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Alongshore variation in barnacle populations is determined by surf zone hydrodynamics

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Abstract. Larvae in the coastal ocean are transported toward shore by a variety of mechanisms. Crossing the surf zone is the last step in a shoreward migration and surf zones may act as semipermeable barriers altering delivery of larvae to the shore. We related variation in the structure of intertidal barnacle populations to surf zone width (surf zone hydrodynamics proxy), wave height, alongshore wind stress (upwelling proxy), solar radiation, and latitude at 40 rocky intertidal sites from San Diego, California to the Olympic Peninsula, Washington. We measured daily settlement and weekly recruitment of barnacles at selected sites and related these measures to surf zone width. *Chthamalus* density varied inversely with that of *Balanus*, and the density of *Balanus* and new recruits was negatively related to solar radiation. Across the region, long-term mean wave height and an indicator of upwelling intensity and frequency did not explain variation in *Balanus* or new recruit densities. *Balanus* and new recruit densities, daily settlement, and weekly recruitment were up to three orders of magnitude higher at sites with wide (>50 m), more dissipative surf zones with bathymetric rip currents than at sites with narrow (<50 m) more reflective surf zones. Surf zone width explained 30–50% of the variability in *Balanus* and new recruit densities. We sampled a subset of sites <5 km apart where coastal hydrodynamics such as upwelling should be very similar. At paired sites with similar surf zone widths, *Balanus* densities were not different. If surf zone widths at paired sites were dissimilar, *Balanus* densities, daily settlement, and weekly recruitment were significantly higher at sites with the wider, more dissipative surf zone. The primary drivers of surf zone hydrodynamics are the wave climate and the slope of the shore and these persist over time; therefore site-specific stability in surf zone hydrodynamics should result in stable barnacle population characteristics. Variations in surf zone hydrodynamics appear to play a fundamental role in regulating barnacle populations along the open coast, which, in turn, may have consequences for the entire intertidal community.

Key words: *Balanus*; *Chthamalus*; larval recruitment; larval settlement; latitudinal variation; rip current; surf zone hydrodynamics; upwelling.

INTRODUCTION

Recruitment is a key determinant of the dynamics and structure of adult populations and communities, but recruitment of marine organisms is still not well understood even after more than a century of study. Over 100 years ago, fisheries biologists began attributing wide fluctuations in year class strength to variation in larval success and subsequent recruitment (Hjort 1914). They came to this realization in part because relationships between population sizes (i.e., stock) and recruitment were and remain notoriously poor (Frank and Leggett 1994). Marine ecologists determined that interspecific interactions following larval settlement often played a large role in regulating populations with population size

being set by postsettlement density-dependent interactions (Caley et al. 1996). It was realized in the 1980s, however, that many of these previous studies were conducted at sites where larvae settled abundantly, leading to intense density-dependent interactions (Connell 1985, Young 1990, Booth and Brosnan 1995, Morgan 2001, Underwood and Keough 2001). In regions with low recruitment, researchers found lower postsettlement mortality with populations composed of multiple cohorts of recruits (Yoshioka 1982, Victor 1983, Underwood and Denley 1984, Connell 1985, Gaines and Roughgarden 1985, Menge and Sutherland 1987, Doherty and Fowler 1994). The degree of saturation by larval settlers is now widely recognized as an important element in establishing the dynamics of populations. Processes that generate large temporal and spatial variation in larval supply are, however, not well understood and have become a focus of investigation (Morgan 1995, 2001, Underwood and Keough 2001, Shanks 2013).

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In productive upwelling regimes along the western margins of continents, latitudinal variation in wind-driven upwelling was proposed to determine the amount of larvae lost to offshore transport, and the number of larvae returning to replenish populations of nearshore species was hypothesized to be limited to infrequent wind-relaxation events (Roughgarden et al. 1988, Menge and Menge 2013). Coastwide surveys of larval recruitment of dominant intertidal species appear consistent with this hypothesis; recruitment was higher where upwelling was weaker and intermittent than where it was strong and persistent (Broitman et al. 2001, 2008, Connolly et al. 2001, Menge et al. 2003, Navarrete et al. 2005).

Recent research suggests that alongshore variation in the delivery of larvae to the shore may also be affected by variation in surf zone hydrodynamics (Rilov et al. 2008, Shanks et al. 2010). Surf zone systems range from dissipative to intermediate to reflective (Wright and Short 1984, McLachlan and Brown 2006). Dissipative shores are characterized by a wide surf zone, gradual shore slope and, if a beach, fine-grain sand. Intermediate shores support bathymetrically controlled rip currents, which are associated with alongshore-variable bars, shoals, and rip channels (Wright and Short 1984, McLachlan and Brown 2006). Breaking waves and the dissipation of wave energy as waves cross the surf zone drive onshore flow, which feeds into the rip currents. Flow is seaward in rip currents and shoreward over the shoals between rip currents; rip current flow systems effectively exchange water and material between the inner shelf and the surf zone (MacMahan et al. 2006). Reflective beaches are at the other extreme and are characterized by narrow surf zones, steep shore slopes, coarse sand if a beach and an absence of bathymetrically controlled rip currents, although transient rip currents can be present (Wright and Short 1984, Suanda and Feddersen 2015, Hally-Rosendahl and Feddersen 2016). Transient rip currents form in all surf zones. At more dissipative surf zones with bathymetric rip currents, flow from transient rip currents is likely directed into the bathymetric rip system and augments the flow rates causing more rapid exchange of surf zone water with that offshore. At sites without bathymetric rip currents, transient rip currents act like large patches of turbulence, which can eject water from the surf zone (Hally-Rosendahl et al. 2014, Suanda and Feddersen 2015, Hally-Rosendahl and Feddersen 2016). To compensate for this loss of water, water must enter the surf zone; transient rip currents cause the exchange of surf zone water with offshore water. Rocky shore surf zones are usually steep and, hence, reflective, however, rocky shores surrounded by more dissipative surf zones are common.

We found that population and new recruit densities of barnacles and limpets were 10 or more times higher at more dissipative than reflective shores (Shanks et al. 2010). We hypothesized that the delivery of larvae and other plankton to the intertidal zone is affected by surf zone type, whereby larvae developing in the coastal

ocean and plankton are held away from shore at reflective surf zones while the reverse is true at more dissipative surf zones. Hence, for species with larvae that develop in the coastal ocean, we hypothesized that higher settlement rates, higher densities of new recruits and potentially higher densities of adults would occur at sites with more dissipative surf zones.

Our extensive physical and biological oceanographic studies at a reflective and a more dissipative shore supported this hypothesis. At both sites, daily plankton samples were collected in and seaward of the surf zone and, concurrently, the hydrodynamics of the surf zone and inner shelf were monitored with fixed instruments and dye releases. At the reflective shore (Carmel River State Beach, CRSB) with a very narrow surf zone (Shanks et al. 2015), flow was offshore throughout most of the water column (undertow) and landward near the surface due to breaking waves, but this current regime was only present within the surf zone. Dye studies and daily observations indicated that bathymetric rip currents were not present, however, transient rips may have been present but were brief enough they were not observed. Lower concentrations of coastal phytoplankton and zooplankton occurred inside than outside the surf zone suggesting that surf zone hydrodynamics was a barrier to the delivery of plankton subsidies from the coastal ocean to the surf zone. Concentrations of coastal plankton species were typically an order of magnitude lower within the surf zone than just offshore, even just 20 m offshore (Shanks et al. 2015, 2016, Morgan et al. 2016; Shanks et al., *unpublished data*). Water within the surf zone was exchanged with offshore water more slowly than at a more dissipative surf zone with rip currents (Brown 2014, Brown et al. 2015). Our data suggested that there are two potential mechanisms by which larvae may enter a reflective surf zone: (1) near the surface with breaking waves and (2) near the bottom via benthic streaming (near-bottom wave-driven shoreward flow present outside the surf zone). We hypothesized that concentrations of plankton in surface waters entering the surf zone with breaking waves would be low (Morgan et al. 2016, Shanks et al. 2016). Zooplankton may avoid high surface turbulence as waves break at the outer edge of the surf zone, decreasing their concentration in the surface waters entering the surf zone. We hypothesized that concentrations of competent larvae occurring in bottom waters entering the surf zone may be higher due to benthic streaming. Some competent meroplankters, including cyprids, were more concentrated within the surf zone than offshore on about one-half of the sample dates during the month of sampling, although median cyprid concentrations within the surf zone were only about 57% of that offshore ($SD = 187\%$; Morgan et al. 2016, Shanks et al. 2016). Concentrations of detritus particles and competent larvae in the surf zone were positively correlated, and they were negatively correlated with wave height, raising the possibility that they may have entered the surf zone via benthic

streaming during periods of low wave activity (Navarrete et al. 2015, Shanks et al. 2015).

Where alongshore currents are present in surf zones, water must enter the current from offshore, potentially delivering subsidies to the intertidal zone and later exit the surf zone. Due to the curved shape of the shore at CRSB, an alongshore current was generated within the sampled reflective surf zone. This current originated at the northern end of the beach and exited as an offshore flow toward the southern end of the beach. Although the northern edge of the alongshore current was outside of our sample grid for physical variables, our modeling study (Fujimura et al. 2014) indicated that water from outside the surf zone entered the alongshore flow potentially transporting larvae into the surf zone near where we measured barnacle settlement and abundance as well as phytoplankton concentration in the surf zone, and then it exited farther to the south. In similar settings, a modeling study by Castelle and Coco (2013) indicated that floating objects in the surf zone, such as surface drogues transported by surf zone currents, were ejected onto the inner shelf and did not return to the surf zone. Even though flow at the northern end of the alongshore current was onshore at CRSB, only one barnacle settled in one month and adult density was low (16 individuals/100 cm², 95% CI 0-16 individuals/100 cm²; Shanks et al. 2015). In addition, the concentration of coastal phytoplankton in the surf zone was only 1% (SD 2%) of that seaward of the surf zone on the inner shelf (Shanks et al. 2016). Why barnacle settlement and phytoplankton concentrations were so low at this site despite its association with an onshore current is unclear.

During a different month, we sampled plankton within and just seaward of a more dissipative shore at Sand City, California (Morgan et al. 2016, Shanks et al. 2016). Extensive physical oceanographic measurements were taken during this month and this site has been studied extensively previously (Reniers et al. 2009, MacMahan et al. 2010, Brown et al. 2015). The surf zone at this site is characterized as intermediate with numerous bathymetric rip currents (Wright and Short 1984, McLachlan and Brown 2006). Wave action drives water into the surf zone over shoals separating rip channels. At the landward edge of the surf zone, water enters feeder channels flowing into rip currents where it flows rapidly offshore exiting beyond the breaker line. Dye studies indicated that water was effectively exchanged between the surf zone and the inner shelf by the rip current system (Brown et al. 2015). As a consequence, meroplankton and phytoplankton concentrations within the surf zone were correlated with concentrations in the coastal ocean, and plankton was often concentrated in recirculation cells of the rip current system (Fujimura et al. 2014, Shanks et al. 2016). On 22 of 28 sample days, cyprid concentrations were higher in the surf zone than offshore and median concentrations were about 370% of those offshore (SD 1,622; Morgan et al. 2016). On nearby rocks, the average density of *Balanus* spp.

(mostly *B. glandula*) and barnacle recruits were far higher than at the reflective site (1,114 individuals/100 cm² and 240 individuals/100 cm², respectively).

Here we test the hypotheses that variation in daily barnacle settlement, weekly recruitment, and densities of new barnacle recruits and *Balanus* adults vary with surf zone hydrodynamics. We focused on barnacles because they were abundant at all 40 sites surveyed along ~2,000 km of the west coast of the USA and are a model organism for rocky intertidal ecology. To determine whether surf zone type regulates barnacle populations, study sites ranged from typically studied rocky benches to rocks set within sandy beaches. Weekly barnacle recruitment and daily settlement were tracked at a subset of sites. We placed our population and settlement data in context of alongshore variation in physical processes, which may affect barnacle populations by generating variation in the delivery of larvae to the shore or the survival of settled individuals. Because the strength and persistence of wind driven coastal upwelling has been proposed to affect the delivery of larvae to the shore, we used alongshore wind stress as a proxy for upwelling. Because desiccation stress can cause the mortality of intertidal organisms (Somero 2002, Tomanek and Helmuth 2002), we used average daily solar radiation as a proxy for potential desiccation stress. Because our primary motivation for this study was to investigate the potential role of surf zone hydrodynamics as a driver of population structure in intertidal barnacles, we used average wave height during the spring and summer and surf zone width as indicators of surf zone hydrodynamics.

METHODS

We surveyed intertidal barnacle populations at 40 locations from San Diego, California to the Olympic Peninsula, Washington, USA (Fig. 1; Appendix S1). We conducted the study in 2012 during spring and summer when barnacle reproduction and growth peaks. Some sites consisted of long stretches of rocky shore while other sites were rocks within beaches. We classified sites as “rocky shores” when rocky habitat was at least 50 m long (Schoch et al. 2006) and “beach rocks” when rocky habitat was <50 m long and surrounded by sand (Fig. 2). The rocky shore habitats are benches commonly studied by intertidal ecologists, whereas the beach rocks are less frequently studied.

