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Testing the intermittent upwelling hypothesis: upwelling, downwelling, and subsidies to the intertidal zone

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Abstract. The Intermittent Upwelling Hypothesis (IUH) posits that subsidies of larvae and phytoplankton to intertidal communities should vary unimodally along a gradient of upwelling from persistent upwelling to persistent downwelling with most subsidies occurring where upwelling is of intermediate strength and intermittent. Furthermore, the hypothesis states that larvae and phytoplankton are transported far offshore by strong, persistent upwelling and fail to subsidize nearshore communities, whereas weak upwelling or downwelling reduces nutrients for phytoplankton production limiting food for larvae and nearshore communities. We review studies conducted at sea and onshore and reanalyze published data to test the IUH and evaluate alternative hypotheses. To test the hypothesis, we examine five predictions that must hold if the IUH is true. (1) Larvae should inhabit the surface Ekman layer where they are transported offshore during upwelling. Larvae of many intertidal taxa occur deeper in the water column where currents flow shoreward during upwelling. (2) Larvae of nearshore species should occur farther offshore during upwelling than during relaxation or downwelling. Larvae of many nearshore species remain within several kilometers of shore during both conditions. (3) Larval settlement in intertidal communities should be lower during upwelling than relaxation or downwelling. Daily larval settlement has not observed to be higher during relaxation or downwelling events; settlement has most often been seen to vary with the fortnightly tidal cycle likely due to onshore larval transport by internal tides. (4) Larval settlement and recruitment in intertidal communities should be lower in areas of strong, persistent upwelling than where upwelling is weaker and less persistent. Recruitment of mussels and barnacles to artificial and natural substrates did not vary with the strength of upwelling, but did vary inversely with two measures of desiccation potential, and directly with indicators of surf zone hydrodynamics; larval recruitment was higher where surf zones were more dissipative with rip currents. (5) Phytoplankton subsidies to nearshore communities should be highest where upwelling is moderate and intermittent. Like larval subsidies, phytoplankton subsidies varied spatially with surf zone hydrodynamics rather than upwelling. This reconsideration of the evidence for the IUH finds the hypothesis unsupported.

Key words: barnacles; dessication; hydrodynamics; intertidal; mussels; recruitment; settlement; subsidies; surf zone.

INTRODUCTION

The importance of larval settlement and postsettlement mortality to the dynamics of marine populations and communities has been investigated for over a century (Morgan 2001). Along the west coast of the United States, a considerable body of research demonstrated the importance in the Pacific Northwest of postsettlement mortality in regulating rocky shore communities. In

contrast, in a highly influential paper, Roughgarden et al. (1988) proposed that low larval settlement regulated intertidal communities in California. They hypothesized that larvae developing in strong, persistent upwelling off California are swept so far offshore by surface currents that few of them return to shore to settle. Consequently, populations are recruitment limited in the strong, persistent upwelling along the California coast, whereas an abundant supply of larvae in the weaker, less persistent upwelling in the Pacific Northwest results in postsettlement density-dependent regulation of populations.

A corollary to this hypothesis was that the alongshore distribution of upwelling also affects the delivery of phytoplankton food subsidies to the intertidal zone (Menge

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and Menge 2013). Wind-driven coastal upwelling draws nutrient rich waters from depth to the euphotic zone close to the coast leading to high phytoplankton productivity, standing stocks and subsidies to intertidal communities. However, if upwelling is strong and persistent, blooms are transported far from shore (Botsford et al. 2006), and subsidies of phytoplankton to the intertidal communities are hypothesized to be low. During relaxation of upwelling or downwelling events, the influx of nutrients is low leading to lower phytoplankton productivity, standing stocks and subsidies to intertidal communities. Thus, phytoplankton subsidies to the shore should be higher in regions of moderate intermittent upwelling than where upwelling or downwelling are strong and persistent.

Critical tests of the effects of upwelling on larval recruitment have been conducted at sea as well as onshore, and we review this literature to reconsider the importance of latitudinal variation in upwelling on larval settlement and recruitment and phytoplankton subsidies to rocky shore populations and communities. As well as reviewing published research, we reanalyzed some published data to evaluate new explanations for results formerly attributed to upwelling. The hypothesis originated over 30 years ago with much of the supporting evidence coming from studies conducted along the West Coast of North America, and consequently, we have focused on the California Current Large Marine Ecosystem (CCLME). We address five predictions or expectations of the Intermittent Upwelling Hypothesis that must hold if the hypothesis is true. We selected these five predictions because they are both key tests of the hypothesis and published data are available to actually make the tests. The first two predictions deal with the pelagic phase of larval dispersal and the last three with the delivery of subsidies (larval settlers and phytoplankton) to the shore and their subsequent recruitment. None of the predictions of the IUH was supported by the evidence.

PREDICTION 1: LARVAE SPEND MOST OF THEIR TIME IN THE SURFACE EKMAN LAYER WHERE WIND-DRIVEN UPWELLING CURRENTS TRANSPORT THEM OFFSHORE

When upwelling favorable winds (from the north in the CCLME) blow parallel to shore, due to the Coriolis effect, flow in the surface Ekman layer (upper 10–20 m) is downwind and offshore causing a drop in sea level at the coast and, to compensate, water from below the Ekman layer flows onshore (Mann and Lazier 1991). During downwelling-favorable winds (from the south in the CCLME), the flow regime is reversed. Given this flow regime, larvae in the surface Ekman layer will be transported offshore during upwelling and back toward the shore during relaxation or downwelling, and larvae below the Ekman layer will experience transport in the opposite directions.

For their 1988 paper, Roughgarden et al. (1988) analyzed samples from oblique zooplankton tows collected by CalCOFI (California Cooperative Fisheries Investigation) as part of a long-term study of variations in sardine

and anchovy populations in the CCLME; oblique plankton tows, however, provided no indication of the depth inhabited by larvae caught in the tows. A number of researchers have subsequently collected vertically stratified samples from throughout the water column to test this hypothesis (see for example Morgan et al. 2009b, Shanks and Shearman 2009). These studies determined that larvae of most nearshore species occur below the surface Ekman layer. For example, Shanks and Shearman (2009) found that the larvae of all intertidal barnacles and all stages of these barnacles were caught deeper than the Ekman layer; during upwelling they inhabited the deeper upwelled water that was flowing shoreward and during downwelling they were found deeper as well and may be transported offshore. Morgan et al. (2009b) showed that larvae of most of the 46 species of crustaceans collected by their sampling occurred deeper in the water column throughout the day or rose to the surface at night after strong afternoon upwelling winds subsided (Morgan and Fisher 2010). There were larvae of some species that did occupy the surface layer and they were transported farther offshore before returning to the nearshore late in development. Larvae of most nearshore species of invertebrates do not spend most of their time in the surface Ekman layer, and in fact, many spend little time in the surface Ekman layer. Similar results have been found by Bartilottii et al. (2014) in the upwelling regime of the Iberian Peninsula. These results are not consistent with Prediction 1.

PREDICTION 2. LARVAE OF NEARSHORE SPECIES SHOULD OCCUR FARTHER OFFSHORE DURING UPWELLING THAN DURING RELAXATION OR DOWNWELLING

As support for their hypothesis, Roughgarden et al. (1988), using the CalCOFI samples, correlated the most seaward extent of barnacle larvae from shore with the strength of upwelling and found that larvae tended to occur farthest offshore during strong upwelling. Anchovies and sardines in the CCLME tend to spawn well offshore, and the CalCOFI samples analyzed by Roughgarden et al. were designed to capture these larvae. As a consequence, the most nearshore station sampled by CalCOFI tended to be 5 nautical miles (9 km) offshore (Roughgarden et al. 1988). Intertidal barnacle larvae are released nearshore in the coastal boundary layer, where cross-shore currents are generally slow due to friction with the bottom and shore (Nickols et al. 2012, 2013); given current speeds in the coastal boundary layer, it should take days for larvae to be transported far enough offshore to be caught during CalCOFI sampling. Perhaps the CalCOFI samples were collected so far offshore that they actually missed the bulk of the barnacle larvae. Because the cross-shelf distribution and abundance of barnacle larvae was not determined, their samples may represent the few unfortunate individuals that were larval wastage.

Subsequent studies filled this gap by sampling at stations from several hundred meters to 70 km offshore in the CCLME (Morgan et al. 2009a, b, Shanks and

Shearman 2009, Morgan 2014), other upwelling regimes (Poulin et al. 2002, Bartilottii et al. 2014, Morgan 2014) and elsewhere (Shanks et al. 2002, Shanks et al. 2003, Shanks and Brink 2005). These studies determined that the larvae of barnacles and many other nearshore species of invertebrates remain close to shore rather than being transported offshore by strong upwelling currents. For example, Shanks and Shearman (2009) found that all larval stages of all the intertidal barnacles were found close to shore, within several km of shore, and that their average distance offshore (generally <2 km) did not vary with upwelling or downwelling. Similar results were obtained for barnacles as well as many other species of nearshore crustaceans in other studies (Morgan et al. 2009a, b, Fisher et al. 2014). Moreover, these latter studies found that larvae of species developing over the mid or outer continental shelf did not occur farther offshore during strong upwelling conditions either.

The conclusion from these studies is that upwelling does not sweep larvae of many, perhaps most, intertidal species far offshore. By avoiding the surface Ekman layer, larvae of most species are not carried offshore by upwelling but, instead, remain within several kilometers of shore throughout their pelagic development. These results are not consistent with Prediction 2.

