is correct, then at the shore we should see maximum chain length at the beginning of a pulse and shorter chains thereafter. In 3 of the 4 pulses of *Pseudo-nitzschia* spp., chain length followed exactly this pattern, which is consistent with our interpretation that the pulses were due to shoreward transport from an offshore bloom.

The combination of data reported in this paper, detailed seawater temperature data from the study site, daily settlement of cyprids at 2 intertidal sites, daily measurements of cyprid abundance in the nearshore and surf zone, and daily phytoplankton abundance in the nearshore and within the surf zone, is unique and provided us with the opportunity to investigate at the same place and time the mechanisms of delivery to the shore of larvae of an intertidal organism (barnacle cyprids) and phytoplankton as represented by the HAB species *Pseudo-nitzschia* spp. A number of studies have presented data purported to demonstrate that cyprids are transported onshore by upwelling-relaxation events, reviewed by Shanks (2009), but these studies followed recruitment at weekly or longer intervals and suffer from aliasing as well as an unknown amount of mortality between settlement and the recruitment measurement (Shanks 2009). Many studies that have measured cyprid settlement daily have, however, found significant correlations between settlement and the fortnightly tidal cycle (Shanks 1986, 2009, Pineda 1991, Pineda & Caswell 1997, Ladah et al. 2005, Tapia & Navarrete 2010), suggesting that transport was due to the internal tides. These studies found weak or no evidence to support delivery of cyprids by upwelling-relaxation events, although Hawkins & Hartnoll (1982) observed higher settlement during onshore winds. A proponent of the hypothesis that upwelling-relaxation transports cyprids to shore might argue that relaxation events did not occur during those studies, which documented fortnightly periodicity in settlement. Here we have temperature data that clearly indicate that we had transport of water by the internal tides and by upwelling-relaxation events.

These 2 transport mechanisms are easily distinguished from one another due to the differential timing of their physical forcing (tidal cycle and wind direction, respectively). Both transport mechanisms were active at the study site, but cyprid delivery to the shore was only correlated to the fortnightly tidal cycle; delivery to the shore appears to have been due to the internal tides not upwelling-relaxation. The reverse was true for *Pseudo-nitzschia* spp.; this taxon and the associated phytoplankton community appeared to have been delivered to the shore by upwelling-relaxation events, not by internal tides.

This begs the question why cyprids would have been transported onshore by one mechanism while *Pseudo-nitzschia* was transported onshore by a different one. Recent studies have demonstrated that in the California Current, cyprids as well as the larvae of many intertidal invertebrates are primarily found within a few kilometers of shore (Shanks & Brink 2005, Morgan et al. 2009, Shanks & Shearman 2009). Our data suggest that cyprids were transported onshore by the internal tides and, at our study site, these were likely generated just offshore in the Carmel Submarine Canyon; the cyprids were likely present only close to shore as was the transport mechanism. In contrast, the likely source of the *Pseudo-nitzschia* was offshore at the upwelling front as has been seen in other locations (Gentien et al. 2005, Adams et al. 2006). This would place them well seaward of the likely generation site for the internal tides at this study site. At this distance from shore, the only active onshore transport mechanism would have been the upwelling front propagating toward shore during upwelling-relaxation events. In Oregon, USA, both cyprids and *Pseudo-nitzschia* were transported onshore by the internal tides, but in Oregon, internal waves are generated at the shelf break and, hence, both the likely source of the *Pseudo-nitzschia*, the upwelling front, and cyprids were in the path of internal waves.

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LITERATURE CITED

- Adams NG, MacFadyen A, Hickey BM, Trainer VL (2006) The nearshore advection of a toxigenic *Pseudo-nitzschia* bloom and subsequent domoic acid contamination of