At each site, we photographed barnacles while characterizing the intertidal zone and adjacent surf zone. Field sampling and analysis of photographs were similar to that described in Shanks et al. (2010). Briefly, at least 10 photographs were taken haphazardly within the barnacle zone, i.e., the intertidal strata where barnacles were most abundant (Connolly and Roughgarden 1998). The goal was to take a series of photographs that were in aggregate representative of the entire barnacle population within the strata where they were most abundant. Photographs (~10 × 25 cm) of rocks with different

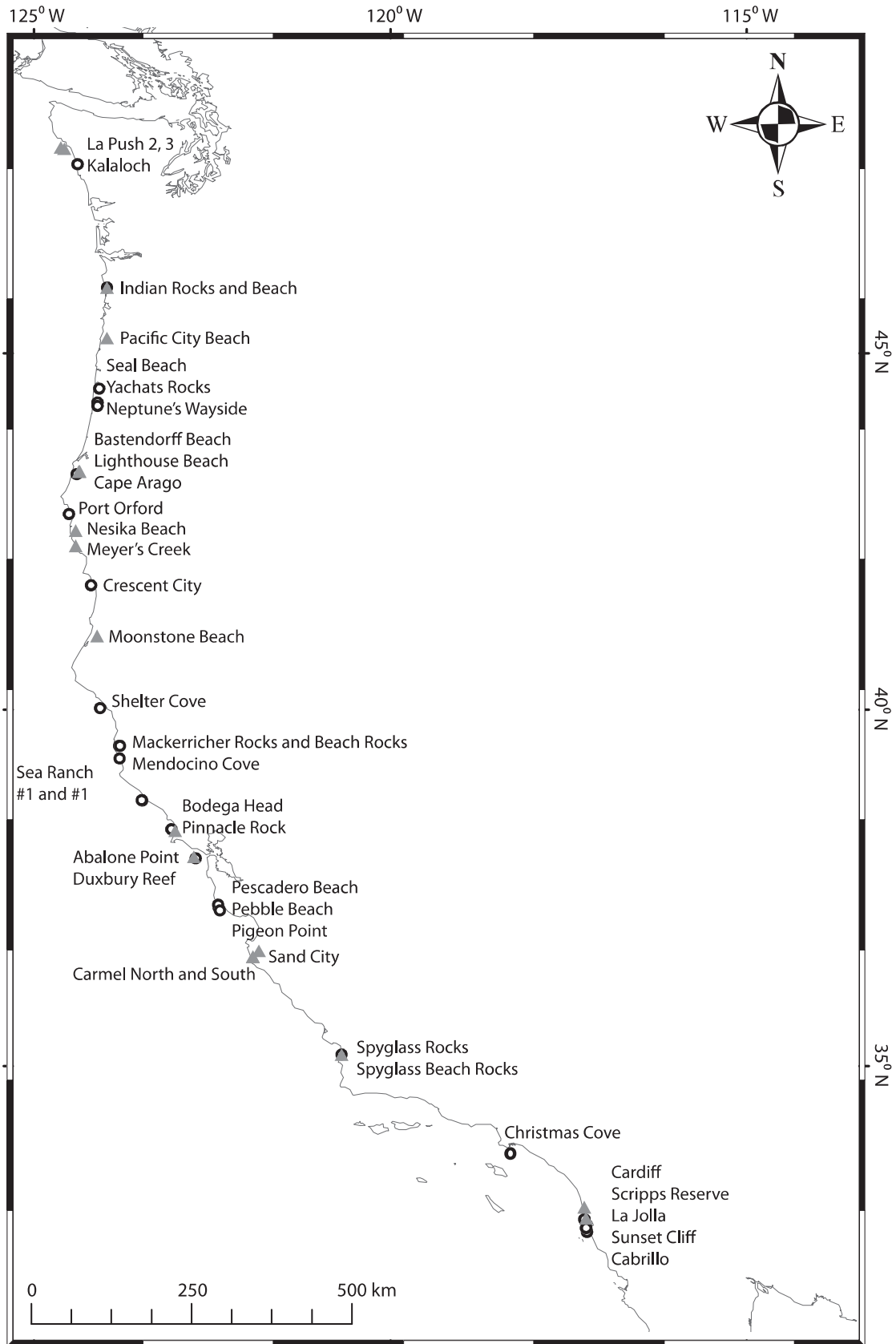


FIG. 1. Study site locations in Washington, Oregon, and California, USA. Circles and triangles represent sites where we sampled rocky shores and beach rocks, respectively. Sample site latitudes, longitudes, and average surf zone widths ($\pm$ SD) are presented in Appendix S1.

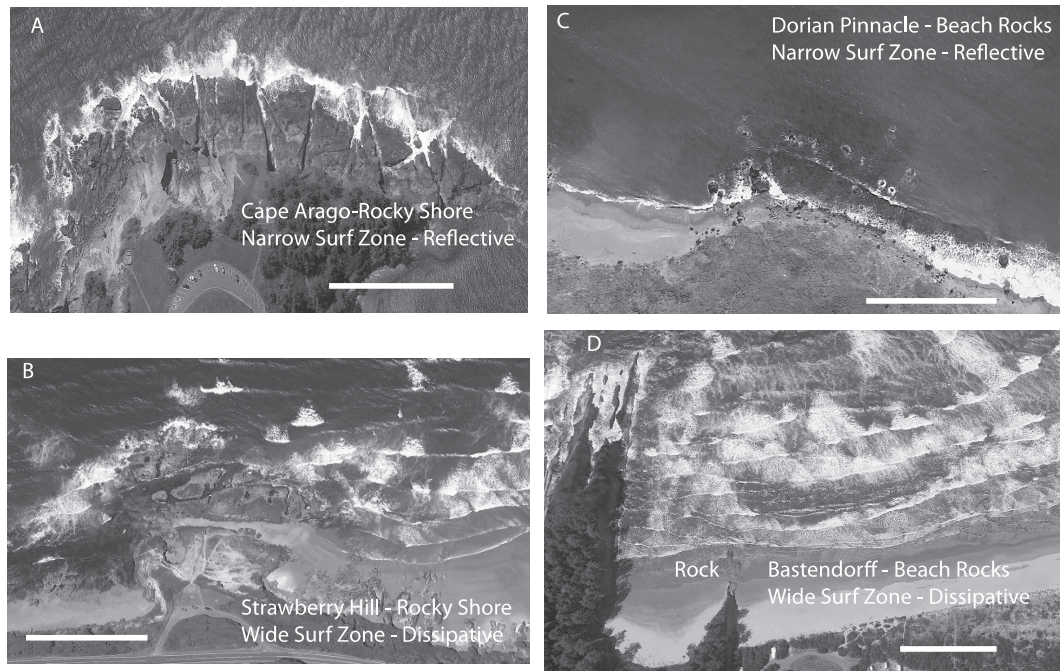


FIG. 2. Photographs of rocky shore and beach rocks at reflective and dissipative surf zones. (A) Cape Arago, a rocky shore with a narrow reflective surf zone. (B) Strawberry Hill, a rocky shore with a wide dissipative surf zone. (C) Dorian Pinnacle, beach rock site with a narrow reflective surf zone. (D) Bastendorff, beach rock site with a wide dissipative surf zone. We classified sites as “rocky shores” when rocky habitat was at least 50 m long (Schoch et al. 2006) and “beach rocks” when rocky habitat was <50 m long and surrounded by sand. The scale bars are about 100 m. Images are from Google Earth.

orientations relative to the sun and waves were taken using a digital camera and strobe. In this way, we tried to minimize the random effects of solar and wave exposure in our data. An object of known size was placed in each photograph to act as a scale bar during digital analysis. Photographs were analyzed with ImageJ software (National Institute of Health). Using enlarged images, we identified *Chthamalus* or *Balanus* using shell color (*Chthamalus* brown-gray; *Balanus* white to gray) and the shape of the operculum (*Chthamalus* oval, *Balanus* diamond; descriptions available online).⁶ We could identify species down to a size of about 1.5 mm diameter and we defined these smaller individuals, which are approximately four weeks old, as “new recruits.” To determine densities, using ImageJ, we placed a 1×1 cm grid over the photograph, and we enumerated and recorded the sizes of barnacles within grid transects. If barnacles were abundant, we counted and measured at least 200 individuals in a randomly selected subset of the grid. This counting procedure is similar to that used when counting

phytoplankton on a slide and yields a sample standard deviation between 10% and 20% (Venrick 1978). If densities were low, we enumerated and measured all individuals in the photograph. When barnacles were not too dense, basal widths of barnacles were measured, however, adult barnacles were so densely packed at some sites that the base of the individuals could not be seen. When densely packed, barnacles tend to grow as flared cylinders with a narrow base and a wider top. In this growth pattern, they form hummocks and are often poorly connected to the substrate (Bertness et al. 1998). At these sites, we measured the maximum width of the barnacle. From these data we determined size frequency distributions and the density of *Chthamalus* and *Balanus*. New recruits occurred on bare rock, but they were also common or abundant on adult barnacles. The density of new recruits is per quadrat and not per area of bare rock within the quadrat.

To complement the photographic data collected during the survey, we measured daily settlement during summer 2011 at six sites and weekly recruitment from late July through September 2010 at eight sites that were characterized by more dissipative and reflective surf zones (see

⁶ <http://www.eeb.ucsc.edu/pacificrockyintertidal/target/target-species-chthamalus-balanus.html#target-barn-top>

Table S2 in Appendix S1 for latitudes, longitudes, and surf zone widths). Daily settlement was quantified at two sites in Carmel Bay, California (6 June–15 July) adjacent to the reflective beach (CRSB) where we conducted an intensive month-long study (Shanks et al. 2015), two sites each near Coos Bay, Oregon (6 June–5 September) and Bodega Bay, California (19 June–11 September). Weekly recruitment was quantified in central California near Bodega Bay (30 July–24 September) and five sites in southern Oregon (July–1 October). Settlers and recruits were counted in marked quadrats on bare rocks situated within the intertidal zone where barnacles were most abundant; in this way the daily settlement and weekly recruitment data could be most confidently compared with the photographic survey data. Settlers and recruits were too small to reliably identify to species. After enumeration they were removed from the settlement surface with a stiff wire brush. We regressed daily settlement and weekly recruitment (dependent variable) with physical variables (independent variable) to test the effect of surf zone hydrodynamics.

Measurements of standard metrics of surf zone morphodynamics at each study site generally followed the methods of Shanks et al. (2010). We made these measurements in the field when we visited each sample site and then compared these data to measurements taken from Google Earth images. We measured the width and slope of the intertidal zone. Using a survey tape, intertidal width ($n = 5$ measurements per site) was measured from the water line to the top of the intertidal zone on rocky shores (i.e., the upper limit of the intertidal community) and to the highest strandline or drift line (i.e., the line of debris deposited by the waves at high tide) on sandy beaches. Using standard surveying techniques (e.g., surveyor's level and stadia rod), we measured the slope of the shore ($n = 5$ measurements per site) from the high tide line or highest strand line to the water's edge (defined above). As an index of the width of the surf zone, we measured the time it took waves to cross the surf zone. Wave crossing time was measured from when a wave first broke until it reached the swash line ($n = 10$ waves measured per site). We used images from Google Earth during spring and summer to determine the average width of the surf zone and intertidal zone as well as the number and spacing of rip currents at each site. In these images, surf zone width was measured immediately seaward of the sample site. Width was from the most seaward breaking wave to the swash line (see Appendix S1 for Google Earth images illustrating this technique), and width of the intertidal zone was measured from the swash line to the highest drift line. The number of useable Google Earth images varied from 3 to 14 and were taken between 2007 and 2014. Measurements from these images were used to calculate the average and standard deviation of surf zone width (Appendix S1: Fig. S3). As an indication that bathymetric rip current recirculation systems were present, we measured the number and average spacing of bathymetric rip currents within 1 km of

each side of the study sites in Google Earth images (see Appendix S2 illustrating this technique). Bathymetric rip currents were clearly apparent in only some images. We used three criteria to identify them: (1) deeper channels under bathymetric rip currents and feeder channels were visible during low tide (Appendix S2: Fig. S3), (2) waves did not break in the deeper water of bathymetric rip channels (Appendix S2: Fig. S3), and (3) plumes of sediment jetted seaward of the surf zone by rip currents. These criteria also were used to identify bathymetric rip currents in the field.

Because of the latitudinal extent of sampling (2,000 km), it was not feasible to sample each site at the same tidal elevation and wave conditions. All measurements made in the field and from the Google Earth images have an inherent level of variation; this variability is in part caused by our sampling methods, but also just because surf zone conditions are variable. We determined the reliability of our surf zone measurements in several ways. Using all of the Google Earth images at each site, we calculated the average and 95% confidence interval of surf zone width. We verified measurements of average surf zone width from Google Earth images by calculating the correlation coefficient between the square root of surf zone width and field measurements of the time it took waves to cross the surf zone. Similarly, we verified measurements of average beach width from Google Earth images by calculating the correlation coefficient between these data and measurements that we made in the field. To verify that our proxies of surf zone characteristics were comparable, we calculated the correlation coefficient between the width and slope of the intertidal zone and the average width of the adjacent surf zone as determined from the Google Earth images.