The dispersal of those larvae of intertidal and shallow subtidal species that remain within several kilometers of shore is under the influence of nearshore hydrodynamics and this leads to a number of consequences. (1) During upwelling, the warm, lower density surface layer of the ocean is pushed offshore and is replaced by cold, denser, upwelled water. These two water masses meet, forming an upwelling front between the cold upwelled water onshore and the warm surface water transported offshore around 10–15 km from shore (Mann and Lazier 1991). As the upwelling season progresses in the CCLME, large eddies, known as jets and squirts, develop in the California Current, which transport continental shelf water far seaward (Korso and Huyer 1986, Strub et al. 1991, Strub and James 2000). Current drifters set seaward of the upwelling front tend to be entrained in these jets and squirts and are carried far from shore (Barth and Smith 1998, Barth et al. 2000), as would larvae of many rockfish species that develop beyond the upwelling front (Fiedler 1986, Haury et al. 1986). In contrast, drifters set landward of the upwelling front tend to be carried back toward shore where they often run aground (Barth and Smith 1998, Barth et al. 2000). Because larvae of most nearshore taxa complete development well landward of the upwelling front, they should seldom encounter jets and squirts and instead be transported onshore like the drifters set landward of the upwelling front (Austin and Barth 2002). (2) During upwelling, the most rapid alongshore current is within the upwelling jet associated with the upwelling front, but the jet does not affect the rate of alongshore larval transport for the many intertidal species that complete their pelagic development in waters kilometers landward of the jet (Korso et al. 1997). (3) Larvae of

intertidal and nearshore species are released in the coastal boundary layer, retarding seaward and alongshore dispersal (Morgan et al. 2009a, Nickols et al. 2013, Hameed et al. 2016). (4) During the upwelling season, roughly every week or two winds shift from upwelling to downwelling favorable (Mann and Lazier 1991). During upwelling favorable winds in the CCLME, nearshore currents flow to the south, and during downwelling, they reverse and flow north (in the Southern Hemisphere wind driven upwelling systems currents are reversed). Larvae of most intertidal fishes and benthic invertebrates that spawn during the upwelling season are likely transported alongshore both north and south as wind reversals occur during their four- to six-week planktonic phase (average 45 d) (Shanks and Eckert 2005). By capturing this variation in current direction, larvae may tend to remain closer to their point of release (Largier 2003).

How do slowly swimming larvae remaining below the surface Ekman layer stay roughly the same distance offshore rather than being transported shoreward during upwelling and seaward during downwelling? As water shoals close to shore, the baroclinic currents generated by Ekman transport are suppressed (Austin and Lentz 2002) limiting cross-shelf transport of larvae. Water within the coastal boundary layer is, however, exchanged during wind reversals (Csanady 1974), which should transport larvae embedded in the water mass along with it if larvae behaved as passive particles. Larvae do not remain attached to a water mass indicating that they are far from passive. Shanks and Brink (2005) repeatedly sampled a transect perpendicular to shore for over a week while winds shifted from upwelling to downwelling and back to upwelling. The water mass adjacent to shore was exchanged with each wind shift, whereas, slowly swimming bivalve larvae of nearshore taxa remained roughly the same distance offshore rather than tracking water masses as they were exchanged. Although these observations were made on the east coast of North America, which is not a predominantly wind-driven upwelling system, the horizontal baroclinic cross-shelf currents generated by upwelling were still at least an order of magnitude faster than larval swimming speeds (Shanks and Brink 2005). The authors hypothesized that by swimming vertically in the much slower downwelling (upwelling) currents converging (diverging) against the shore, larvae may have been able to maintain their position close to shore despite the exchange of water masses. A similar mechanism may be occurring in wind-driven upwelling systems associated with eastern boundary currents like the California Current.

PREDICTION 3. DAILY SETTLEMENT OF LARVAE IN THE INTERTIDAL ZONE SHOULD BE LOWER DURING UPWELLING AND HIGHER DURING DOWNWELLING CONDITIONS

Upwelling surface currents were hypothesized to cause enough offshore transport for larvae to be lost to coastal populations resulting in low settlement at the shore,

whereas the reverse is hypothesized to occur during relaxation from upwelling or downwelling conditions (Farrell et al. 1991, Roughgarden et al. 1991). There are two mechanisms that may transport larvae shoreward during a downwelling or upwelling relaxation event. As described above, a front is formed offshore separating the cold upwelled water from the warm surface water that has been pushed offshore. Following an upwelling event (e.g., onset of downwelling or upwelling relaxation), the cool upwelled water sinks back to a stable vertical distribution and the warm water beyond the upwelling front flows back toward shore as a density current (Shanks et al. 2000). If, prior to the commencement of new upwelling, larvae are released into the warm surface water and remain there, they will be transported offshore during subsequent upwelling and they will occur in the lens of warm water on the seaward side of the upwelling front. With relaxation of upwelling-favorable winds, they will be transported back toward shore by the density current. When this lens of warm water contacts shore and remains in contact with the shore, settlement in intertidal communities should be higher. The warm water flowing back toward shore takes the form of a moving convergent front with surface flow toward the front from both the warm and cool water sides of the front (Shanks et al. 2000). Larvae carried into the convergent front can be transported shoreward by the moving convergence (Shanks et al. 2000). This will also lead to higher settlement at the shore during downwelling events, but the settlement should appear as a brief pulse as the front arrives onshore.

A number of studies have measured barnacle settlement and the abundance of crab megalopae at the shore daily or every two days and results are not consistent with Prediction 3 (Shanks 1983, 1986, 1998, 2006, 2009a, b, Farrell et al. 1991, Pineda 1991, 1994, Roegner et al. 2007, Shanks et al. 2014). These studies consistently found that the delivery of settlers tends to occur in brief pulses of one to several days, and the pulses are cross-correlated with the tidal amplitude cycle of spring to neap tides. The fortnightly periodicity in settlement is most likely due to onshore transport by the internal tides either by moving convergences over these internal waves or by internal bores generated by breaking internal waves (Shanks 1983, Pineda 1991). Contrary to expectations, larval settlement was not related to relaxation events; it was actually higher during upwelling, but the positive effect of upwelling winds on settlement was only apparent after the much stronger fortnightly tidal effect had been removed from the time series (Shanks 2009a). For the purpose of this review of the IUH, the important point is not that onshore transport of larvae often appears to be due to tidally generated internal waves, rather it is that when settlement and larval abundance have been measured daily, there is no evidence for the hypothesized higher settlement during downwelling and relaxation events.

An apparent exception to these observations was a paper by Farrell et al. (1991) in which they interpreted

their data to indicate that barnacle settlement was higher following a downwelling event, although they did not statistically test this effect. Subsequent time-series analysis revealed that there was a clear fortnightly effect of the spring-neap tidal amplitude cycle in this data set as well and no effect of upwelling and downwelling (Shanks 2009a).

At a coastal site near Duck, North Carolina, Shanks et al. (2000) sampled an upwelling front propagating toward shore during an upwelling relaxation event. The front formed a moving convergence zone that transported blue crab (*Callinectes sapidus*) megalopae toward shore as predicted by the IUH. Daily abundance of blue crab megalopae sampled during the same period and at the same sample site, however, varied with the fortnightly tidal cycle (Shanks 1998) suggesting the megalopae were regularly transported shoreward by the internal tides. Indeed, observations off Beaufort, North Carolina demonstrated that moving convergences generated by internal waves transported blue crab megalopae as well as a number of other larval types shoreward (Shanks 1988). We conclude from these studies that moving convergences generated by any mechanism can transport larvae (Shanks et al. 2000). However, over the continental shelf, moving convergences are more frequently generated by the internal tides than relaxation events, and this mode of onshore transport shows up in time series of daily settlement and abundance of larvae as a fortnightly signal.

Although the IUH suggests that peaks in the abundance of settlers at the shore should occur during downwelling and relaxation events, researchers have consistently found that abundance varies with a fortnightly periodicity related to the tidal amplitude cycle. Abundance peaks related to downwelling or upwelling relaxation events were not observed. Thus, Prediction 3 is not supported.

PREDICTION 4. WHERE UPWELLING IS STRONG AND PERSISTENT, SETTLEMENT AND RECRUITMENT IN THE INTERTIDAL ZONE SHOULD BE LOWER THAN WHERE UPWELLING IS LESS PERSISTENT

The rationale behind this prediction is that, where upwelling is strong and persistent, larvae of intertidal organisms are pushed out to sea and lost to the population; but where upwelling is weaker and less persistent, larvae are transported shoreward and settle during more frequent relaxation conditions (Roughgarden et al. 1988). The strength and persistence of upwelling changes with latitude (Checkley and Barth 2009), and therefore, so might larval recruitment to adult populations (Roughgarden et al. 1988). Where or when larval supply is high, recruitment to adult populations will be high (Menge and Menge 2013). Alongshore variation in the apparent recruitment of barnacles and mussels, which appears to be related to alongshore variation in upwelling, has been presented as among the strongest evidence supporting the

IUH (reviewed in Menge and Menge 2013). Several papers have compared latitudinal variation in the recruitment of barnacles or mussels to the distribution of upwelling within the CCLME (Connolly et al. 2001, Menge et al. 2004, Broitman et al. 2008) as well as along the coast of Chile (Navarrete et al. 2005). The consensus is that where upwelling is strong and persistent recruitment is lower than in areas of weak upwelling.