- intertidal bivalves. *Afr J Mar Sci* 28:271–276
- Bertness MD, Gaines SD, Wahle RA (1996) Wind-driven settlement patterns in the acorn barnacle *Semibalanus balanoides*. *Mar Ecol Prog Ser* 137:103–110
- Bowman MJ, Esaias WE (eds) (1978) Oceanic fronts in coastal processes. Springer-Verlag, Berlin
- Cairns JL, LaFond EC (1966) Periodic motions of the seasonal thermocline along the southern California coast. *J Geophys Res* 71:3903–3915
- Castilla JC, Varas MA (1998) A plankton trap for exposed rocky intertidal shores. *Mar Ecol Prog Ser* 175:299–305
- Chereskin TK (1983) Generation of internal waves in Massachusetts Bay. *J Geophys Res* 88:2649–2661
- Connolly SR, Menge BA, Roughgarden J (2001) A latitudinal gradient in recruitment of intertidal invertebrates in the northeast Pacific Ocean. *Ecology* 82:1799–1813
- Emery WJ, Thomson RE (1997) Data analysis methods in physical oceanography. Elsevier Science, New York, NY
- Farrell TM, Bracher D, Roughgarden J (1991) Cross-shelf transport causes recruitment to intertidal populations in central California. *Limnol Oceanogr* 36:279–288
- Fryxell G, Villac M, Shapiro L (1997) The occurrence of the toxic diatom genus *Pseudo-nitzschia* (Bacillariophyceae) on the West Coast of the USA, 1920–1996: a review. *Phycologia* 36:419–437
- Gentien P, Donaghay P, Yamazaki H, Raine R, Reguera B, Osborn T (2005) Harmful algal blooms in stratified environments. *Oceanography* 18:172–183
- Gordon RL, Marshall NF (1976) Submarine canyons: internal wave traps? *Geophys Res Lett* 3:622–624
- Hall RA, Carter GS (2011) Internal tides in Monterey Submarine Canyon. *J Phys Oceanogr* 41:186–204
- Haurly LR, Briscoe MG, Orr MH (1979) Tidally generated internal wave packets in Massachusetts Bay. *Nature* 278:312–317
- Hawkins SJ, Hartnoll RG (1982) Settlement patterns of *Semibalanus balanoides* (L.) in the Isle of Man (1977–1981). *J Exp Mar Biol Ecol* 62:271–283
- Holloway PE, Pelinovsky E, Talipova T, Barnes B (1997) Nonlinear models of internal tide and internal solitary wave evolution over a continental slope. *Proc 7th Int Offshore Polar Eng Conf, Honolulu, HI. The International Society of Offshore and Polar Engineers, Honolulu, HI*, p 130–138
- Kingsford MJ, Choat JH (1986) The influence of surface slicks on the distribution and onshore movement of small fish. *Mar Biol* 91:161–171
- Kropfli RA, Ostrovski LA, Stanton TP, Skirta EA, Keane AN, Irisov V (1999) Relationships between strong internal waves in the coastal zone and their radar and radiometric signatures. *J Geophys Res* 104:3133–3148
- Kunze E, Rosenfeld LK, Carter GS, Gregg MC (2002) Internal waves in Monterey Submarine Canyon. *J Phys Oceanogr* 32:1890–1913
- Ladah LB, Tapia FJ, Pineda J, López M (2005) Spatially heterogeneous, synchronous settlement of *Chthamalus* spp. larvae in northern Baja California. *Mar Ecol Prog Ser* 302:177–185
- Lee OS (1961) Observations on internal waves in shallow water. *Limnol Oceanogr* 6:312–321
- Leichter JJ, Wing SR, Miller SL, Denny MW (1996) Pulsed delivery of subthermocline water to Conch Reef (Florida Keys) by internal tidal bores. *Limnol Oceanogr* 41:1490–1501
- Leichter JJ, Shellenbarger G, Genovese SJ, Wing SR (1998) Breaking internal waves on a Florida (USA) coral reef: a plankton pump at work? *Mar Ecol Prog Ser* 166:83–97
- Morgan SG (1995) Life and death in the plankton: larval mortality and adaptation. In: McEdward L (ed) *Ecology of marine invertebrate larvae*. CRC Press, Boca Raton, FL, p 157–192
- Morgan SG (2001) The larval ecology of marine communities. In: Bertness MD, Gaines SD, Hay ME (eds) *Marine community ecology*. Sinauer, Sunderland, MA, p 159–182
- Morgan SG, Fisher JL, Mace AJ, Akins LJ, Slaughter AM, Bollens SM (2009) Cross-shelf distributions and recruitment of crab postlarvae in a region of strong upwelling. *Mar Ecol Prog Ser* 380:173–185
- Narváez DA, Navarrete SA, Largier J, Vargas CA (2006) Onshore advection of warm water, larval invertebrate settlement, and relaxation of upwelling off central Chile. *Mar Ecol Prog Ser* 309:159–173
- Omand MM, Leichter JJ, Franks PJS, Guza RT, Lucas AJ, Feddersen F (2011) Physical and biological processes underlying the sudden surface appearance of a red tide in the nearshore. *Limnol Oceanogr* 56:787–801
- Osborne AR, Burch TL (1980) Internal solitons in the Andaman Sea. *Science* 208:451–460
- Parrish RH, Nelson CS, Bakun A (1981) Transport mechanisms and reproductive success of fishes in the California Current. *Biol Oceanogr* 1:175–203
- Parson TR, Takahashi M, Hargrave B (1984) *Biological oceanographic processes*. Pergamon Press, New York, NY
- Pedlosky J (1987) *Geophysical fluid dynamics*. Springer, New York, NY
- Pineda J (1991) Predictable upwelling and the shoreward transport of planktonic larvae by internal tidal bores. *Science* 253:548–549
- Pineda J (1994) Spatial and temporal patterns in barnacle settlement rate along a southern California rocky shore. *Mar Ecol Prog Ser* 107:125–138
- Pineda J (1995) An internal tidal bore regime at nearshore stations along western U.S.A.: predictable upwelling within the lunar cycle. *Cont Shelf Res* 15:1023–1041
- Pineda J (2000) Linking larval settlement to larval transport: assumptions, potentials, and pitfalls. *Oceanogr East Pac* 1:84–105
- Pineda J, Caswell H (1997) Dependence of settlement rate on suitable substrate area. *Mar Biol* 129:541–548
- Queiroga H, Cruz T, dos Santos A, Dubert J and others (2007) Oceanographic and behavioural processes affecting invertebrate larval dispersal and supply in the western Iberia upwelling system. *Prog Oceanogr* 74:174–191
- Roughgarden J, Gaines SD, Possingham H (1988) Recruitment dynamics in complex life cycles. *Science* 241:1460–1466
- Ryan JP, Dierssen HM, Kudela RM, Scholin CA and others (2005) Coastal ocean physics and red tides: an example from Monterey Bay, California. *Oceanography* 18:246–255
- Shanks AL (1983) Surface slicks associated with tidally forced internal waves may transport pelagic larvae of benthic invertebrates and fishes shoreward. *Mar Ecol Prog Ser* 13:311–315
- Shanks AL (1986) Tidal periodicity in the daily settlement of intertidal barnacle larvae and an hypothesized mechanism for the cross-shelf transport of cyprids. *Biol Bull (Woods Hole)* 170:429–440
- Shanks AL (1988) Further support for the hypothesis that internal waves can transport larvae of invertebrates and