We obtained wave and wind data from NOAA buoys closest to our study sites (National Data Buoy Center, Appendix S1: Table S3; buoy data *available online*).⁷ Wave and weather buoys are spaced about 120 km apart. The upwelling index was obtained from the Pacific Fisheries Environmental Laboratory for the spring and summer of 2012, when the photographic sampling occurred (data *available online*).⁸ Average wave height was included as a physical variable, because dissipative surf zones tend to be at sites with larger waves (Wright and Short 1984, Woodroffe 2002). We calculated hourly alongshore wind stresses using data from buoys and standard equations (Pedlosky 1987); alongshore wind stress forces upwelling (Barber and Smith 1981, Csanady 1981, Austin and Lentz 2002). In the standard equation for wind stress, drag varies with wind speed as ocean roughness increases with wind speed. Because a constant drag coefficient was used, values should be considered pseudo-wind stresses. We regressed alongshore wind stress and wave height data against latitude and used these relationships to calculate values of

⁷ <http://www.ndbc.noaa.gov>

⁸ <http://www.pfeg.noaa.gov>

alongshore wind stress and wave height for each of our sample sites. Barnacles, as is typical for intertidal organisms, can suffer from desiccation stress, and hence, variation in their alongshore abundance may vary with desiccation. As a proxy for desiccation stress, we used average daily solar radiation, which was obtained for each site from the National Solar Radiation Data Base.⁹

We present the data on latitudinal change in upwelling using both the classic Bakun upwelling index and alongshore wind stress, but we used alongshore wind stress in our data analysis. The upwelling index is determined every 3° of latitude (about 300 km) providing only six data points spanning our coast wide transect. More problematic is that, south of Pt. Conception, the upwelling index is calculated for locations to the west of the Channel Islands, seaward of the Southern California Bight, whereas our study sites were located on the mainland within the Bight, about 120 km east of the sites for which the upwelling index is calculated. During the upwelling season, winds south of Pt. Conception and seaward of the Channel Islands are strongly upwelling favorable, as they are along the coast to the north, whereas, upwelling winds are less common within the Bight (Hickey 1998). For example, NOAA buoy NDBC 46053 is within the Bight about 20 km off Santa Barbara, whereas buoy NDBC 46054 is about 50 km farther west and seaward of the Channel Islands. At the inshore buoy, average alongshore wind stress during the 2012 spring and summer was weakly downwelling favorable (−0.06 dynes), whereas it was strongly upwelling favorable (1.04 dynes) at the offshore buoy. This difference in winds between the nearshore buoy and the one beyond the Channel Islands is typical of the southern California Bight; within the Bight, winds closer to shore are generally weaker and often downwelling favorable generating a persistent poleward current along the coast while wind west of the Channel Islands, over the Equatorward-flowing California Current, tend to be upwelling favorable (Hickey 1998).

We tested if wave height, alongshore wind stress, intertidal width, intertidal slope, surf zone width, and solar radiation (dependent variables) varied with latitude (independent variable) by calculating correlation coefficients using linear or nonlinear regressions. The relationships between wave height and alongshore wind stress and latitude were nonlinear and first order polynomials were fitted to these data. The relationships between latitude and the other four variables were linear. Because the density of *Chthamalus* was negatively related to *Balanus* density dropping to zero at high densities of *Balanus* (see *Results*), we limited the statistical analysis of barnacle density to just the density of *Balanus*. Correlation coefficients were estimated by linear regressions to investigate the relationships between barnacle population structure (e.g., log density of *Balanus* and log density of new recruits; dependent variables) and latitude, upwelling

strength (alongshore wind stress), wave height, solar radiation, and log-transformed surf zone width (independent variables). *Balanus* density varied significantly with latitude and solar radiation and solar radiation varied with latitude (see *Results*). To isolate the effect of solar radiation from the latitudinal effect, a second set of correlation coefficients was calculated by linear regressions using the residuals from the regression between *Balanus* and new recruit densities and solar radiation (dependent variables) and physical variables (independent variables). We calculated correlation coefficients separately for *Balanus* and new recruit density (log transformed data) at rocky shore sites ($n = 23$) and sites with rocks in beaches ($n = 17$) and the log transformed surf zone width. For these analyses, we ran a number of regressions and significance was set by a Holm-Bonferroni correction to be conservative in our conclusions.

In more dissipative surf zones with bathymetric rip currents, surf zone diatoms, surf zone specialists, become concentrated within the eddies generated by rip current systems (Talbot and Bate 1987a, b). At Sand City, where we intensively studied a more dissipative surf zone with bathymetric rip currents, coastal phytoplankton taxa (e.g., *Skeletonema*, *Pseudo-nitzschia*), and zooplankton (e.g., calanoid copepods and their nauplii) were more concentrated within the sampled rip current (Morgan et al. 2016, Shanks et al. 2016) suggesting the possibility that cyprids, due to the rip current eddy system, may become concentrated within more dissipative surf zones. For surf zone diatoms, the concentration process is dependent on their production of mucus, which traps bubbles floating them at the surface. The bathymetric rip current eddy system tends to trap both mucus-bound surf zone diatoms and floating surface drifters within the eddy (Talbot and Bate 1987a, Brown et al. 2015). The structure of barnacle populations on rocks at more dissipative surf zones may be affected by the capacity of rip current systems to retain floating material there by enhancing the concentration of cyprids adjacent to rocks within beaches. We also calculated the surf zone retention parameter (surf zone width/spacing between rip currents), as an index of the capacity of a surf zone with bathymetric rip currents to retain floating material (Castelle et al. 2014). For study sites with bathymetric rip currents, we calculated the retention parameter and regressed this index against the density of new recruits (log-transformed data) and the percentage of the populations that were new recruits.

During the photographic survey, we sampled closely spaced stations (0.13–4.6 km apart) at eight sites. Given the close proximity of stations, the adjacent coastal ocean should be similar so that differences between the stations could be attributed to surf zone hydrodynamics. To achieve this goal, we selected sites that were not close to persistent upwelling centers or associated with prominent capes and were not located within coves or bays that might have topographically generated fronts at their mouths (McCulloch and Shanks 2003, Shanks et al.

⁹ http://rredc.nrel.gov/solar/old_data/nsrdb/

2003). Google Earth images of these samples sites are presented in Appendix S3. In most cases, sites were paired. Near Coos Bay Oregon, we photographed populations at three sites (Bastendorff Beach, Lighthouse Beach, and Cape Arago). In addition, we measured daily settlement and weekly recruitment at Bastendorff Beach and Pack Trail, which are separated by 3.9 km. Surf zone widths were narrow at both of the study sites at one-half of the locations, and narrow and wider surf zone were present at the other sites. If coastal hydrodynamics affect subsidies of larvae to shore, then population characteristics at closely spaced study sites should be similar, despite differences in surf zone width. However, if surf zone hydrodynamics affect populations as we hypothesized, then sites with similar surf zone widths should have similar population characteristics, and at sites with different surf zone widths (i.e., a narrow surf zone near a wide surf zone), population densities, weekly recruitment, and daily settlement should be higher at the site with a wide surf zone. Population densities, weekly recruitment, and average daily settlement between nearby sites were compared using a *t* test on log-transformed data. Because we predicted the direction of each comparison a priori, we used one-way probabilities. A Holm-Bonferroni correction was applied to the analyses.

RESULTS

Central to our analysis is the characterization of surf zone morphotypes, ranging from more reflective to more dissipative. We determined that data from Google Earth images were valid measures of both intertidal and surf zone widths by comparing measurements taken in the field and with those taken from Google Earth images. Beach width measured during field sampling explained 90% of the variation in the average beach width measured from Google Earth images (Fig. 3). The characteristics of surf zones and the adjacent intertidal zones were interdependent. The width of the intertidal zone and slope of the intertidal zone, and the slope of the intertidal zone and the width of the surf zone were negatively correlated (Fig. 3), as typically occurs for these indicators of surf zone morphodynamics (Wright and Short 1984). Because of the interdependence of these variables, in subsequent statistical analyses between the biological and physical variables, we used only surf zone width as an indicator of surf zone hydrodynamics; wider surf zones are more dissipative, narrower are more reflective. Field measurements of variation in the time for waves to cross surf zones explained >80% of the variation in average surf zone width determined from Google Earth images (Fig. 3). We ranked sites from narrowest to widest surf zones (average and 95% confidence intervals) as determined from Google Earth images. Surf zones narrower than 50 m (more reflective and without bathymetric rip currents) tended to remain narrow despite day-to-day variation in the width of surf zones from changes in the impinging waves and tidal phase; in only

five of the 28 surf zones narrower than 50 m did the 95% confidence interval cross 50 m (Fig. 3A). Wide surf zones (more dissipative), which often had bathymetric rip currents, tended to remain wide despite day-to-day variability in the wave field; in only one of 14 surf zones wider than 50 m did the 95% confidence interval dip below 50 m (Fig. 3A).

Latitudinal variation in physical parameters may cause latitudinal variation in intertidal barnacle populations. Average wave height varied with latitude accounting for 77% of the variability; average wave height was lowest at the southern end of the sample range in the Southern California Bight, reached a peak between about 40° and 45° N and then began to level off or decrease to the north (Fig. 4A). The upwelling index and alongshore wind stress also varied with latitude. The upwelling index was high from 33° to 40° N and decreased northward (Fig. 4B). Recall that the upwelling index for 33° N was calculated for a location seaward of the Channel Islands and outside the Southern California Bight, whereas our sample sites at that latitude were within the Southern California Bight. Latitude explained about 60% of the variability in alongshore wind stress (Fig. 4B); alongshore wind stress was low (<0, downwelling-favorable winds) at buoys within the Southern California Bight (around 34° N) where our samples sites were located, increased to a maximum (upwelling-favorable winds) around 40° N, and decreased northward with a low value near 0 by 48° N. Intertidal width and surf zone width increased significantly with latitude (Fig. 4C, E), but latitude explained only a small percentage of the variability (16% and 13%, respectively). The slope of the shore decreased with 31% of the variability explained by latitude (Fig. 4D). Average daily solar radiation decreased with latitude with >90% of the variability explained by latitude (Fig. 4F).

On both rocky shores and beach rocks, small barnacles and new recruits appeared to compose a larger percentage of populations at sites with wider surf zones (Fig. 5). The transition from a wide surf zone with a high abundance of new recruits (defined as <1.5 mm) to a narrow surf zone with few new recruits appeared to be around 50 m surf zone width.

In other geographic settings, *Chthamalus* and *Balanus* have been observed to compete for space in the intertidal zone with *Balanus* tending to outcompete *Chthamalus* (Connell 1961, Dayton 1971, Farrell 1991, Menge 2000). At high *Balanus* densities, the density of *Chthamalus* often dropped to zero (Fig. 6A); 11 sites had *Balanus* densities >500 individuals/100 cm² and *Chthamalus* were absent at eight of these sites and densities were low at the remaining three sites (average 52 individuals/100 cm²). In addition, log *Balanus* density explained 63% of the variation in the percentage of *Chthamalus* in populations (Fig. 6B). Sites with high *Balanus* densities were associated with more dissipative surf zones, and consequently, an analysis of the effect of surf zone hydrodynamics on *Chthamalus* density would be confounded by the

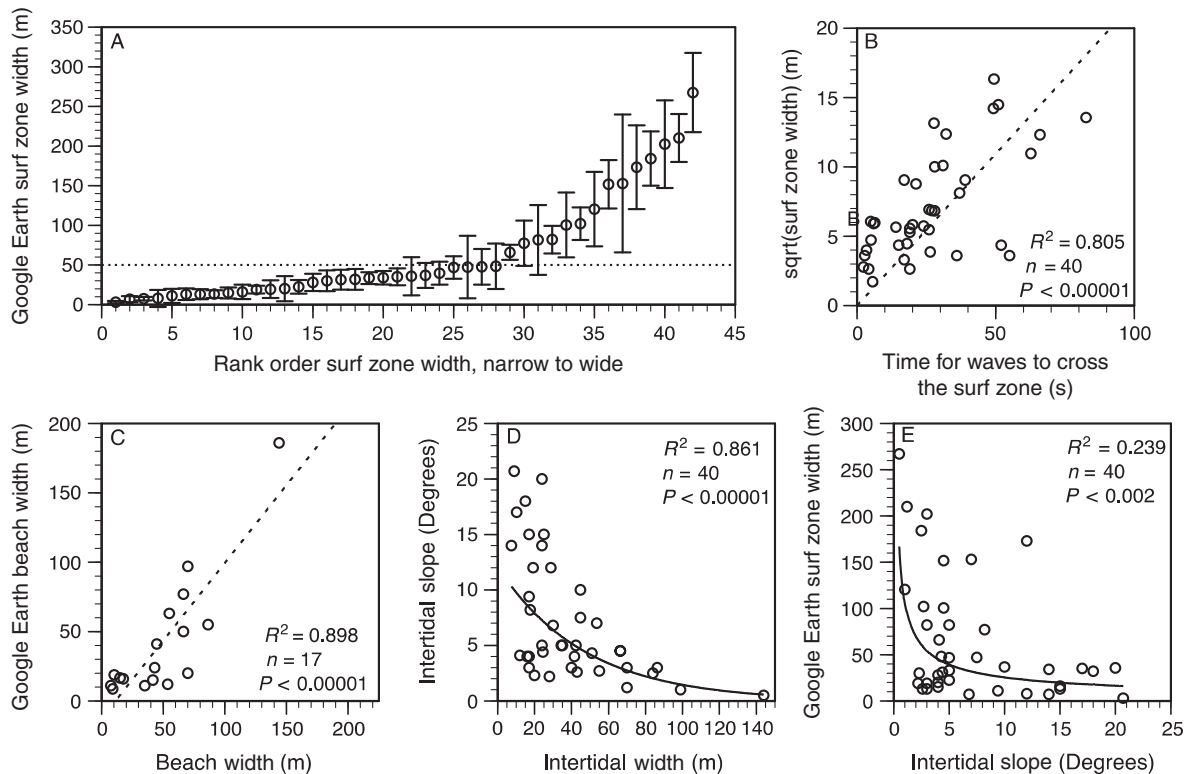


FIG. 3. (A) Surf zone width (average and 95% confidence interval) at the study sites as measured from Google Earth images ordered from the narrowest to the widest surf zone. Bathymetric rip currents tended to be absent from the more reflective surf zones narrower than 50 m (dotted line) and were present in nearly all surf zones wider than 50 m (one exception, Nesika Beach). (B) Time for waves to cross surf zones plotted with the square root (sqrt) of surf zone width (m). (C) Beach width measured in the field plotted with the average beach width measured from Google Earth images. (D) Average width of the intertidal zone plotted with the average slope of the intertidal zone as measured in the field. (E) Average slope of the intertidal zone (field measurements) plotted with the average width of the surf zone as measured from Google Earth images. Statistical results in each figure are from linear or nonlinear regressions.

abundance of *Balanus*. Because *Chthamalus* abundance varied inversely with that of *Balanus*, the subsequent statistical analysis focuses only on *Balanus* density.