Although the recruitment data do appear to support the IUH, there are problems both with the data and with the interpretation of the data that warrant reconsideration. As described above, the vertical and cross-shelf distribution of larvae do not match the predictions of the IUH. Larvae were not in the surface Ekman layer and upwelling did not transport them offshore; instead most larvae were found below the surface Ekman layer and remained within several kilometers of shore. In addition, when settlement was measured daily, higher settlement rates did not occur during downwelling events, but rather settlement rate followed a fortnightly pattern suggestive of transport to shore by the internal tides. Hence, the underlying rationale used to explain the potential effect of upwelling intensity on alongshore variation in recruitment is not supported by empirical data collected at sea and onshore.

Much of the data on recruitment of barnacles has been collected using Safety-Walk plates, plexiglas plates covered with non-skid Safety-Walk tape (3M Co. Minnesota; reviewed in Menge and Menge 2013). The rough surface of the tape appears to be an ideal settlement surface for cyprids that prefer rugose substrates, but unfortunately, the tape heats up rapidly in the sun reaching surface temperatures (e.g., 40°–50°C) lethal to settled cyprids in tens of minutes (Shanks 2009b). Despite this potential artifact, Broitman et al. (2008) found significant correlations between recruitment and cyprid settlers on recovered Safety-Walk plates. Although the heating problem may have been over emphasized (Shanks 2009b), recruitment data using Safety-Walk plates should be interpreted cautiously because solar energy varies with latitude as does the typical coastal weather at a site, including fog often associated with upwelling.

Investigators recently have begun to examine the potential effects of surf zone hydrodynamics on the delivery of larvae and phytoplankton subsidies to shore (Rilov et al. 2008, Shanks et al. 2010, 2016, 2017b, c, Morgan et al. 2016, 2017a). Surf zones vary from reflective (steeply angled shores with narrow surf zones) to more dissipative (gently sloping shores with wide surf zones). Surf zone hydrodynamics can both limit the onshore migration of larvae from the coastal ocean with the surf zone as a barrier, or not hinder shoreward migration (Shanks et al. 2010, 2017a, Morgan et al. 2016, 2017a). Most rocky shores are steep and, hence, reflective, and hydrodynamics coupled with larval behavior tend to hinder the delivery of larvae, including cyprids and mussels, to the shore. In contrast, more dissipative shores, including rock platforms associated with wide dissipative surf zones, often

contained bathymetric rip currents that concentrate larvae in eddies (Fujimura et al. 2014, Morgan et al. 2016, 2017b). Barnacle larval settlement, recruits, and population densities were significantly higher at more dissipative than reflective surf zones (Shanks et al. 2017a).

Several studies used variations in recruitment at sites from central California (about 35°N latitude) northward into Oregon to support the IUH (reviewed in Menge and Menge 2013). The intensity of upwelling and its persistence decreased along this latitudinal transect; it was higher in central and northern California and decreased northward with, the papers suggest, a sharp drop occurring north of Cape Blanco, Oregon (Fig. 1). Recruitment tended to be higher north of Cape Blanco, consistent with the IUH. However, daily solar radiation (Shanks et al. 2017a) and maximum intertidal temperatures as measured with Robomussels (Helmuth 1998, Helmuth et al. 2000, 2016) also decreases along this latitudinal gradient of stations (Fig. 1). In addition, due either to chance or latitudinal variation in coastal geomorphology, many of the stations surveyed north of Cape Blanco are rock platforms within wide, more dissipative, surf zones (Fig. 1), where settlement was high due to surf zone hydrodynamics (Shanks et al. 2017a). Last, runoff of nutrients from high precipitation may fuel phytoplankton production that is several times greater in the waters over the Oregon and Washington continental shelf (Hickey and Banas 2008), providing more food for adults and larvae thereby increasing reproductive output or larval survival (Morgan 2001). Thus along this latitudinal transect of stations, there are consistent trends in four variables all of which have the potential to increase recruitment to the north.

At least two studies conducted along a longer latitudinal transect sampled sites with enough variation in these variables that it might be possible to untangle their effects. (1) Broitman et al. (2008) sampled mussel (*Mytilus*) and barnacle (*Balanus*) recruitment to Tuffy scrub pads and Safety-Walk plates, respectively, at stations distributed from south of Point Conception and within the Southern California Bight to northern Oregon. Note that this study occurred before it was discovered that Safety-Walk plates heat up rapidly in the sun (Shanks 2009a, b) and that surf zone hydrodynamics affect intertidal populations and the delivery of larvae to the shore (Rilov et al. 2008, Shanks et al. 2010). (2) Recently, Shanks et al. (2017a) surveyed the structure of barnacle populations, density of adult *Balanus* and recruit density (individuals <1.5 mm diameter) from San Diego to northern Washington.

These studies sampled sites within the Southern California Bight where the hydrodynamics are quite different from the coast to the north of Point Conception or seaward of the Channel Islands. Within the Bight, flow along the coast is from the south, winds are weaker and more variable, and upwelling is much weaker and less frequent, downwelling conditions are more common (Checkley and Barth 2009). Along the coast northward from Point

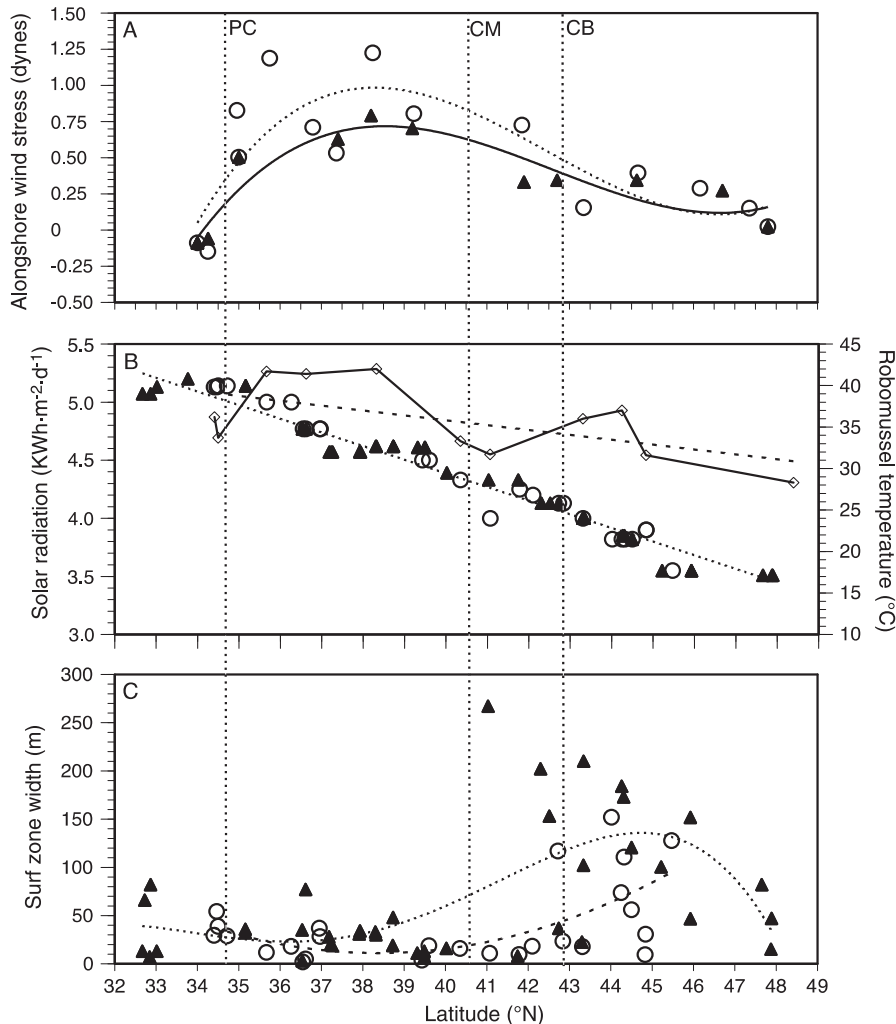


FIG. 1. Regressions of three environmental variables at study sites along the west coast of the United States. Samples stations are those from Broitman et al. (2008) (open circles) and Shanks et al. (2017a) (solid triangles). (A) Alongshore wind stress during three years of the data (2001–2003) from Broitman et al. (2008), reanalyzed here, and from the study by Shanks et al. (2017a). The dotted and dashed lines are the results of regressions (see Table 2 for regression equations) between the alongshore wind stress data and latitude for the Broitman et al. and Shanks et al. data, respectively. Wind stress values are from wind data collected by NOAA weather buoys. $1 \text{ dyne} = 1 \times 10^{-5} \text{ N}$. (B) Average daily solar radiation at each station sampled by Broitman et al. and Shanks et al. with the results of a regression between latitude and solar radiation (dotted line). Open diamonds are the average maximum low tide Robomussel temperatures (see methods in Prediction 4) with the results of a regression between latitude and the average maximum low tide Robomussel temperatures (dashed line, see Table 2 for regression equation). (C) Average surf zone width as determined from Google Earth images. Note the increase in the frequency of stations with wide ($\geq 100 \text{ m}$), more dissipative, surf zones north of Cape Mendocino. The dotted and dashed lines are the results of regressions between surf zone width and latitude for the Broitman et al. and Shanks et al. data, respectively. A description of the techniques used to measure surf zone width and the reliability of the data are presented in Shanks et al. (2017a, c). The vertical dotted lines indicate the locations of prominent capes (PC, Point Conception; CM, Cape Mendocino; CB, Cape Blanco).

Conception, upwelling-favorable winds during spring and summer increase in magnitude to around 38°N near Bodega Bay and then decrease northward (Fig. 1).