- fish onshore. *Fish Bull* 86:703–714
- Shanks AL (1995) Mechanisms of cross-shelf dispersal of larval invertebrates and fish. In: McEdward LR (ed) *Ecology of marine invertebrate larvae*. CRC Press, Boca Raton, FL, p 323–368
- Shanks AL (ed) (2001) *An identification guide to the larval marine invertebrates of the Pacific Northwest*. Oregon State University Press, Corvallis, OR
- Shanks AL (2009) Barnacle settlement versus recruitment as indicators of larval delivery. II. Time-series analysis and hypothesized delivery mechanisms. *Mar Ecol Prog Ser* 385:217–226
- Shanks AL, Brink L (2005) Upwelling, downwelling, and cross-shelf transport of bivalve larvae: test of a hypothesis. *Mar Ecol Prog Ser* 302:1–12
- Shanks AL, McCulloch A (2003) Fortnightly periodicity in the abundance of diatom and dinoflagellate taxa at a coastal study site. *J Exp Mar Biol Ecol* 296:113–126
- Shanks AL, Shearman RK (2009) Paradigm lost? Cross-shelf distributions of intertidal invertebrate larvae are unaffected by upwelling or downwelling. *Mar Ecol Prog Ser* 385:189–204
- Shanks AL, Largier J, Brink L, Brubaker J, Hooff R (2000) Demonstration of the onshore transport of larval invertebrates by the shoreward movement of an upwelling front. *Limnol Oceanogr* 45:230–236
- Shanks AL, Morgan SG, MacMahan J, Reniers AJHM (2010) Surf zone physical and morphological regime as determinants of temporal and spatial variation in larval recruitment. *J Exp Mar Biol Ecol* 392:140–150
- Shearman RK, Lentz S (2004) Observations of tidal variability on the New England shelf. *J Geophys Res* 109: C06010, doi: 10.1029/2003JC001972
- Simpson JE (1997) *Gravity current in the environment and the laboratory*. Cambridge University Press, Cambridge
- Sournia A (ed) (1978) *Phytoplankton manual*. UNESCO, Paris
- Tapia F, Navarrete S (2010) Spatial patterns of barnacle settlement in central Chile: persistence at daily to inter-annual scales relative to the spatial signature of physical variability. *J Exp Mar Biol Ecol* 392:151–159
- Tilstone GH, Figueiras FG, Fraga F (1994) Upwelling-downwelling sequences in the generation of red tides in a coastal upwelling system. *Mar Ecol Prog Ser* 112: 241–253
- Trevorrow MV (1998) Observations of internal solitary waves near the Oregon coast with an inverted echo sounder. *J Geophys Res* 103:7671–7680
- Tweddle JF, Strutton PG, Foley DG, O'Higgins L and others (2010) Relationships among upwelling, phytoplankton blooms, and phycotoxins in coastal Oregon shellfish. *Mar Ecol Prog Ser* 405:131–145
- Underwood AJ, Keough MJ (2001) Supply-side ecology: the nature and consequences of variations in recruitment of intertidal organisms. In: Bertness MD, Gaines SD, Hay ME (eds) *Marine community ecology*. Sinauer, Sunderland, MA, p 183–200
- Venrick EL (1978) How many cells to count? In: Sournia A (ed) *Phytoplankton manual*. UNESCO, Paris, p 7–16
- Winant CD (1974) Internal surges in coastal waters. *J Geophys Res* 79:4523–4526
- Wolanski E, Delesalle B (1995) Upwelling by internal waves, Tahiti, French Polynesia. *Cont Shelf Res* 15:357–368
- Yoshioka PM (1982) Role of planktonic and benthic factors in the population dynamics of the bryozoan *Membranipora membranacea*. *Ecology* 63:457–468

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