The literature suggests that *Chthamalus* may have a refuge from competition with *Balanus* higher in the intertidal zone where they are more tolerant of desiccation stress (Dayton 1971, Farrell 1991, Menge 2000). In addition, the density of both species may vary with the latitudinal variation in average daily solar radiation, which we use as a simple proxy for desiccation stress. The log *Chthamalus* density was positively correlated with average daily solar radiation, with 22% of the variation in density explained by average daily solar radiation, whereas log *Balanus* density was negatively correlated with >30% of the variation in their density explained by average daily solar radiation (Fig. 6C, D).

Almost 30% of the variation in the log density of *Balanus* could be accounted for by latitude (Fig. 7A), however, when the residuals from the significant regression between *Balanus* density and average daily solar radiation were regressed against latitude, the relationship was no longer significant (Fig. 7B). Neither log *Balanus* density nor their residuals from the solar radiation

regression were related to the average alongshore wind stress (a proxy for upwelling) or average wave height (Fig. 7C–F). Both log *Balanus* density and the residuals from the solar radiation regression were, however, related to log average surf zone width with about 58% and 20% of their variability, respectively, explained by surf zone width (Fig. 7G, H).

The density of new recruits was also negatively related to the average daily solar radiation ($R^2 = 0.205$, $n = 40$, $P < 0.004$). There was not a significant regression between the log of the density of new recruits and latitude nor was there a significant relationship when the residuals from the regression with solar radiation were regressed against latitude (Fig. 8A, B). Neither the log density of new recruits nor the residuals from the solar radiation regression were related to the average alongshore wind stress (a proxy for upwelling) or average wave height (Fig. 8C–F). However, both the log of new recruit density and their residuals from the solar radiation regression were related to the log of the average surf zone width explaining 38% and 30% of their variability, respectively (Fig. 8G, H). In these later two plots, there is one point that appears to be an outlier (indicated by

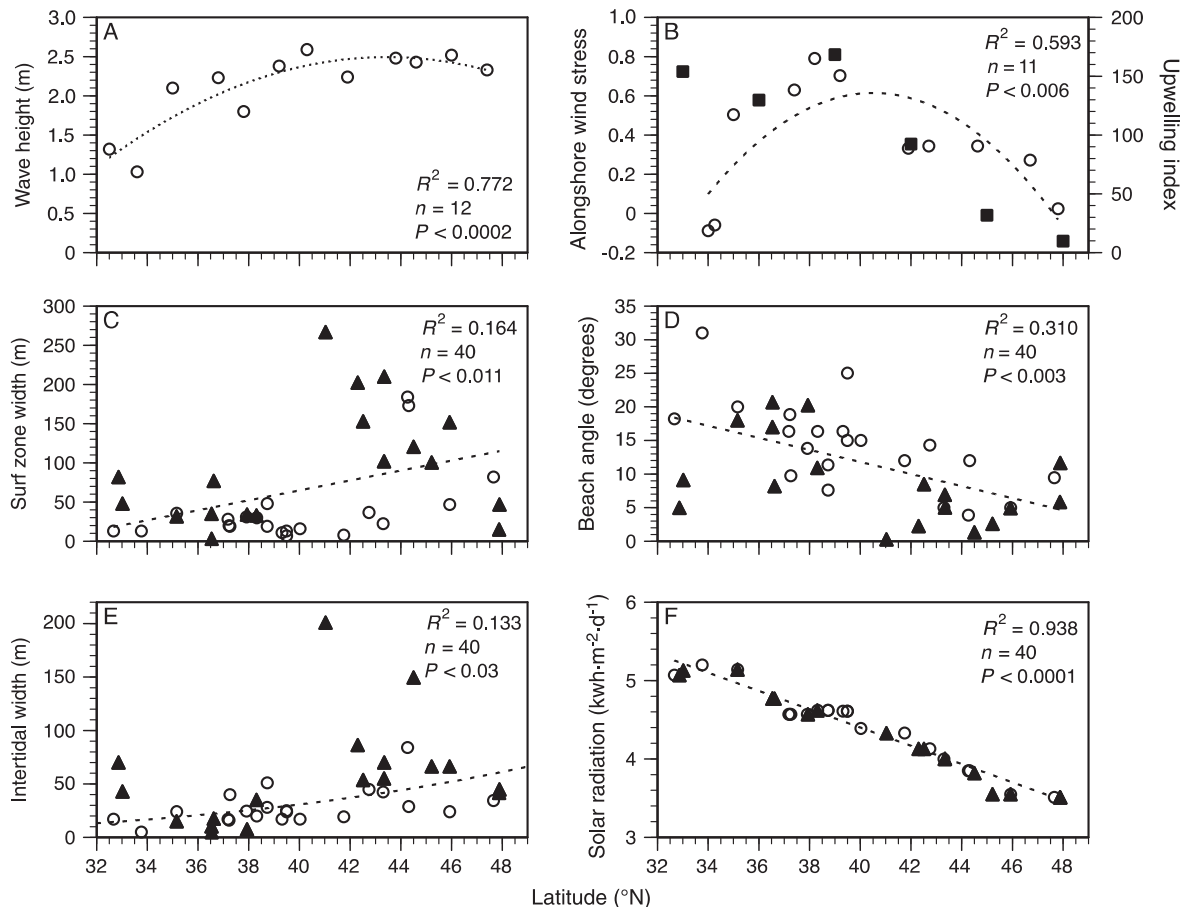


FIG. 4. Latitudinal distribution of physical variables. (A) Average wave height during spring and summer. The relationship between latitude and average wave height was nonlinear ($y = -0.14x^2 + 0.93x - 17.71$). (B) Average alongshore wind stress (open circles) and upwelling index (solid squares) during spring and summer. The relationship between latitude and alongshore wind stress was nonlinear ($y = -0.012x^2 + 0.986x - 19.35$). We did not relate latitude to the upwelling index (see methods). Latitudinal variation in (C) average surf zone width determined from Google Earth images taken during spring and summer (see Appendix S2), (D) slope of the intertidal zone, and (E) width of the intertidal zone, both measured on the day each site was sampled. (F) Average daily solar radiation. In C–F, open circles and solid triangles indicate beach rocks and rocky shore sites, respectively. Dashed lines are regressions between all data and latitude.

arrows in Fig. 8G, H). These data are from Nesika Beach, Oregon, which was unique; the surf zone was wide but lacked bathymetric rip currents. Calculating the regression without this site, log surf zone width explained 53% and 44% of the variability in log new recruit density and the residuals (Fig. 8G, H).

We reanalyzed the relationship between surf zone width (log-transformed) and log barnacle densities separately for beach rock and rocky shores sites (Fig. 9), log surf zone width at rocky shores explained 38% and 32% of the variability in log *Balanus* and log new recruit densities, respectively. The log surf zone width at beach rock sites explained 68% and 32% of the variability, and it explained 74% and 63% of the variability without the data from Nesika Beach.

Brushing settlement and recruitment surfaces removed cyprids and new recruits, but may not have removed chemical signatures of their presence. These chemicals

may have attracted settlers, inflating subsequent counts. If this were the case, we might see a steady increase in settlement/recruitment over the time series as the chemical signal accumulated. Increasing numbers of settlers and recruits is not apparent in any of either the daily settlement or weekly recruitment time series (Figs. 10 and 11), densities rise and fall, but did not increase over the time series and, in fact, in several time series numbers decreased over time. Shanks (Shanks 2009b) also found no evidence that removal of cyprids by brushing enhanced subsequent settlement.

Average daily settlement of barnacle larvae was lower at shores with more reflective than dissipative surf zones; it ranged from 0.05 to 2.7 settlers/d at the five more reflective sites and was 23 settlers/d at the more dissipative site (Bastendorff Beach; Fig. 10). Maximum daily settlement at more reflective sites ranged from 1 to 22 settlers/day, whereas it was 1,009 settlers/d at Bastendorff

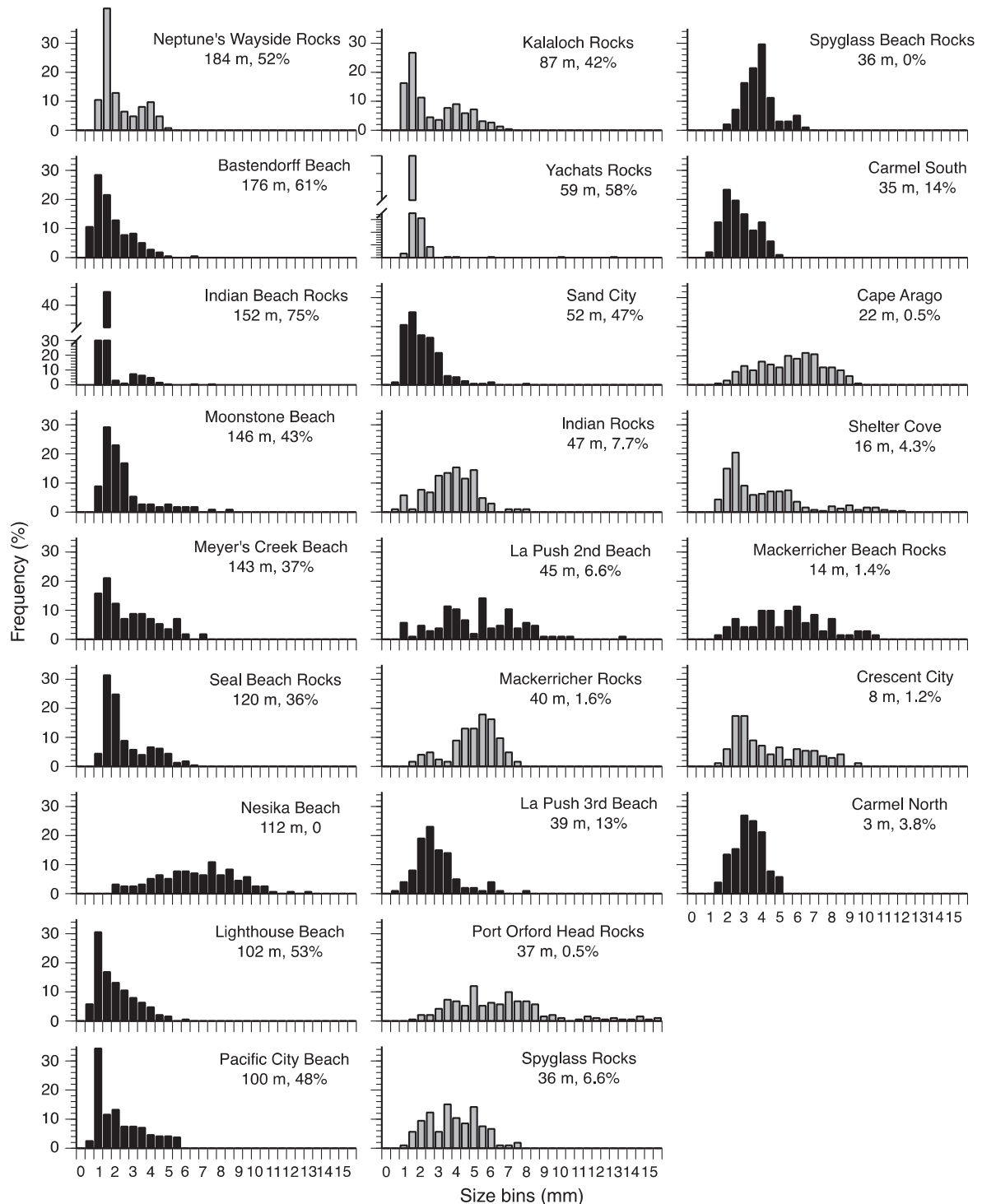


Fig. 5. Size frequency distributions of barnacles at a subset of the sites sampled (25 of 40 sites). Gray bars are data collected from rocky shores and black bars are from beach rocks. Below the site name is the width of the surf zone in meters and the percentage of the barnacle population that were new recruits (individuals <1.5 mm diameter). Sites are arranged from the widest to the narrowest surf zone.

Beach. Average weekly recruitment was lower at the seven more reflective sites, ranging from 11 to 41 recruits/week, than at the two sites with more dissipative

surf zones where average weekly recruitment was 196 and 281 recruits/week (log-transformed data, one-way analysis, $t = 3.57$, $P < 0.008$, $df = 7$; Fig. 11).