Along this latitudinal transect, solar energy decreases monotonically from south to north (Fig. 1), although the actual exposure of intertidal organisms to solar energy is likely more complex depending in part on the timing of daytime low tides (higher exposure occurs when low spring tides occur during the hottest time of

the day; Helmuth et al. 2000; average daily solar radiation was obtained from the National Solar Radiation Data Base, *available online*).⁴ To capture this effect, we analyzed temperature data collected using Robomussels (mussel models with an embedded thermistor; Helmuth et al. 2016) at a number of study sites. Using these data, we calculated the average maximum low tide

⁴http://rredc.nrel.gov/solar/old_data/nsrdb/

temperature (Fig. 1). To make this calculation, we first determined the average and standard deviation of temperature over the entire time series at each site, added twice the standard deviation to the average temperature, and calculated the average of all the temperatures higher than this temperature, which we have defined as the average maximum low tide temperature.

We measured surf zone width as a proxy for surf zone hydrodynamics, wider surf zones are more dissipative and narrow more reflective. Detailed description of the methods used to measure surf zone width and reliability of the data are presented in Shanks et al. (2017a, c). Briefly, we used images from Google Earth during spring and summer to determine the average width of the surf zone immediately seaward of the sample sites. Width was from the most seaward breaking wave to the swash line. The number of useable Google Earth images varied from 3 to 14 and were taken between 2007 and 2014. The distribution of surf zone widths at the study sites is likely a reflection of the distribution of coastal geomorphology (Fig. 1). For example, the geomorphology of the Big Sur coast (roughly Point Piedras Blancas, 35.7° N to Point Lobos, 36.5° N) is very steep with few sandy beaches or more dissipative surf zones. North of Cape Mendocino (40.35° N) dissipative surf zones are more common and a number of sites north of Cape Blanco frequently sampled by intertidal ecologists are rock platforms associated with wide more dissipative surf zones (e.g., Cape Meares, Yachats, Strawberry Hill, and Tokakee Klootchana).

We reanalyzed data from Broitman et al. (2008) and Shanks et al. (2017a) to examine the effect of solar radiation, average maximum low tide temperature, surf zone hydrodynamics as indicated by surf zone width, and the strength of upwelling as indicated by alongshore wind stress (see Shanks et al. [2017a] for discussion of alongshore wind stress vs. the Bakon index as proxies for upwelling) on recruitment of *Balanus* and mussels along the West Coast. Data for (1) average solar radiation and surf zone width was available for each study site (see Shanks et al. 2017a, for methods), (2) average alongshore wind stress during the spring and summer was calculated using data from 15 NOAA weather buoys (see Shanks et al. 2017a for methods), and (3) Robomussel temperature data are from 11 sites (Table 1). To assign values of alongshore wind stress and average maximum low tide temperature to each study site from Broitman et al. (2008) and Shanks et al. (2017a), we calculated regressions between latitude (independent variable) and

TABLE 1. Average maximum low tide temperature as measured by Robomussels at stations sampled by Helmuth et al. (2016) along the west coast of North America.

Station name	Latitude (°N)	Longitude (°W)	Maximum low tide temperature (°C)
Coal Oil Point	34.4067	119.8783	36.2
Jalama	34.4952	120.4969	33.7
Piedras	35.6658	121.2867	41.7
Hopkins	36.6219	121.9053	41.4
Bodega Reserve	38.3185	123.0740	42.0
Cape Mendocino	40.348	124.3650	33.3
Trinidad	41.0621	124.1493	31.7
Cape Arago	43.3066	124.4024	36.0
Strawberry	44.2499	124.1136	37.0
Boilers Bay	44.8306	124.0601	31.6
Landing Beach	48.3938	124.7355	28.3

Note: see methods in Prediction 4.

the physical variables of average maximum low tide temperature and alongshore wind stress (dependent variables) and then used these regression equations to calculate the values of the physical variables at each site (see Shanks et al. 2017a for methods; Table 2). We calculated the alongshore wind stress and average maximum low tide temperature for each of the three years of data (2001–2003) that we analyzed from Broitman et al. (2008), calculated the average of these values and used these averages in the regression analysis.

Broitman et al. (2008) surveyed the latitudinal and seasonal variation in *Mytilus* and *Balanus* recruitment from 1997 through 2004, but all 26 sites were only sampled from 2001 to 2003. The following analysis is limited to these years. Data were presented as heat maps of the log of the monthly recruitment rates (Broitman et al. 2008), so we estimated the recruitment rates by comparing the heat map color scale to the color for the month with highest annual recruitment. We calculated linear regressions between the log of recruitment of *Mytilus* and *Balanus* in the Broitman et al. and Shanks et al. data sets (dependent variables) and the averages of daily solar radiation, maximum low tide temperature, alongshore wind stress, and log surf zone width (independent variables).

In the Broitman et al. (2008) data, recruitment of *Mytilus* and *Balanus* were negatively related to average daily solar radiation and average maximum low tide temperature with >60% to almost 70% of the variation in recruitment explained by these variables (Fig. 2).

TABLE 2. Regression equations used to calculate alongshore wind stress and average maximum low tide temperature at stations sampled in Broitman et al. (2008) and Shanks et al. (2017a).

Regression	<i>n</i>	<i>R</i> ²	<i>P</i>	Regression equation
Alongshore wind stress, Broitman et al. (2008) analysis	11	0.848	<0.0004	$y = 0.003028 x^3 + (-0.3857 x^2) + (16.217 x) - 224.479$
Alongshore wind stress, Shanks et al. (2017a) analysis	15	0.634	<0.00006	$y = 0.00224 x^3 + (-0.2865 x^2) + (12.0948 x) - 168.1436$
Maximum low tide temperature	11	0.362	0.05	$y = -0.587 x + 59.83$

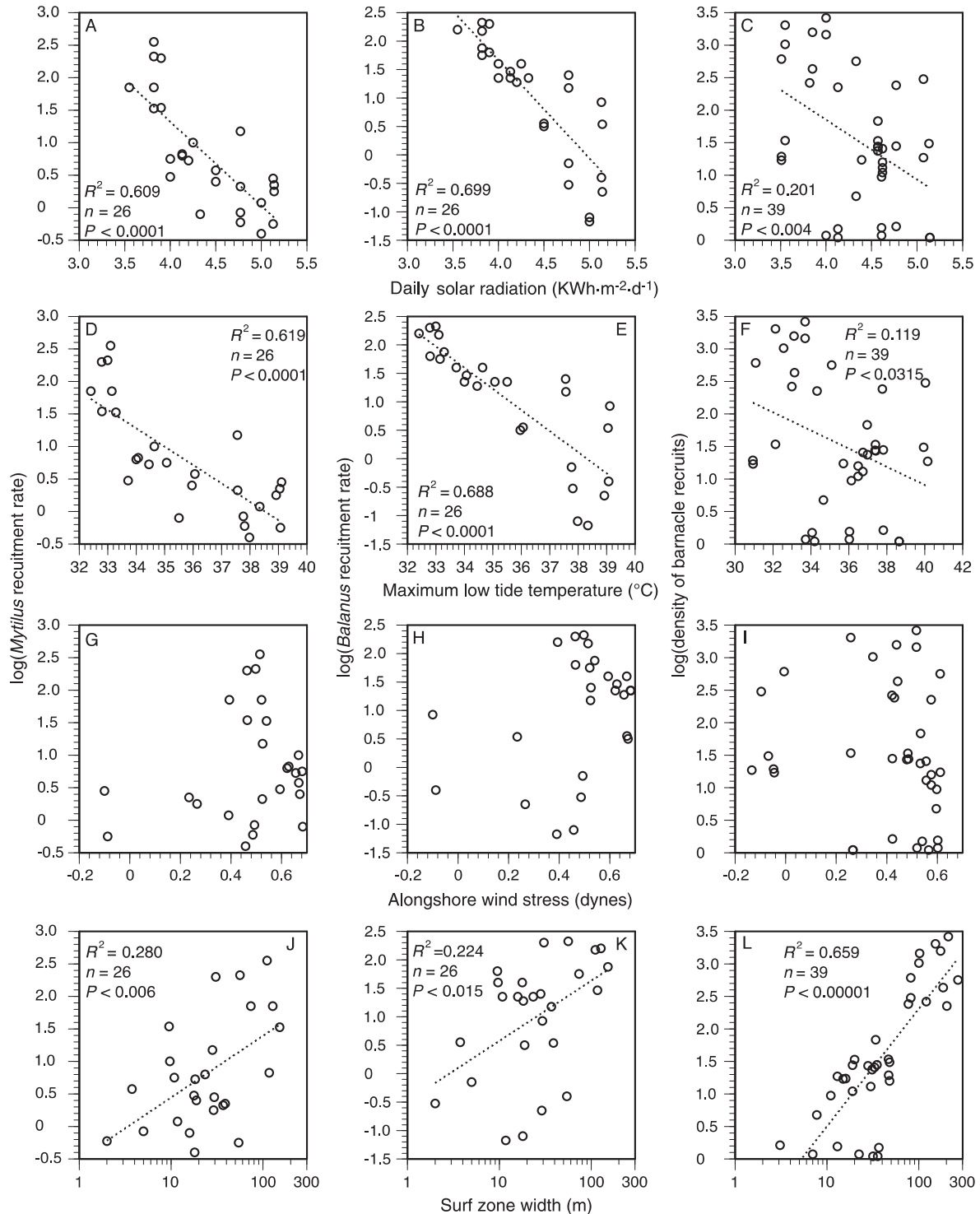


FIG. 2. Variation in the density of *Mytilus* and *Balanus* recruits (A, D, G, J and B, E, H, K, respectively, data from Broitman [2008]) and barnacle recruits (C, F, I, and L, data from Shanks et al. [2017a]) with four physical variables from the west coast of the USA. (A–C) Average daily solar radiation. (D–F) Average maximum low tide temperature from Robomussels (see methods in Prediction 4). (G–I) Average alongshore wind stress in dynes ($1 \text{ dyne} = 1 \times 10^{-5} \text{ N}$). Positive (negative) values are upwelling (downwelling) favorable. (J–L) Surf zone width as determined from Google Earth images (see Shanks et al. 2017a, c for methods). Note that if a Bonferroni correction was applied to the set of four regressions calculated for each data set then the regression in F would not be significant (corrected alpha = 0.0125).