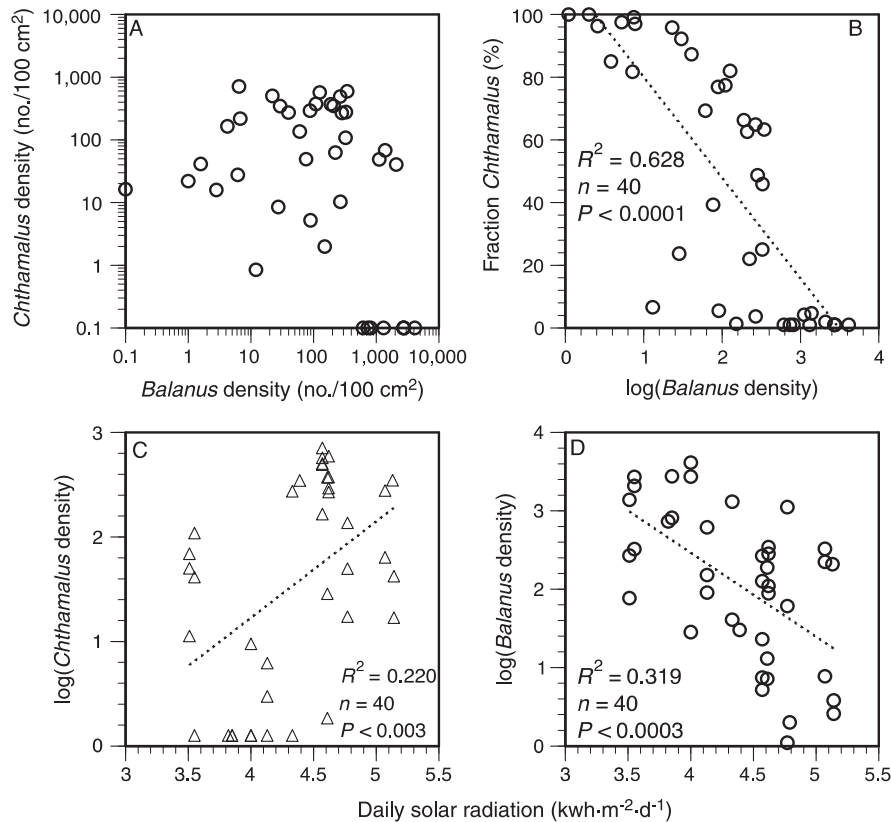


FIG. 6. (A) Variation in the density of *Chthamalus* with the density of *Balanus*. (B) Variation in the percentage of the barnacles at a site that were *Chthamalus* relative to the density of *Balanus*. The relationship is nonlinear ($y = 346.1e^{-1.45x}$). (C) and (D) Variation in *Chthamalus* and *Balanus* densities, respectively, with average daily solar radiation.

The summed daily settlement over a month and the average weekly recruitment were positively correlated with surf zone width (Fig. 12A); surf zone width explained $\geq 80\%$ of the variability in daily settlement and weekly recruitment. The regression between average weekly recruitment and the density of new recruits from the photographic survey (data collected at the same sites) was also significant and explained $>90\%$ of the variability (Fig. 12B). Last, the regressions between summed daily settlement over a month and the density of new recruits and *Balanus* from the photographic survey (data collected at the same sites) were significant, explaining at least 80% of the variability (Fig. 12C).

The density of *Balanus* between closely spaced sites with surf zones of similar width did not differ (Fig. 13A–D). Where the surf zone width differed between closely spaced sites, narrow (<50 m) vs. wide (>80 m), *Balanus* densities, average weekly recruitment, and average daily settlement were all significantly higher, often 10 or more times higher, at sites with wide surf zones (Fig. 13E–J).

Where surf zone width was <50 m, bathymetric rip currents were not observed either when we sampled sites or in the Google Earth images. In contrast, most wider surf zones had from 2 to 6 rip currents within 1 km of the

sample site and one site (Sand City, California) had 18 rip currents (Fig. 14A). Nesika Beach was unique because bathymetric rip currents were not observed, even though the surf zone was wide (153 m). Arrows in Figs. 8, 9, and 14 indicate data from this site. At sites with bathymetric rip currents, new recruits on average accounted for 45% (SD $\pm 20\%$) of the populations, but only 10% (SD $\pm 7\%$) of populations were new recruits at sites without bathymetric rip currents (Fig. 14A). Even at the more reflective sites without bathymetric rip currents, however, density of new recruits was positively correlated ($R^2 = 0.286$, $n = 23$, $P < 0.004$) with surf zone width (Fig. 14B). At the sites with bathymetric rip currents, 64% and 72% of the variability in the log density of new recruits and the percentage of populations that were new recruits, respectively, can be explained by variation in the retention parameter (Fig. 14C, D), an index of the capacity of the surf zone to retain floating material. There appear to be two types of sites irrespective of beach rocks and rocky shores: (1) sites with wide surf zones and bathymetric rip currents where new recruits were abundant and density of adults was high, and (2) sites usually (but not always) with narrow surf zones and without bathymetric rip currents, where new recruits composed a small percentage of populations and adult density was generally much lower.

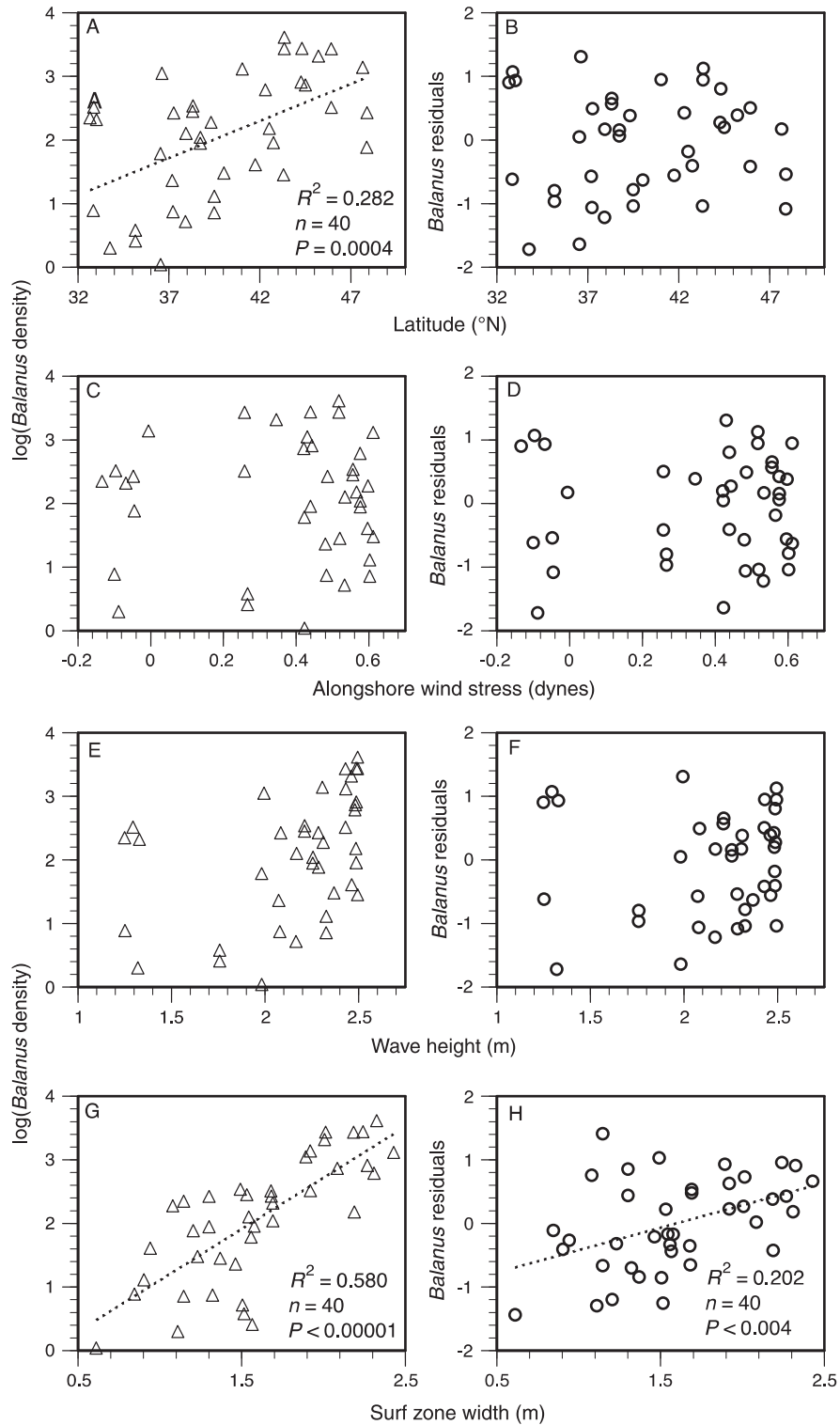


FIG. 7. Plots on the left are physical variables (latitude, average alongshore wind stress, average wave height, and log-transformed average surf zone width) plotted against the density of *Balanus* (no./100 cm²; log-transformed data). Plots on the right are the same physical variables plotted against the residuals from the regression between average daily solar radiation and *Balanus* density (Fig. 5D).

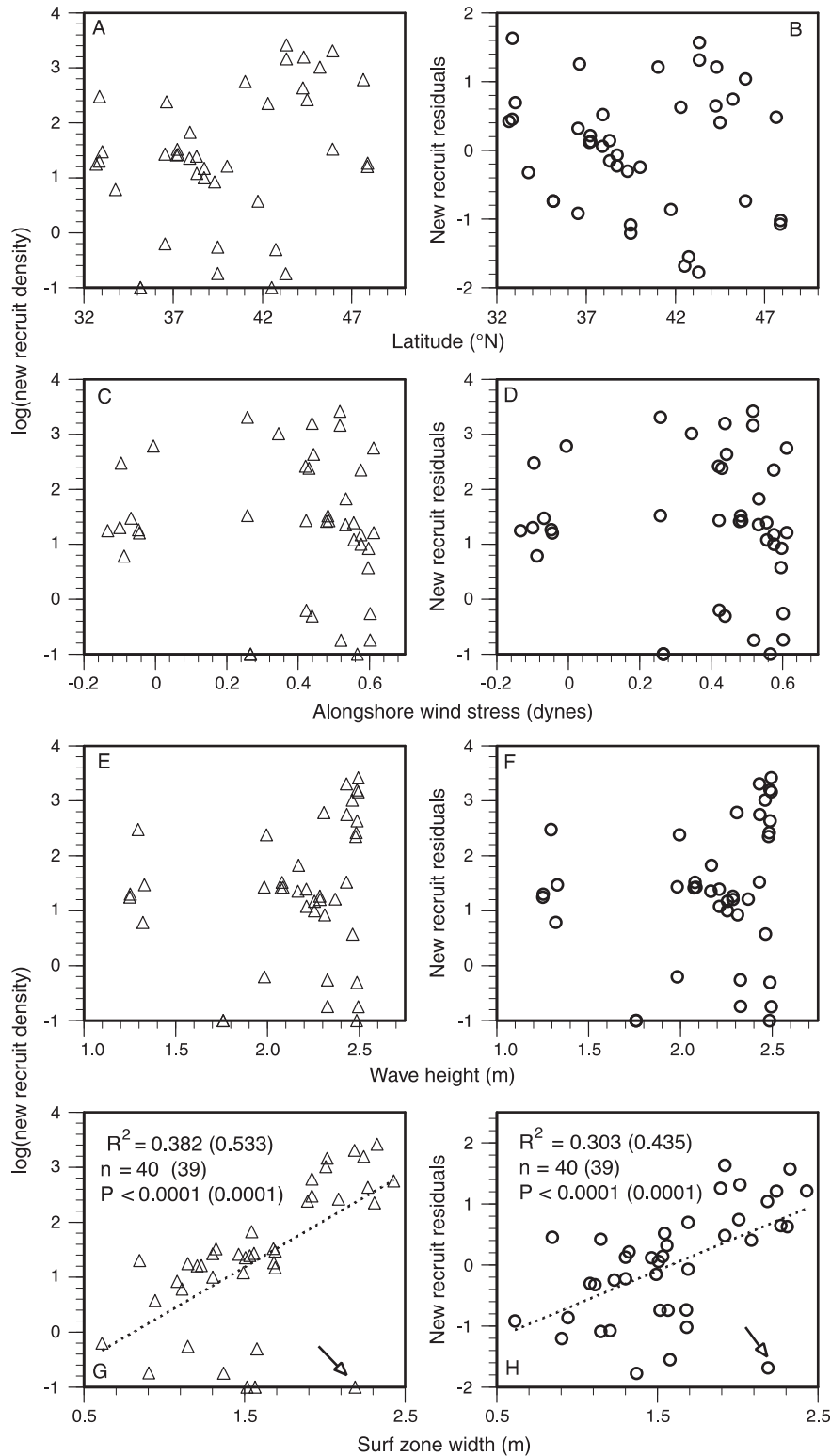


FIG. 8. Plots on the left are physical variables (latitude, average alongshore wind stress, average wave height, and log transformed average surf zone width) plotted against the log-transformed density of new recruits (no./100 cm²). Plots on the right are the same physical variables plotted against the residuals from the regression between average daily solar radiation and new recruit density ($R^2 = 0.205$, $n = 40$, $P < 0.004$). The regressions were calculated for all sites and without Nesika Beach (datum indicated by arrow; regression results in parentheses) where the wide surf zone lacked bathymetric rip currents.

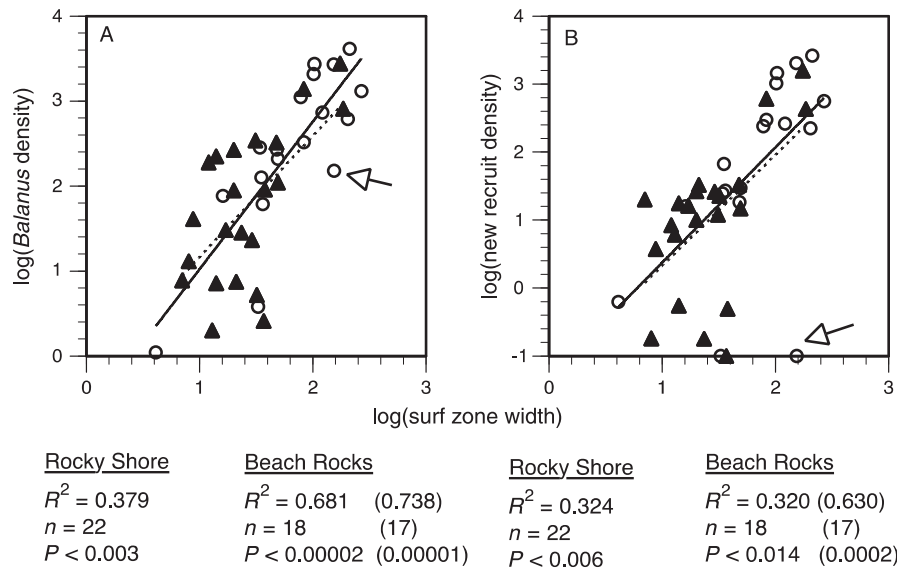


FIG. 9. The log of (A) *Balanus* density (no./100 cm²) and (B) new recruits density (no./100 cm²) plotted against the log-transformed surf zone width (m) for rocky shore (solid triangles) and beach rock (open circles) sites. The regressions were calculated for all sites and without Nesika Beach (indicated by arrow; regression results in parentheses) where the wide surf zone lacked bathymetric rip currents.