Given the heating of Safety-Walk plates when in the sun, the strong relationship between daily solar radiation and average maximum low tide temperature and *Balanus* recruitment was expected. What was not expected was that the recruitment of *Mytilus* to scrub pads responded similarly. The open structure of scrub pads may not retain much moisture; perhaps exposing the mussel recruits to desiccation stress. In contrast, the abundance of barnacle recruits (individuals <1.5 mm) surveyed on natural rock substrate by Shanks et al. (2017a) varied weakly with daily solar radiation (~20% of the variation explained) and the average maximum low tide temperature (12% of the variation explained). There were no significant regressions between alongshore wind stress and any of the recruitment data (Fig. 2). All three measures of recruitment, however, varied significantly with surf zone width, although relationships to recruitment were weaker in the Broitman et al. (2008) study (30% and 22% of the variation explained for mussels and barnacles, respectively) than the Shanks et al. data on barnacle recruits (66% of the variation explained). This difference might be related to the much stronger effects of daily solar radiation and average maximum low tide temperature on recruitment to artificial substrates in the Broitman et al. (2008) study than to the natural recruitment measured by Shanks et al. (2017a).

Broitman et al. (2008) found that the density of cyprid settlers on the recruitment plates correlated with recruitment to the plates. Our reanalysis of their data found that recruitment varied with surf zone width, hence, by logical extension, settlement likely also correlates with surf zone width. This matches the findings by Shanks et al. (2017a); the density of recruits on natural rock substrates and the weekly recruitment and daily settlement of barnacles to cleared rock quadrates all varied with surf zone width, an indicator of surf zone hydrodynamics.

In an attempt to control for the effect of variation in coastal hydrodynamics (i.e., upwelling and downwelling) on barnacle recruitment and settlement, Shanks et al. (2017a) surveyed closely spaced pairs of stations (several kilometers to hundreds of meters apart) with different types of surf zones. At some station pairs, they also measured weekly recruitment and daily settlement to natural rock surfaces. Surf zone widths at some of the pairs of stations were similarly narrow while in other cases one station had a wide surf zone (more dissipative) and the other narrow (more reflective). If barnacle larval settlement and recruitment depends on coastal hydrodynamics (e.g., upwelling strength and persistence) then, given the close spacing of the stations, these measures of barnacle recruitment and settlement should have been the same at each station pair. If instead these measures vary with surf zone hydrodynamics, then these measures should be similar at station pairs with narrow surf zones but different at station pairs with wide and narrow surf zones (higher settlement and recruitment at the wide surf zone) and this is exactly what was observed (Shanks et al. 2017a). This comparative experiment clearly illustrated the importance

of surf zone hydrodynamics on barnacle larval settlement and recruitment in the intertidal zone.

In this reanalysis of recruitment data from Broitman et al. (2008) and Shanks et al. (2017a), we found no support for an effect of upwelling strength as measured by alongshore wind stress on recruitment, a strong effect of two measures of potential desiccation stress on recruitment to artificial surfaces (Tuffy scrub pads and Safety-Walk plates), a weak effect of potential desiccation stress on natural barnacle recruitment, a strong effect of surf zone hydrodynamics as indicated by surf zone width on natural barnacle recruitment and a weaker significant effect on recruitment to artificial surfaces. These results are not consistent with Prediction 4, but are consistent with surf zone hydrodynamics regulating barnacle larval delivery to the intertidal zone along the west coast of the United States.

PREDICTION 5. WHERE OFFSHORE PHYTOPLANKTON CONCENTRATIONS ARE HIGHER DUE TO CURRENTS OR UPWELLING, SUBSIDIES OF PHYTOPLANKTON TO THE INTERTIDAL ZONE WILL BE HIGHER

Resources from the coastal ocean subsidize communities and populations in the intertidal zone (Polis et al. 1997, Krenz et al. 2011). The waters of the coastal ocean are sources of food (plankton and detritus) and settling larvae that can sustain populations. Temporal and especially spatial variation in these bottom-up subsidies have profound effects on the form and function of intertidal populations (Menge 2000). Researchers have attributed variations in subsidies to the shore to alongshore variations in the hydrodynamics over the continental shelf (Bustamante et al. 1995, Menge et al. 1999, 2003, Connolly et al. 2001, Broitman et al. 2008, Menge and Menge 2013). Where phytoplankton populations are larger due to the hydrodynamics of offshore waters, subsidies to the intertidal zone are hypothesized to be higher (Menge and Menge 2013). When or where phytoplankton subsidies are higher, the growth rate of filter-feeding foundation species are higher and their reproductive output is larger (Leslie et al. 2005, Bracken et al. 2012).

Above, we have discussed subsidies of larvae to the shore and related variation in these subsidies to alongshore variation in surf zone hydrodynamics. Subsidies of phytoplankton to the shore may also vary with surf zone hydrodynamics. In two month-long intensive studies of a reflective and more dissipative surf zone around the Monterey Peninsula, California, concentrations of coastal phytoplankton in the surf zone (subsidies) at a reflective shore were generally 10 times lower than in the waters just seaward of the surf zone, whereas at a more dissipative surf zone the reverse was true (Shanks et al. 2016, 2017b).

To experimentally test if phytoplankton subsidies to the intertidal zone are set by surf zone hydrodynamics, we attempted to control for phytoplankton concentrations in the coastal ocean (Shanks et al. 2017c) by comparing closely spaced stations (median separation 1 km, minimum

30 m) around Cape Arago, Oregon where surf zone width varied from a few meters to more than 200 m (i.e., reflective to more dissipative surf zones). Station spacing was close enough that the concentration of phytoplankton in the coastal waters was likely quite similar (see Shanks et al. [2017c] for a discussion of this assumption). Hence, if subsidies were set by concentrations on the inner shelf, then concentrations at the study sites should have been similar, but if they were set by surf zone hydrodynamics, the concentrations should vary with surf zone width. We found that 65–90% of the variation in the concentration of coastal phytoplankton taxa (*Pseudo-nitzschia*, *Chaetoceros*, and dinoflagellates) in the surf zone was explained by surf zone width.

We reanalyzed data from Bracken et al. (2012), who sampled the concentration of chlorophyll *a* (chl *a*) in surf zones adjacent to rocky shores in Oregon. We found that >85% of the variation in chl *a* concentration was explained by surf zone width (Shanks et al. 2017c). In addition, Bracken et al. (2012) found that mussel growth varied directly with chl *a* concentration; hence, mussel growth must also have varied with surf zone width. C. Salant (*unpublished data*) measured reproductive output of mussels and barnacles at the same sites sampled by Shanks et al. (2017c), and found that reproductive output varied with phytoplankton subsidies, which in turn varied with surf zone width, as in Shanks et al. (2017c). She also found that the concentration of coastal phytoplankton species in reflective surf zones was significantly lower than seaward on the inner shelf and the reverse was true at more dissipative surf zones, as did Shanks et al. (2016, 2017b).

Harmful algal bloom taxa (HABs) are coastal phytoplankton, and their concentration at the shore varies with surf zone hydrodynamics (Shanks et al. 2016). Most exposure of humans to HAB toxins occurs when people consume shellfish, mostly intertidal shellfish, which have consumed HAB species. Thus, the contamination of shellfish by HABs likely varies with surf zone hydrodynamics (Shanks et al. 2016).

At least over fairly short geographic distances (e.g., Monterey Peninsula, central Oregon, and Cape Arago), surf zone phytoplankton concentrations have varied directly with surf zone hydrodynamics: phytoplankton subsidies were much lower at more reflective than dissipative surf zones irrespective of the concentration in the coastal ocean. Perhaps when tested over longer distances where concentrations of phytoplankton in the coastal ocean are indeed different, while controlling for surf zone hydrodynamics, the effect of coastal phytoplankton concentrations on subsidies to the intertidal zone will become apparent. To more rigorously test the effect of surf zone hydrodynamics on the concentration of phytoplankton in surf zones, sampling still needs to be conducted both within surf zones of different types and seaward in the coastal ocean along a gradient of offshore phytoplankton concentration.

Perhaps the closest data set to this ideal is that presented in Menge and Menge (2013). There are no

measurements of offshore phytoplankton concentration, but the stations sampled extend from northern California to northern Oregon and include stations from either side of the South Island of New Zealand. These sites cover a range of upwelling conditions from sites with weak upwelling to downwelling (New Zealand stations), strong persistent upwelling (California stations) and intermittent upwelling (Oregon stations). To test for the effect of surf zone hydrodynamics on phytoplankton subsidies, we digitized data in Fig. 4 from Menge and Menge (2013) using ImageJ and determined average surf zone widths from Google Earth images of the study sites (See Shanks et al. 2017a, c for methods).