At both rocky shore and beach rock sites, new recruit density explained much of the variation in the density of barnacle populations on rocky shores, beach rocks, and all sites combined (Fig. 15A). Sites deviated from the regression line significantly less where rip currents were present than absent (Fig. 15B).

DISCUSSION

By sampling 40 diverse rocky shores with different types of surf zones along the west coast of the United States, we found that densities of *Balanus* and new recruits were significantly higher, often >10 times higher, at shores that were more dissipative than reflective. Daily settlement and weekly recruitment of barnacles were also 10–100 times higher at more dissipative than reflective shores, indicating that, at a subset of the study sites, the patterns observed during our latitudinal survey were maintained over months. Density of populations, daily settlement, and weekly recruitment were higher at wide, more dissipative surf zones even when sites were separated by <5 km of shore; spacing close enough that the hydrodynamics of the adjacent ocean should be quite similar. The proportion of barnacle populations that were new recruits increased as shores became more dissipative. The low densities of adults and new recruits at reflective shores suggest that these populations were recruitment limited. Furthermore, we documented the importance of bathymetric rip current systems in regulating recruitment; at sites with bathymetric rip current systems (dissipative and intermediate surf zones), new recruit density was much higher than at sites where rip current systems were absent. Even on reflective shores

without bathymetric rip current systems, however, new recruit density increased with surf zone width. Thus, variation in surf zone hydrodynamics appears to play an important role in regulating barnacle populations.

Bathymetric rip current systems tend to develop in more dissipative surf zones when waves approach shore at a low angle, i.e., wave crests parallel to shore (MacMahan et al. 2006). As waves approach shore at a steep angle (wave crests at an angle to the shore), an alongshore current within the surf zone is generated due to the alongshore variation in momentum and bathymetric rip currents are suppressed. Under these conditions, the exchange of surf zone water with offshore water is reduced (MacMahan et al. 2006). Nesika Beach appears to be such a site; the surf zone is wide, but both bathymetric rip currents and new recruits were absent. Thus, bathymetric rip current systems appear to be critical to the free exchange of plankton between the inner shelf and surf zone; without bathymetric rip currents, surf zone hydrodynamics limit delivery of plankton subsidies from the ocean to shore (Shanks et al. 2015, 2016, Morgan et al. 2016).

How do bathymetric rip current systems promote the delivery of barnacle larvae to the shore and what limits delivery at more reflective surf zones without bathymetric rip currents? Our complementary dye studies demonstrated that flow within bathymetric rip currents is seaward and water from the surf zone is transported just beyond the breakers where it mixes with coastal waters (Brown et al. 2015). To maintain continuity, wave dynamics push water back into the surf zone over the shoals separating rip channels (MacMahan et al. 2010). Bathymetric rip current systems cause from 10% to 20% of the water in the surf zone to be exchanged per hour

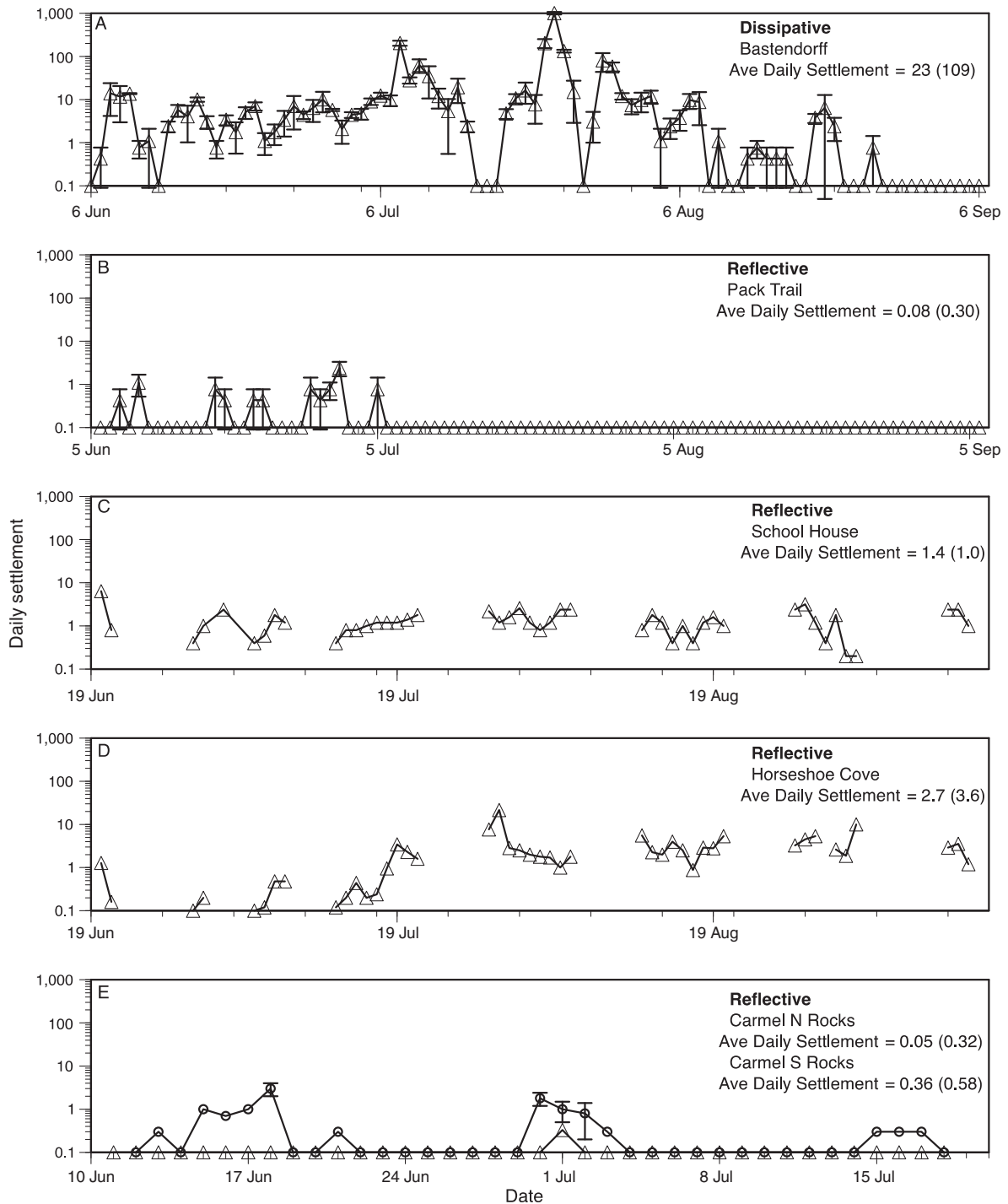


FIG. 10. Average daily settlement of barnacles on marked quadrats of bare rock from June through July or September 2011 to sites with (A–D) more reflective and (E) dissipative surf zones (see Appendix S1 for surf zone widths). Average surf zone width ($\pm$ SD) as determined from Google Earth images and average daily settlements are presented for each site. In A, B, and E, average daily settlement is the daily average from three settlement surfaces ($\pm$ SD).

(MacMahan et al. 2010), thereby effectively exchanging surf zone water for coastal water. Zooplankton and phytoplankton in coastal water are transported into the surf zone where they can become highly concentrated within

the bathymetric rip current eddy (Morgan et al. 2016, Shanks et al. 2016). At study sites with bathymetric rip currents, we found a strong positive relationship between the retention parameter and both the density of new

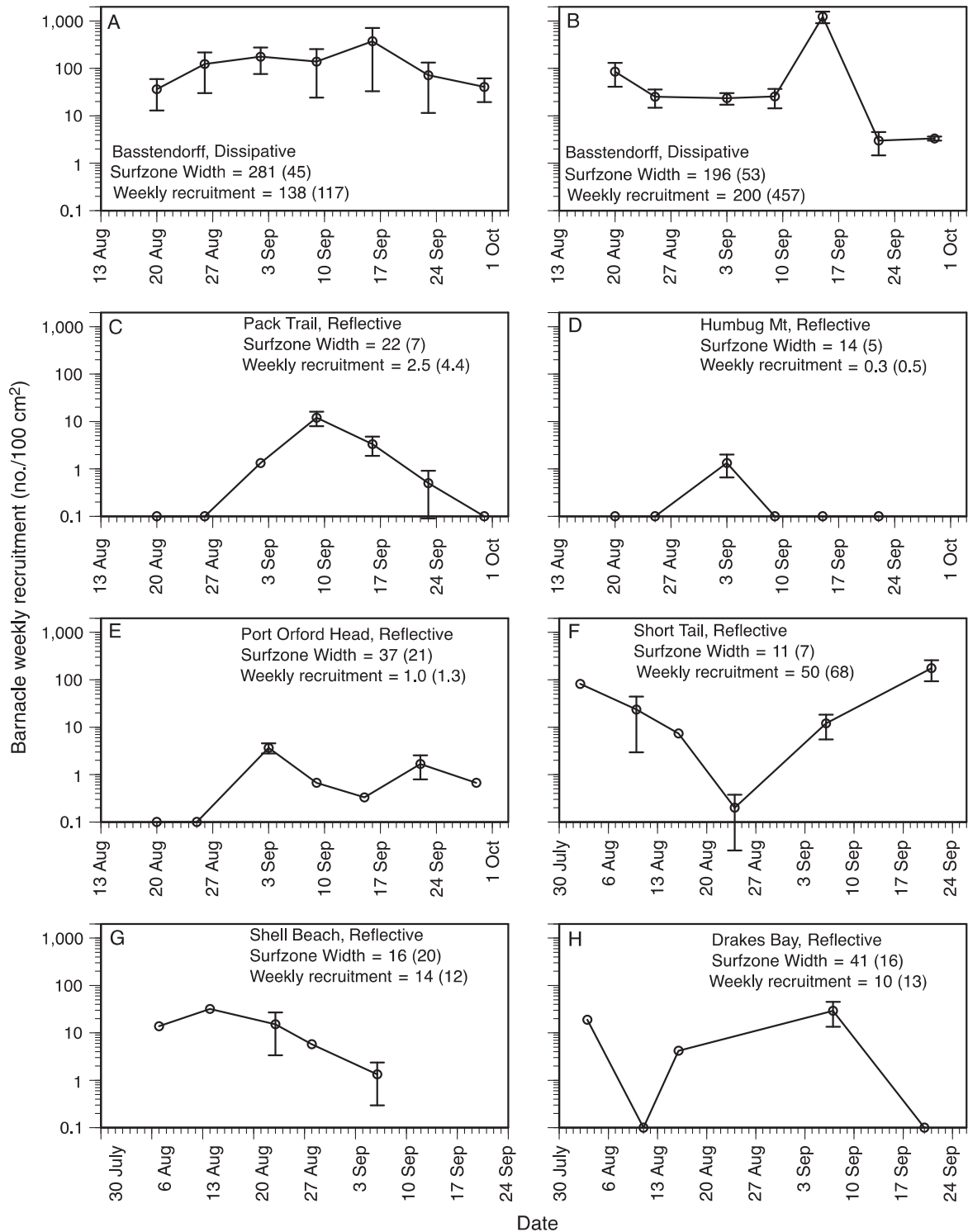


FIG. 11. Average weekly recruitment of barnacles on quadrats of bare rock from July through September 2010 to sites with (A and B) more dissipative and (C–H) reflective surf zones (see Appendix S1 for surf zone widths). Average surf zone width ($\pm$ SD) as determined from Google Earth images and grand average weekly recruitment ($\pm$ SD) are presented for each site.

recruits and the percentage of the populations composed of new recruits, suggesting that barnacle populations at these sites were likely effected by both the effective

transport of coastal plankton into the surf zone and, potentially, by their retention and concentration within the bathymetric rip current eddy system.