Menge and Menge (2013) found that surf zone concentrations of chl *a* were related to both the Bakun upwelling index and an index they created that measures the intermittency of upwelling, the Intermittency index. The relationships were complex with lower chl *a* concentrations at low and high values of both the Bakun upwelling and Intermittency Indices (Fig. 3A, B redrawn from Menge and Menge [2013]). At stations in central Oregon with similar or identical values of the Bakun upwelling and Intermittency Indices, however, the chl *a* concentration varied by a factor of 5 from 5 to 25 $\mu\text{g/L}$ (Fig. 3). This pattern of chl *a* concentration might be due to the chance distribution of wide and narrow surf zones among the study sites. In Fig. 3C and D, we plotted surf zone width with the Bakun upwelling and Intermittency Indices; at low and high values of the indices, surf zones coincidentally tended to be narrow while at intermediate values of the indices surf zone width ranged from narrow to quite wide (>150 m). When the surf zone chl *a* concentration (dependent variable) was regressed with surf zone width (independent variable), almost 65% of the variability in chl *a* was explained by surf zone width (Fig. 4A); narrow more reflective surf zones contained lower concentrations of chl *a* than wider more dissipative surf zones.

Perhaps the effect of offshore coastal hydrodynamics would become apparent if we scaled chl *a* concentrations by the effect of surf zone hydrodynamics. We calculated the residuals from the regression between surf zone width (independent variable) and chl *a* concentration (dependent variable) and then calculated regressions between these residuals (dependent variable) and the Bakun upwelling index and the Intermittency index (independent variables); these regressions were not significant (Fig. 4B, C). Thus, Prediction 5 is not supported, and instead, as with subsidies of larvae to the shore, phytoplankton subsidies to the shore vary with surf zone hydrodynamics.

CONCLUSION

Our reconsideration of the evidence for the IUH finds that the hypothesis is not supported. (1) Larvae of many intertidal taxa are not found in the surface Ekman layer where larvae would have to occur if upwelling were to transport them offshore and (2) larvae of intertidal invertebrate species do not occur farther offshore during

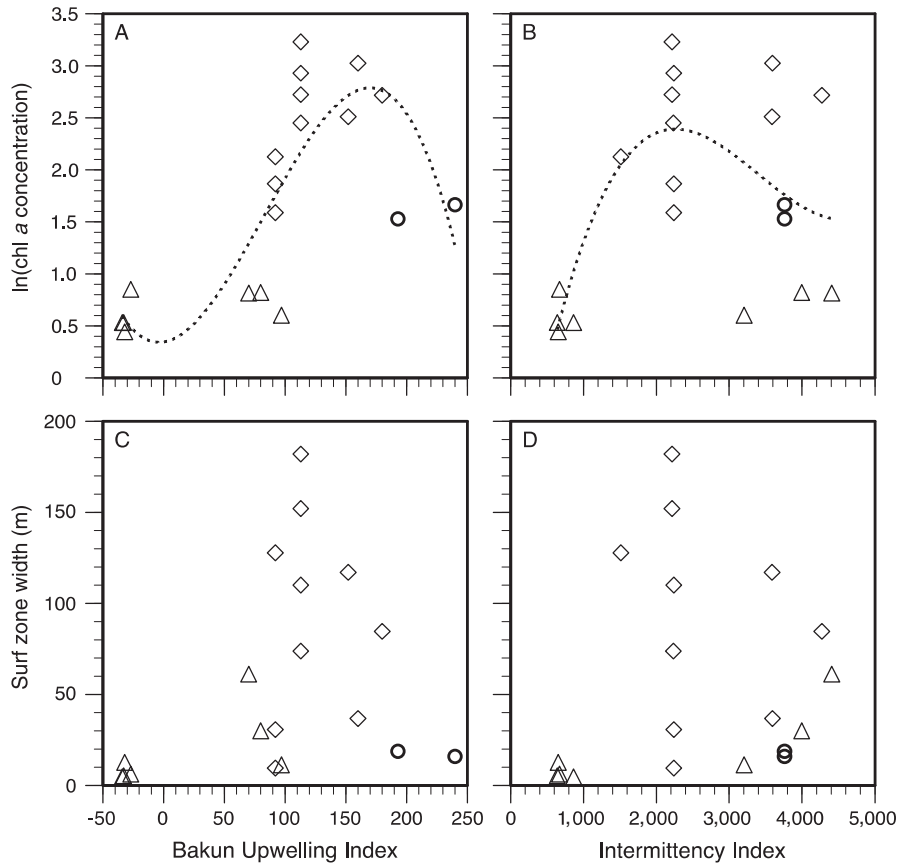


FIG. 3. Variation in chl *a* concentration ($\mu\text{g/L}$) and surf zone width relative to two upwelling indices, (A) the Bakun Upwelling index and (B) the Intermittency index (redrawn from Menge and Menge [2013]). The dotted lines are the results of a regression analysis. See Menge and Menge (2013) for a description of methods and statistical analysis. The Bakun Upwelling index is a measure of the strength of upwelling while the Intermittency index was developed by Menge et al. (2003) as a measure of the frequency of upwelling. Triangles are data from the South Island of New Zealand, diamonds are from Oregon, USA stations, and circles from northern California, USA stations. In panels C and D, the Bakun Upwelling and Intermittency indices, respectively, are plotted with average surf zone width at the sampled stations as determined from Google Earth images (see Shanks et al. 2017a, c for methods).

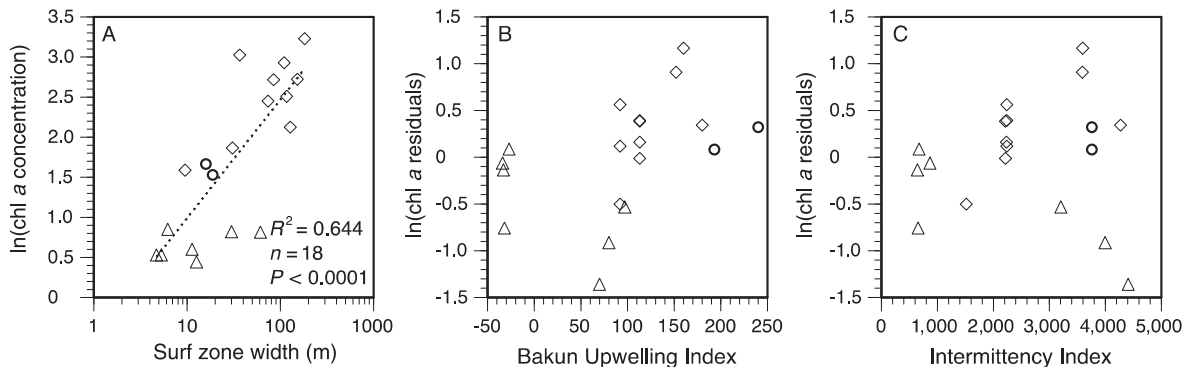


FIG. 4. Variation in chl *a* concentration ($\mu\text{g/L}$; data from Menge and Menge 2013) relative to three environmental variables. (A) Average surf zone width as determined from Google Earth images of the stations sampled by Menge and Menge (2013). See Shanks et al. (2017a, c) for methods of determining surf zone width from Google Earth images. Using the regression equation from panel A, we calculated residuals and then regressed these (dependent variable) against (B) the Bakun Upwelling index and (C) the Intermittency index (independent variable, data from Menge and Menge 2013). Neither regression was significant.

upwelling and closer to shore during downwelling as proposed. (3) Daily settlement of barnacle cyprids and the abundance of crab megalopae at the shore are not higher during downwelling and lower during upwelling, but, instead vary with a fortnightly periodicity likely due to onshore transport by tidally generated internal waves. (4) Recruitment of mussels and barnacles to artificial settlement substrates varied inversely with two measures of desiccation potential, did not vary with the strength of upwelling and downwelling, but did vary directly with surf zone width, an indicator of surf zone hydrodynamics; larval subsidies were significantly higher where surf zones were more dissipative. (5) Like larval subsidies, phytoplankton subsidies to the shore varied with surf zone hydrodynamics. Shelf hydrodynamics clearly affect phytoplankton abundance, but in the data currently available, this variation in abundance is overshadowed by the effect of surf zone hydrodynamics on the delivery of subsidies to the shore. The IUH has persisted for three decades even though critical tests of transport processes were not, until fairly recently, conducted at sea, alternative hypotheses were not seriously evaluated including studies indicating that behavior is effective at regulating cross-shelf transport of larvae (Shanks 1995, Queiroga and Blanton 2004, Morgan 2014, Morgan et al. 2017b) and other zooplankton (Peterson et al. 1979, Peterson 1998).

To test the IUH, we have focused on the CCLME where the preponderance of studies have been conducted, the hypothesis was originated by researchers on the west coast of the United States and the authors of this paper conduct their research there. Given that the hydrodynamics of wind-driven coastal upwelling/downwelling is essentially the same at each of the eastern boundary current systems, we suspect that what is true for the CCLME likely applies to these other systems as well, although this assumption needs testing. Of particular interest is what happens in systems, such as those off South Africa and Peru/Chile where the oxygen minimum layer is frequently present below the mixed layer across the continental shelf; does this layer of low oxygen water prevent larvae from swimming downward to avoid the surface Ekman layer? If larvae are unable to avoid the surface Ekman layer, then they may, as predicted by the IUH, be transported seaward during upwelling events.

The effect of surf zone hydrodynamics on the delivery of subsidies (phytoplankton and larvae) to the shore should be similar everywhere. The effects are primarily due to the physics of surf zones and physical processes are conservative. Researchers influenced by the IUH have viewed alongshore changes in intertidal community structure as gradients or clines driven by the gradual changes in the strength and persistence of upwelling along a coast. In our work on the effects of surf zone hydrodynamics on subsidies to the shore, we have not seen gradients and instead find the variation in the structure of intertidal communities along a coastline to be a mosaic driven apparently largely by the form of the surf zone adjacent to the shore. The form that a surf zone takes, dissipative

to reflective, is largely driven by the slope of the bottom beneath the surf zone. Coastal geomorphology can be consistent over long distances. For example, the entire Big Sur coast of California is steep and nearly all of the surf zones at beaches and rocky shores are narrow and more reflective. In other areas, the geomorphology can change over short distances. This appears to be the case from roughly Cape Mendocino, California through Oregon. Here we have found rocky shorelines with reflective surf zones adjacent to rock platforms imbedded in more dissipative surf zones (e.g., Strawberry Hill vs. Boilers Bay). In these situations, over surprisingly short distances (tens of meters), we have seen order of magnitude changes in the delivery of subsidies (larval settlers and phytoplankton food) to the shore (Shanks et al. 2017a, c). What our studies suggest is that shores with more dissipative surf zones and higher subsidies tend to have intertidal communities dominated by filter feeders (particularly barnacles) while shores with more reflective surf zones tend to have communities with far fewer filter feeders and denser populations of benthic macrophytes (Shanks et al. 2010; E. Conser, *unpublished data*). Our research on surf zones has forced us to see the world of intertidal ecology from a very different perspective, one where benthic pelagic coupling and intertidal community structure is largely controlled by very nearshore hydrodynamics, which in turn is controlled by geomorphology.

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LITERATURE CITED

- Austin, J. A., and J. A. Barth. 2002. Variations in the position of the upwelling front on the Oregon shelf. *Journal of Geophysical Research* 107:1–15.
- Austin, J. A., and S. J. Lentz. 2002. The inner shelf response to wind-driven upwelling and downwelling. *Journal of Physical Oceanography* 22:2171–2193.
- Barth, J. A., and R. L. Smith. 1998. Separation of a coastal upwelling jet at Cape Blanco, Oregon, USA. *South African Journal of Marine Science* 19:5–14.
- Barth, J., S. Pierce, and R. Smith. 2000. A separating coastal upwelling jet at Cape Blanco, Oregon and its connection to the California Current System. *Deep Sea Research II* 47:783–810.
- Bartilottii, C., A. dos Santos, M. Castro, Á. Peliz, and A. M. P. Santos. 2014. Decapod larval retention within distributional bands in a coastal upwelling ecosystem. *Marine Ecology Progress Series* 207:233–247.
- Botsford, L. W., C. A. Lawrence, E. P. Dever, A. Hastings, and J. Largier. 2006. Effects of variable winds on biological productivity on continental shelves in coastal upwelling systems. *Deep Sea Research II* 53:3116–3140.
- Bracken, M. S., B. A. Menge, M. M. Foley, C. J. B. Sorte, J. Lubchenco, and D. R. Schiel. 2012. Mussel selectivity for high-quality food drives carbon inputs into open-coast intertidal ecosystems. *Marine Ecology Progress Series* 459:62.

- Broitman, B. R., C. A. Blanchette, B. A. Menge, J. Lubchenco, C. Krenz, M. Foley, P. T. Raimondi, D. Lohse, and S. D. Gaines. 2008. Spatial and temporal patterns of invertebrate recruitment along the west coast of the United States. *Ecological Monographs* 78:403–421.
- Bustamante, R. H., et al. 1995. Gradients of intertidal primary productivity around the coast of South Africa and their relationships with consumer biomass. *Oecologia* 102:189–201.
- Checkley, D. M. J., and J. A. Barth. 2009. Patterns and processes in the California Current System. *Progress in Oceanography* 83:49–64.
- Connolly, S. R., B. A. Menge, and J. Roughgarden. 2001. A latitudinal gradient in recruitment of intertidal invertebrates in the northeast Pacific Ocean. *Ecology* 82:1799–1813.
- Csanady, G. T. 1974. Mass exchange episodes in the coastal boundary layer, associated with current reversals. *Rapports et Proces-Verbaux des. Scientifique de la Mer* 167:41–45.
- Farrell, T. M., D. Bracher, and J. Roughgarden. 1991. Cross-shelf transport causes recruitment to intertidal populations in central California. *Limnology and Oceanography* 36:279–288.
- Fiedler, P. C. 1986. Offshore entrainment of anchovy by displacement eddy. *California Cooperative Oceanic Fisheries Investigations Reports* 77:3248–3255.
- Fisher, J. L., W. T. Peterson, and S. G. Morgan. 2014. Does larval advection explain latitudinal differences in recruitment across upwelling regimes? *Marine Ecology Progress Series* 503:123–137.
- Fujimura, A., A. Reniers, C. Claire Paris, A. L. Shanks, J. MacMahan, and S. Morgan. 2014. Numerical simulations of larval transport into a rip-channeled surf zone. *Limnology and Oceanography* 56:1434–1447.
- Hameed, S. O., J. W. White, S. H. Miller, K. J. Nickols, and S. Morgan. 2016. Inverse approach to estimating larval dispersal reveals limited population connectivity along 700 km of wave-swept open coast. *Proceedings of the Royal Society B*. <https://doi.org/10.1098/rspb.2016.0370>
- Haury, L. R., J. Pelaez, C. J. Koblinsky, and D. Wiesenhan. 1986. Biological consequences of a recurrent eddy off Point Conception, California. *Journal Geophysical Research* 91:12937–912956.
- Helmuth, B. S. T. 1998. Intertidal mussel microclimate predicting the body temperature of a sessile invertebrate. *Ecological Monographs* 68:51–74.
- Helmuth, B., C. D. G. Harley, P. M. Halpin, and M. O'Donnell. 2000. Climate change and latitudinal patterns of intertidal thermal stress. *Science* 298:1015–1017.
- Helmuth, B. F. C., et al. 2016. Long-term, high frequency in situ measurements of intertidal mussel bed temperatures using biomimetic sensors. *Scientific Data*. <https://doi.org/10.1038/sdata.2016.87>
- Hickey, B. M., and N. S. Banas. 2008. Why is the northern end of the California Current System so productive? *Oceanography* 21:90–93.
- Korso, P. M., and A. Huyer. 1986. CTD and velocity surveys of seaward jets off northern California, July 1981 and 1982. *Journal of Geophysical Research* 91:7680–7690.
- Korso, P., J. Barth, and P. Strub. 1997. The coastal jet: Observations of surface currents over the Oregon Continental Shelf from HF radar. *Oceanography* 10:53–56.
- Krenz, C., B. A. Menge, T. L. Freidenburg, J. Lubchenco, F. Chan, M. M. Foley, and K. J. Nielsen. 2011. Ecological subsidies to rocky intertidal communities: Linear or non-linear changes along a consistent geographic upwelling transition? *Journal of Experimental Marine Biology and Ecology* 409:361–370.
- Largier, J. 2003. Considerations in estimating larval dispersal distances from oceanographic data. *Ecological Applications* 13:S71–S89.
- Leslie, H. M., E. N. Breck, C. Chan, J. Lubchenco, and B. A. Menge. 2005. Barnacle reproductive hotspots linked to nearshore ocean conditions. *Proceedings National Academy of Sciences USA* 102:10534–10539.
- Mann, K. H., and J. R. N. Lazier. 1991. *Dynamics of marine ecosystems*. Blackwell Scientific Publications, Boston, Massachusetts, USA.
- Menge, B. A. 2000. Top-down and bottom-up community regulation in marine rocky intertidal habitats. *Journal of Experimental Marine Biology and Ecology* 250:257–289.
- Menge, B. A., and D. N. L. Menge. 2013. Dynamics of coastal meta-ecosystems: the intermittent upwelling hypothesis and a test in rocky intertidal regions. *Ecological Monographs* 83:283–310.
- Menge, B., D. B. A. J. Lubchenco, E. Sanford, E. Dahlhoff, P. Halpin, G. Hudson, and J. Runaford. 1999. Top-down and bottom-up regulation of New Zealand rocky intertidal communities. *Ecological Monographs* 69:297–330.
- Menge, B., et al. 2003. Coastal oceanography sets the pace of rocky intertidal community dynamics. *Proceedings of the National Academy of Sciences USA* 100:12229–12234.
- Menge, B., C. Blanchette, P. Raimondi, T. Freidenburg, S. Gaines, J. Lubchenco, D. Lohse, D. Hudson, M. Foley, and J. Pamplin. 2004. Species interaction strength: Testing model predictions along an upwelling gradient. *Ecological Monographs* 74:663–684.
- Morgan, S. G. 2001. The larval ecology of marine communities. Pages 159–181 in M. D. Bertness, S. D. Gaines, and M. E. Hay, editors. *Marine community ecology*. Sinauer, Sunderland, Massachusetts, USA.
- Morgan, S. 2014. Behaviorally mediated larval transport in upwelling systems. *Advances in Oceanography* 17. <https://doi.org/10.1155/2014/364214>
- Morgan, S. G., and J. L. Fisher. 2010. Larval behavior regulates nearshore retention and offshore migration in an upwelling shadow and along the open coast. *Marine Ecology Progress Series* 404:109–126.
- Morgan, S., J. Fisher, S. Miller, S. McAfee, and J. Largier. 2009a. Nearshore larval retention in a region of strong upwelling and recruitment limitation. *Ecology* 90:3489–3502.
- Morgan, S., J. L. Fisher, A. J. Mace, L. J. Akins, A. M. Slaughter, and S. M. Bollens. 2009b. Cross-shelf distributions and recruitment of crab larvae in a region of strong upwelling. *Marine Ecology Progress Series* 380:173–185.
- Morgan, S. G., A. L. Shanks, A. G. Fujimura, A. J. H. M. Reniers, J. MacMahan, C. D. Griesemer, M. Jarvis, and J. Brown. 2016. Surfzone hydrodynamics as a key determinant of spatial variation in rocky intertidal communities. *Proceedings of the Royal Society B*. <https://doi.org/10.1098/rspb.2016.1017>
- Morgan, S. G., A. L. Shanks, A. G. Fujimura, A. J. H. M. Reniers, J. MacMahan, and F. Feddersen. 2017a. Plankton subsidies to surfzone and intertidal communities. *Annual Review in Marine Science*. <https://doi.org/10.1146/annurev-marine-010816-060514>
- Morgan, S. G., A. L. Shanks, A. G. Fujimura, A. J. H. M. Reniers, J. MacMahan, C. D. Griesemer, M. Jarvis, and J. Brown. 2017b. Surf zones regulate larval supply and zooplankton subsidies to nearshore communities. *Limnology and Oceanography*. <https://doi.org/10.1002/lno.10609>
- Navarrete, S., E. Wieters, B. Broitman, and J. Castilla. 2005. Scales of benthic-pelagic coupling and the intensity of species interactions: From recruitment limitation to top-down control. *Proceedings of the National Academy of Sciences USA* 102:18046–18051.
- Nickols, K. J., B. Gaylord, and J. L. Largier. 2012. The coastal boundary layer: predictable current structure decreases alongshore transport and alters scales of dispersal. *Marine Ecology Progress Series* 464:17–35.