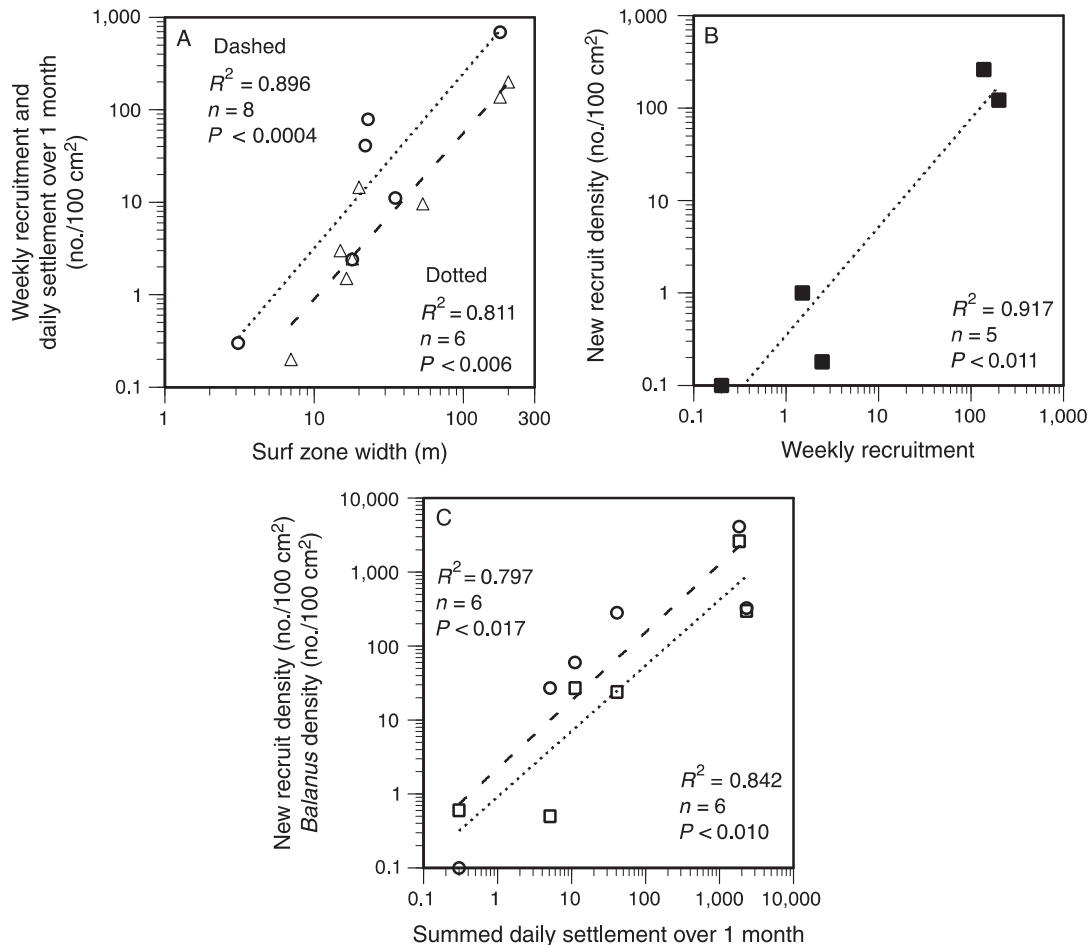


FIG. 12. (A) Average weekly recruitment and daily settlement summed over a month plotted with surf zone width. Recruitment and settlement were measured on fixed quadrats on rocks. The results of regressions are presented (dashed line open triangles weekly recruitment and dotted line open circles summed daily settlement). (B) Average weekly recruitment measured on fixed quadrats on rocks plotted with the density of new recruits from the photographic survey. Both sets of data were collected at the same sites. (C) Daily settlement summed over a month plotted with the density of new recruits (open square) and *Balanus* adult density (open circle) both from the photographic survey. Both sets of data were collected at the same sites.

Transient and topographic rip currents occur in reflective surf zones, increasing the exchange of water between the surf zone and inner shelf (Hally-Rosendahl et al. 2014, Suanda and Feddersen 2015, Hally-Rosendahl and Feddersen 2016). Though we might expect these rip currents to enhance the exchange of larvae, thereby increasing settlement and recruitment, we did not see evidence of this. Instead, we found low densities of *Balanus* and new recruits and low weekly recruitment and daily settlement at sites with reflective surf zones. In an earlier study (Shanks et al. 2014), we measured daily settlement at rocky sites adjacent to a reflective beach (CRSB). One of these sites was located exactly at the location where water from seaward of the surf zone entered an alongshore current within the surf zone. Despite the onshore flow at this site, there was only one settler over a month of sampling. Why transient and topographic rip currents apparently had little effect on recruitment to surf zones is not clear.

The low settlement and recruitment rates of barnacles at more reflective surf zones suggest that they are prevented from entering the surf zone. Dye studies at the intensively studied reflective surf zone (CRSB) indicated that water inside and just outside the surf zone was exchanged (Brown 2014), yet concentrations of both zooplankton and phytoplankton were much lower within the surf zone (Morgan et al. 2016, Shanks et al. 2016). Most larvae swim slowly, so that they are unlikely to be swimming away from the surf zone; instead, surf zone hydrodynamics may limit their entry into the surf zone. At this reflective surf zone, we observed offshore flow, undertow within the bulk of the water column, and onshore surface flow into the surf zone (Shanks et al. 2015). Plankton close to the sea surface may be transported into the surf zone by both the onshore flow generated by breaking waves and onshore winds, but those deeper in the water column may be pushed away from

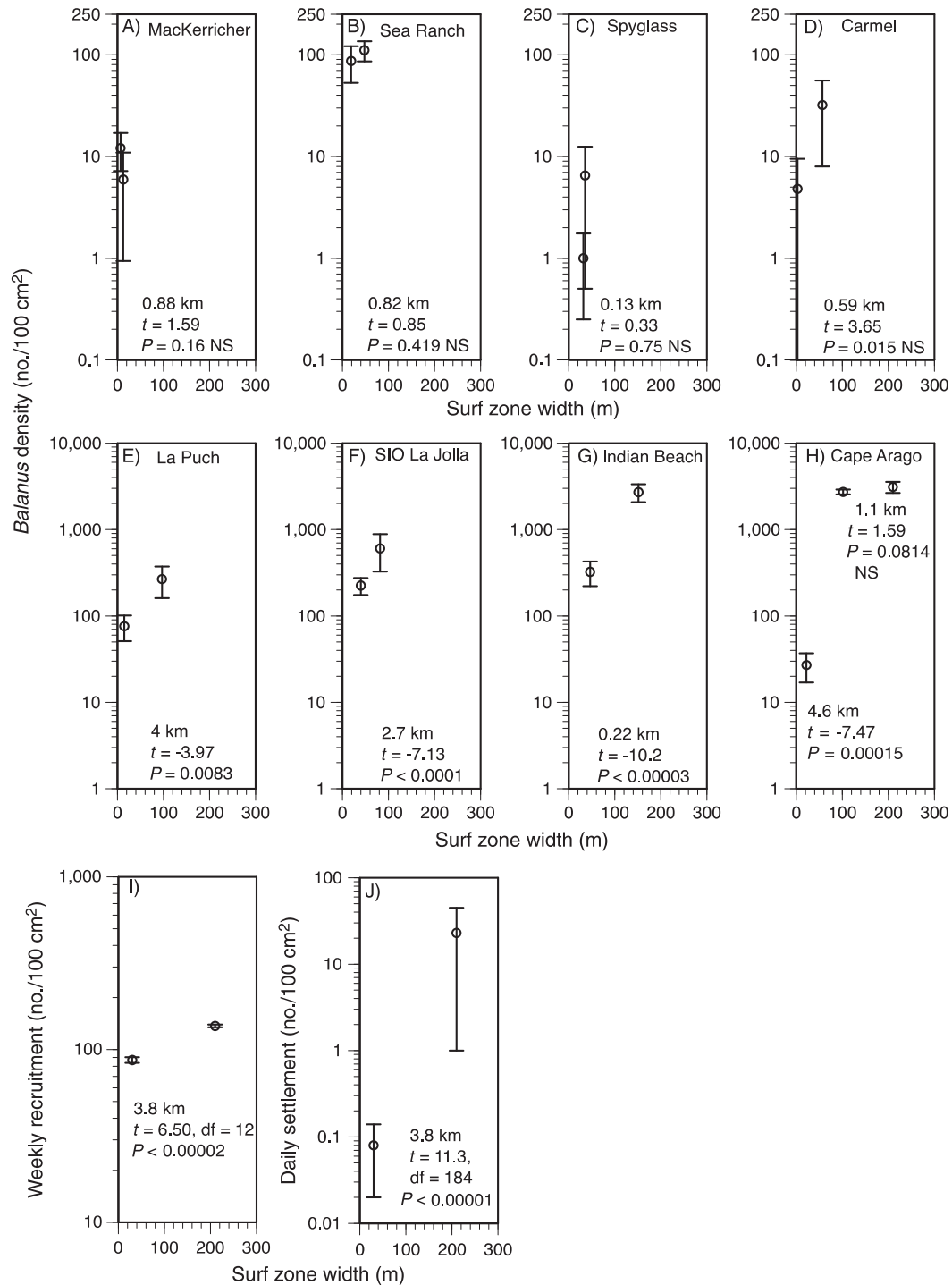


FIG. 13. Surf zone width plotted against (A–H) average *Balanus* density (and 95% confidence interval), (I) average weekly recruitment (and 95% confidence interval), and (J) average daily settlement (and 95% confidence interval) at sites that were located near each other (<5 km apart). In panels A–D, surf zones at both sites were narrow (<50 m) while panels E–H present data from closely spaced sites where surf zones at one or more sites were wide (>100 m) compared to a site with a narrow surf zone (<50 m). Weekly recruitment (I) and daily settlement (J) were measured on marked quadrats on bare rock during the summers of 2010 and 2011, respectively, at Pack Trail (narrow surf zone) and Bastendorff (wide surf zone). The results of t tests run on the log-transformed data are presented in each figure. We predicted that, where surf zone width at adjacent sites was different, barnacle density, average weekly recruitment, and average daily settlement would be higher at the wide surf zone; for these tests we used a one-way analysis with a Holm-Bonferroni correction to determine significance. Google Earth images and a more detailed description of each set of sample sites are presented in Appendix S3.

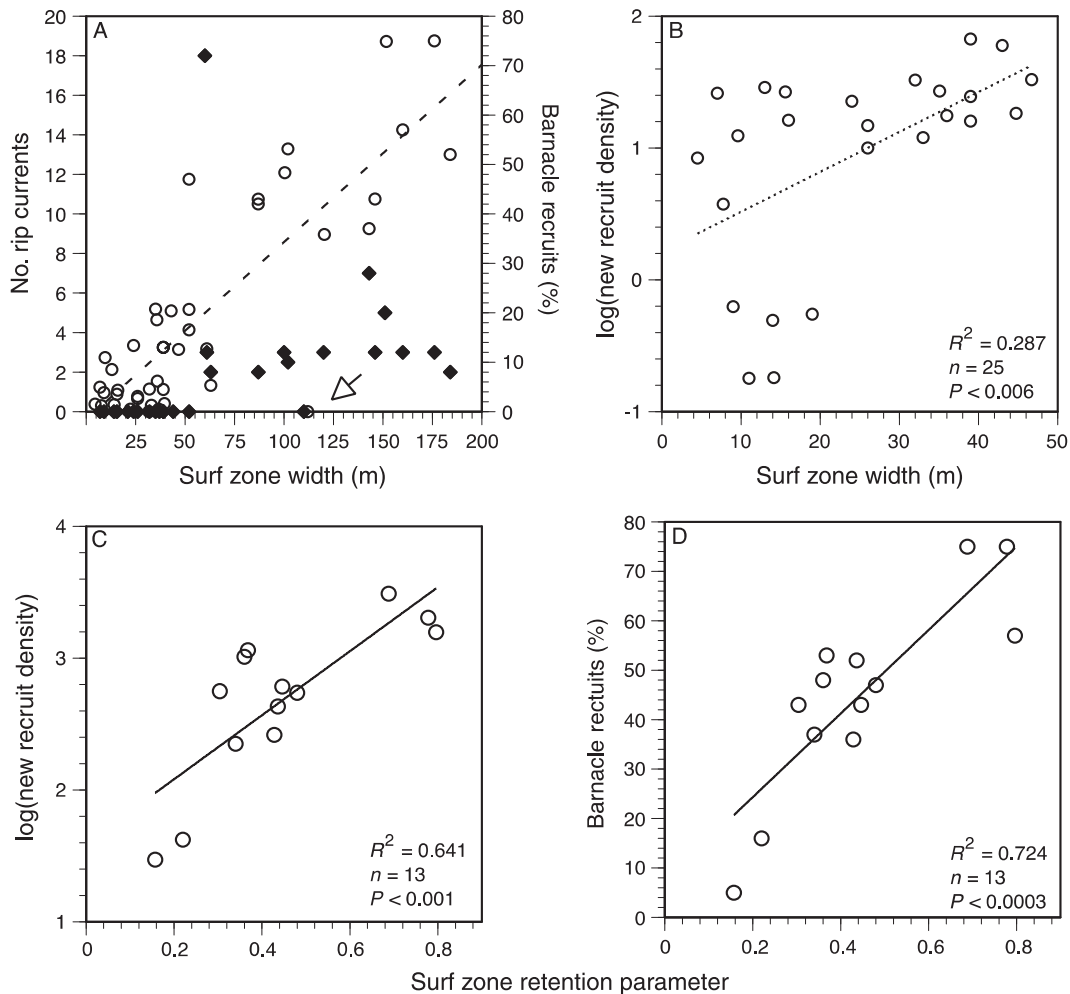


FIG. 14. (A) The number of bathymetric rip currents present (solid diamonds) and percentage of the barnacle populations that were new recruits (open circles, individuals <1.5 mm diameter) plotted against surf zone width. The arrow indicates Nesika Beach, Oregon where the surf zone was wide but bathymetric rip currents were absent. (B) The log density of new recruits (individuals <1.5 mm diameter; no./100 cm^2) for sites without bathymetric rip currents plotted against surf zone width. (C and D) Density of new recruits (log-transformed) and the percentage of populations that were new recruits plotted against the retention parameter.

the outer edge of the surf zone by the undertow. A variety of meroplankters swim down in strong turbulence (Fuchs and Gregory 2016), which they would encounter at the outer edge of the surf zone. We hypothesized (Shanks et al. 2015, Morgan et al. 2016) that such a behavior, if common among zooplankton, would tend to move zooplankters out of the surface water flowing into the surf zone and down into the water column where the undertow would tend to push them away from the surf zone. If this hypothesis is correct, then we would expect to see low near surface concentrations of meroplankters at the seaward edge of more reflective surf zones and larval concentrations in the surf zone should be similar to the concentrations of larvae in the near surface waters just beyond the breakers, the water that actually enters the surf zone.