- Nickols, K. J., S. H. Miller, B. Gaylord, S. G. Morgan, and J. L. Largier. 2013. Spatial differences in larval supply within the coastal boundary layer impact availability to shoreline habitats. *Marine Ecology Progress Series* 494:191–203.
- Peterson, W. T. 1998. Life cycle strategies of copepods in coastal upwelling zones. *Journal of Marine Systems* 15:313–326.
- Peterson, W. T., C. B. Miller, and A. Hutchinson. 1979. Zonation and maintenance of copepod populations in the Oregon upwelling zone. *Deep Sea Research* 26A:467–494.
- Pineda, J. 1991. Predictable upwelling and the shoreward transport of planktonic larvae by internal tidal bores. *Science* 253:548–551.
- Pineda, J. 1994. Spatial and temporal patterns in barnacle settlement rate along a southern California rocky shore. *Marine Ecology Progress Series* 107:125–138.
- Polis, G. A., W. B. Anderson, and R. D. Holt. 1997. Towards an integration of landscape and food web ecology: the dynamics of spatially subsidized food webs. *Annual Review of Ecology and Systematics* 28:289–316.
- Poulin, E., A. T. Palma, G. Leiva, D. Narvaez, R. Pacheco, S. A. Navarrete, and J. C. Castilla. 2002. Avoiding offshore transport of competent larvae during upwelling events: The case of the gastropod *Concholepas concholepas* in Central Chile. *Limnology and Oceanography* 47:1248–1255.
- Queiroga, H., and J. Blanton. 2004. Interactions between behaviour and physical forcing in the control of horizontal transport of decapod crustacean larvae. *Advances in Marine Biology* 47:107–214.
- Rilov, G., S. Dudas, B. Menge, B. Grantham, J. Lubchenco, and D. Schiel. 2008. The surf zone: a semi-permeable barrier to onshore recruitment of invertebrate larvae? *Journal of Experimental Marine Biology and Ecology* 361:59–74.
- Roegner, G. C., D. A. Armstrong, and A. L. Shanks. 2007. Wind and tidal influences on larval crab recruitment to an Oregon estuary. *Marine Ecology Progress Series* 351:177–188.
- Roughgarden, J., S. D. Gaines, and H. Possingham. 1988. Recruitment dynamics in complex life cycles. *Science* 241:1460–1466.
- Roughgarden, J., J. T. Pennington, D. Stoner, S. Alexander, and K. Miller. 1991. Collisions of upwelling fronts with the intertidal zone: The cause of recruitment pulses in barnacle populations of central California. *Acta Oecologia* 12:35–51.
- Shanks, A. L. 1983. Surface slicks associated with tidally forced internal waves may transport pelagic larvae of benthic invertebrates and fishes shoreward. *Marine Ecology Progress Series* 13:311–315.
- Shanks, A. L. 1986. Tidal periodicity in the daily settlement of intertidal barnacle larvae and an hypothesized mechanism for the cross-shelf transport of cyprids. *Biological Bulletin* 170:429–440.
- Shanks, A. L. 1988. Further support of the hypothesis that internal waves can transport larvae of invertebrates and fish onshore. *Fisheries Bulletin* 86:703–714.
- Shanks, A. L. 1995. Mechanisms of cross-shelf dispersal of larval invertebrates and fish. Pages 324–367 in L. R. McEdward, editor. *Ecology of marine invertebrate larvae*. CRC Press, Boca Raton, Florida, USA.
- Shanks, A. L. 1998. Abundance of post-larval *Callinectes sapidus*, *Penaeus* spp., *Uca* spp., and *Labinia* spp. collected at an outer coastal site and their cross-shelf transport. *Marine Ecology Progress Series* 168:57–69.
- Shanks, A. 2006. Mechanisms of cross-shelf transport of crab megalopae inferred from a time series of daily abundance. *Marine Biology* 148:1383–1399.
- Shanks, A. L. 2009a. Barnacle settlement vs. recruitment as indicators of larval delivery: time series analysis and hypothesized delivery mechanisms. *Marine Ecology Progress Series* 385:217–226.
- Shanks, A. L. 2009b. Barnacle settlement vs. recruitment as indicators of larval delivery: effects of post-settlement mortality and recruit density. *Marine Ecology Progress Series* 385:205–216.
- Shanks, A. L., and G. Eckert. 2005. Life-history traits and population persistence of California Current Fishes and Benthic Crustaceans; solution of a marine drift paradox. *Ecological Monographs* 75:505–524.
- Shanks, A. L., and L. Brink. 2005. Upwelling, downwelling, and cross-shelf transport of bivalve larvae: test of a hypothesis. *Marine Ecology-Progress Series* 302:1–12.
- Shanks, A. L., and R. K. Shearman. 2009. Paradigm lost? Cross-shelf distributions of intertidal invertebrate larvae were unaffected by upwelling or downwelling. *Marine Ecology Progress Series* 385:189–204.
- Shanks, A. L., J. Largier, and J. Brubaker. 2003. The nearshore distribution of larval invertebrates during an upwelling event. *Journal of Plankton Research* 25:645–667.
- Shanks, A. L., J. Largier, L. Brink, J. Brubaker, and R. Hooff. 2000. Demonstration of the onshore transport of larval invertebrates by the shoreward movement of an upwelling front. *Limnology and Oceanography* 45:230–236.
- Shanks, A. L., J. Largier, L. Brink, J. Brubaker, and R. Hooff. 2002. Observations on the distribution of meroplankton during a downwelling event and associated intrusion of the Chedspeake Bay estuarine plume. *Journal of Plankton Research* 24:391–416.
- Shanks, A. L., S. G. Morgan, J. MacMahan, and A. J. H. M. Reniers. 2010. Surf zone physical and morphological regime as determinants of temporal and spatial variation in larval recruitment. *Journal of Experimental Marine Biology and Ecology* 392:140–150.
- Shanks, A. L., S. G. Morgan, J. MacMahan, A. J. H. M. Reniers, M. Jarvis, J. Brown, and C. Griesemer. 2014. Onshore transport of plankton by internal tides and upwelling-relaxation events. *Marine Ecology Progress Series* 502:39–51.
- Shanks, A. L., S. G. Morgan, J. MacMahan, A. J. H. M. Reniers, R. Kudela, M. Jarvis, J. Brown, A. Fujimura, I. Ziccarelli, and C. Griesemer. 2016. Variation in the abundance of *Pseudo-nitzschia* and domoic acid with surf zone type. *Harmful Algae* 55:172–178.
- Shanks, A. L., S. G. Morgan, J. MacMahan, and A. J. H. M. Reniers. 2017a. Alongshore variation in barnacle populations is determined by surfzone hydrodynamics. *Ecological Monographs*. <https://doi.org/10.1002/ecm.1265>
- Shanks, A. L., S. G. Morgan, J. MacMahan, A. J. H. M. Reniers, M. Jarvis, J. Brown, C. Griesemer, A. Fujimura, and L. Ziccarelli. 2017b. Persistent differences in horizontal gradients in phytoplankton concentration maintained by surfzone hydrodynamics. *Estuaries and Coasts*. <https://doi.org/10.1007/s12237-017-0278-2>
- Shanks, A. L., P. Sheeley, and L. Johnson. 2017c. Phytoplankton subsidies to the intertidal zone are strongly affected by surfzone hydrodynamics. *Marine Ecology*. <https://doi.org/10.1111/maec.12441>
- Strub, P. T., and C. James. 2000. Altimeter-derived variability of surface velocities in the California Current System: 2. Seasonal circulation and eddy statistics. *Deep Sea Research* 47:831–870.
- Strub, P. T., P. M. Kosro, and A. Huyer. 1991. The nature of cold filaments in the California Current system. *Journal of Geophysical Research* 96:14693–614706.