There are a variety of mechanisms that can transport larvae of intertidal organisms from the coastal ocean to

the inner shelf adjacent to surf zones (Shanks 1995), but whether these larvae actually enter the surf zone or not depends on surf zone hydrodynamics. For example, daily barnacle settlement at Bastendorff Beach (dissipative) was high (mean 23 settlers $\cdot \text{d}^{-1} \cdot 100 \text{ cm}^{-2}$, Fig. 10) and varied with the tidal amplitude cycle suggesting that larvae may have been transported to shore by the internal tides (Shanks 2009a). In contrast, at a nearby site (Pack Trail, 3.9 km south) with a reflective surf zone, settlement was >100 times lower (mean 0.08 settlers $\cdot \text{d}^{-1} \cdot 100 \text{ cm}^{-2}$, Fig. 10), and there was no relationship between daily settlement and the tidal amplitude cycle (in cross-correlations between maximum daily tidal range and log-transformed daily settlement, there were no lags with $P < 0.05$). These sites were close enough together that shoreward transport of larvae should have been quite similar, yet daily settlement varied by a factor of 100, suggesting that different surf zone dynamics may have

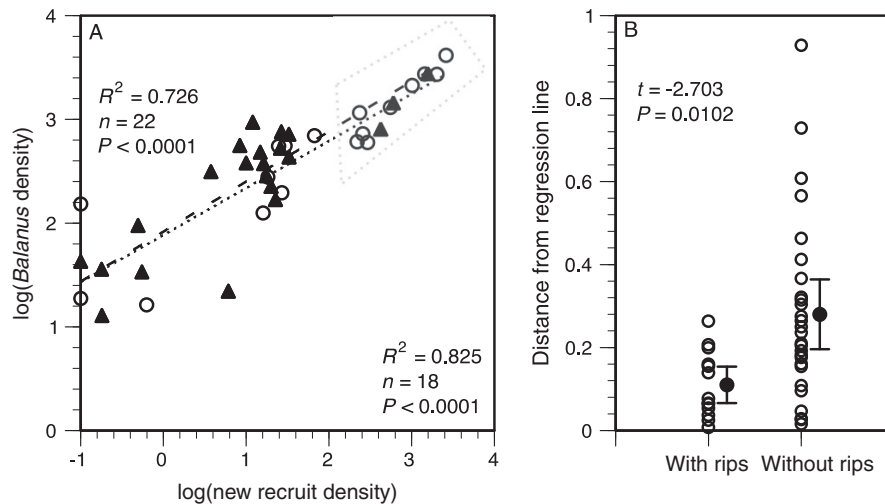


FIG. 15. (A) Regression of log barnacle new recruit density (no./100 cm²) and log *Balanus* density (no./100 cm²) from beach rock (open circles and dotted line) and rocky shore (solid triangles and dashed line) sites. The dotted line "trapezoid" indicates sites with bathymetric rip currents and all other sites lacked bathymetric rip currents. (B) The distance data points are from the regression line (absolute value of the residuals with mean and 95% confidence intervals) with data from sites with bathymetric rip currents and without them plotted separately.

ultimately determined whether larvae entered the surf zone, encountered the rocky shore, and settled. Delivery of larvae to the intertidal zone appears to be at least a two-step process (Pfaff et al. 2015); larvae first are transported across the shelf to the outer edge of the surf zone by one or more of a variety of mechanisms (Shanks 1995) and then are transported or not into the surf zone by a very different process, surf zone hydrodynamics.

Balanus and new recruit densities were higher at more northern than southern latitudes, as has been observed in previous studies (Connolly and Roughgarden 1998, Connolly et al. 2001, Broitman et al. 2008). This latitudinal pattern of barnacle abundance has been attributed to weaker, less persistent upwelling north of Cape Blanco, Oregon. While these studies were longer in duration than the work reported here, they used the upwelling index as a measure of upwelling. However, the index is calculated for sites seaward of the Channel Islands in southern California waters, whereas our samples and those used by several of the above studies, were within the Southern California Bight where upwelling is much weaker (Hickey 1979, Huyer 1983). The hypothesized effect of upwelling and downwelling on the delivery of barnacle larvae to the shore (Roughgarden et al. 1988, Menge and Menge 2013) suggests that new recruits should be abundant in the Bight and this should lead to higher *Balanus* densities. However, population and new recruit densities did not follow the distribution of upwelling-favorable alongshore wind stress measured along the coast and within the Southern California Bight; the structure of barnacle populations was uncorrelated to alongshore variation in upwelling.

The study presented here and previous studies also differed in the way study sites were selected. In previous

studies (Connolly and Roughgarden 1998, Connolly et al. 2001, Menge et al. 2003, Schoch et al. 2006, Broitman et al. 2008), site selection was limited to what we would define as rocky shores. For example in their experimental design, Schoch et al. (2006) selected "low-angle platforms (relatively flat bedrock outcrops) longer than 50 m" as their study sites, however, their "low angle" shores were steeper than those sampled for our study. In Schoch et al. (2006), shore slope varied from about 24° to 31°; whereas in our study, the slope of rocky shores were all <24° and only two of the reflective beach rocks sites had shore slopes falling within their range (Fig. 4D). Given the steepness of the shores sampled in Schoch et al. (2006), the surf zones at all their sampled sites were likely reflective. This and similar research in which a particular subset of shore types were sampled would be unable to distinguish the effects of surf zone hydrodynamics on intertidal ecology.

Solar radiation decreased significantly with latitude and both *Balanus* and new recruit densities varied inversely with solar radiation; *Balanus* and new recruit densities were higher to the north where solar radiation was lower. Schoch et al. (2006) found a similar relationship with air temperature. When the residuals from regressions between barnacle density and solar radiation were regressed against latitude, the latitudinal effect vanished. Hence, the hypothesized latitudinal variation in barnacle abundance reported in a number of studies may not be due to alongshore variation in upwelling (otherwise one would see high barnacle recruit abundance in the Southern California Bight), but are perhaps due to latitudinal variation in solar radiation or some other factor. Solar radiation has long been known to increase mortality of intertidal organisms, especially recent settlers,

from desiccation stress, thermal stress, and ultraviolet radiation damage. However, this simple hypothesized relationship between solar radiation and barnacle densities does not take into effect numerous other ecological factors such as thermal hotspots or the effect of the timing of low tides on the effects of radiation stress (Helmuth 1998, Helmuth et al. 2000), biological interactions (competition, disturbance, and predation), and larval abundance to name a few. Another possible explanation for the latitudinal gradient in barnacle densities could be increased reproductive output or larval survival (Morgan 2001) due to chlorophyll *a* concentrations that are several times higher along the coast of Oregon and Washington than along Northern California (Hickey and Banas 2008) providing more food for adults and larvae.

At more dissipative sites with bathymetric rip currents, barnacles were frequently very tightly packed (10 to >30 individuals/cm²); individuals tended to be tall with narrow bases, they were often easily dislodged, and open patches of bare rock commonly were colonized by numerous new recruits. The observed morphology is typical of individuals in dense populations (Bertness et al. 1998). These populations appeared to turnover rapidly with, given their small size, few individuals living even a year, and settlers rapidly filled gaps in the population. Connell (1985) described populations with densities this high as being controlled by density-dependent factors, primarily intense competition for space. In contrast, at more reflective sites, densities were much lower (~0.3 new recruits/cm² and ~3 *Balanus*/cm²), and at some of these sites, densities were very low (<0.002 new recruits/cm², <0.3 *Balanus*/cm²). Adults that were large enough to be at least 1 year old were more common; they had the typical conical shape with a wide base for attachment and the shell apex was often eroded. Turnover in these populations appeared to be much slower with separate cohorts contributing to a multigenerational population resulting in a weaker relationship between the abundance of new recruit and population density. Alongshore variation in surf zone hydrodynamics, even over distances as small as several hundred meters, appeared to alter the dynamics of barnacle populations; at more dissipative sites, populations appeared to be recruitment regulated with apparent strong density-dependent effects while at more reflective sites populations appeared to be recruitment-limited.

In his 1985 review paper, Connell pointed out that some sites consistently had high or low barnacle recruitment and or adult densities, which he suggested might be due to characteristics of the local hydrodynamics or larval abundance. For some of our sites, we have data from more than one year and, like Connell, these sites consistently had high or low settlement, recruitment and adult densities, and these consistent differences were related to the surf zone hydrodynamics (Table 1). Sites that were dissipative (reflective) had high (low) barnacle settlement, weekly recruitment, and densities in the different sample years.

TABLE 1. Data from sites sampled in this study compared to that collected in previously published and unpublished studies (site name with the average surf zone width, $\pm$ SD, and number of Google Earth images examined, *n*).

Site	Surf zone type	Current data (this paper)	Previous data	References
Dike Rock, Scripps Reserve (82 $\pm$ 26, 9)	dissipative	2012 PS, 306 <i>Balanus</i> /100 cm ² , 299 new recruits/100 cm ²	1983 peak DS >1,000-100 cm ⁻² d ⁻¹ ; 1989 peak DS >1,000/d	Shanks (1986), Pineda (1991)
Bastendorff (210 $\pm$ 46, 9)	dissipative	2012 PS, 4,117 <i>Balanus</i> /100 cm ² , 2,612 new recruits/100 cm ² , 2011 peak DS 1,000-100 cm ⁻² d ⁻¹ ; 2010 peak WR 374-100 cm ⁻² week ⁻¹	2007 peak DS >1,000-100 cm ⁻² d ⁻¹ ; 2008 PS, 846 total/100 cm ² , 245 new recruits/100 cm ² ; 2013 peak DS 650-100 cm ⁻² d ⁻¹	Shanks (2009a), Shanks et al. (2010) A. L. Shanks, unpublished data
Lighthouse (102 $\pm$ 30, 8)	dissipative	2012 PS, 2,726 <i>Balanus</i> /100 cm ² , 1,449 new recruits/100 cm ²	2008 PS, 1,166 total/100 cm ² , 560 new recruits/100 cm ²	Shanks et al. (2010)
Humbug Mt. (14 $\pm$ 5, 4)	reflective	2010 peak WR 1.3-100 cm ⁻² week ⁻¹	2008 PS 133/100 cm ² , new recruits 4/100 cm ²	Shanks et al. (2010)
Port Orford Heads (37 $\pm$ 21, 7)	reflective	2012 PS, 90 <i>Balanus</i> /100 cm ² , 0.5 new recruits/100 cm ²	2008 PS, 79/100 cm ² , 1.1 new recruits/100 cm ²	Shanks et al. (2010)
Pack Trail (22 $\pm$ 7, 7)	reflective	2011 peak DS 4-100 cm ⁻² d ⁻¹ , 2010 peak WR 3-100 cm ⁻² week ⁻¹	2010 peak DS 2.3-100 cm ⁻² d ⁻¹ , 2011 peak WR 1-100 cm ⁻² week ⁻¹	A. L. Shanks, unpublished data

Notes: PS, photographic survey; DS, daily settlement; WR, weekly recruitment. Sites that are dissipative (reflective) have high (low) barnacle densities, settlement, and weekly recruitment across years.

Connell (1985) addressed four questions: (1) What environmental factors affect the density and distribution of “settlers?” (2) How do variations in settlement affect the abundance and distribution of young juveniles? (3) How do variations in either settlement or recruitment affect the abundance and distribution of adults? (4) How do rates of recruitment vary over larger scales of time and space? Results from our study address these questions. (1) The density and distribution of daily barnacle settlement, considered “settlers” by Connell, varied directly with surf zone hydrodynamics; where surf zones were wide with bathymetric rip currents (more dissipative surf zones), daily settlement was an order of magnitude or more higher than at sites, even nearby sites, where surf zones were narrow and more reflective. (2) Daily settlement explained much of the variability (>80%) in the abundance and distribution of young juveniles (i.e., new recruits from the photographic survey). (3) Variations in daily settlement explained much of the variability (>80%) in the abundance of adult *Balanus*. Daily settlement was orders of magnitude higher at sites with more dissipative surf zones than at sites with more reflective surf zones. (4) The abundance of new recruits (not rates, but snapshots of abundance) varied in space along our latitudinal transect and weekly recruitment (data at eight sites) were both much higher at sites with dissipative surf zones. Barnacle settlement, recruitment, and adult densities were all higher at more dissipative than reflective surf zones. The primary drivers of surf zone hydrodynamics are the wave climate and the slope of the shore, which persist over time. We propose that this stability in surf zone hydrodynamics leads to stability in the characteristics of barnacle populations over time.

Variation in surf zone hydrodynamics has been recognized for decades as being crucial to understanding community dynamics of soft-sediment communities (McLachlan and Erasmus 1983, Peterson 1991, Morgan 2001), and it is becoming increasingly apparent that it may be equally important for rocky shore communities (Rilov et al. 2008, Shanks et al. 2010, 2015, 2016, Morgan et al. 2016). Indeed larval supply is just one of several bottom-up subsidies from the coastal ocean, including phytoplankton, zooplankton, detritus and wrack, that regulate the dynamics and structure of rocky shore communities (Bustamante et al. 1995, Menge et al. 1997a, b, 2003), and delivery of these subsidies to the shore likely varies with surf zone hydrodynamics.

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SUPPORTING INFORMATION

Additional supporting information may be found online at: <http://onlinelibrary.wiley.com/doi/10.1002/ecm.1265/full>

DATA AVAILABILITY

Data available from the Dryad Digital Repository: <https://doi.org/10.5061/dryad.tq381>.