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Surf zone physical and morphological regime as determinants of temporal and spatial variation in larval recruitment

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ABSTRACT

Larvae of intertidal species develop in the coastal ocean, and the last body of water they must cross while migrating back to shore is the surf zone. We hypothesized that the surf zone is a semipermeable barrier to this shoreward migration and that differences in water exchange across the surf zone result in temporal and spatial variation in larval delivery to the shore. We tested the hypotheses that larval delivery 1) should increase with larger waves and 2) should be higher on more dissipative beaches than on more reflective beaches. We found a significant positive correlation between the daily averaged ratio of wave height to wave period (H/T) and daily cyprid settlement at Dike Rock, California and Bastendorff Beach, Oregon, USA. We tested the second hypothesis by comparing populations of barnacles, limpets, and benthic algae on rocks on four more dissipative and six more reflective sandy beaches in northern California and southern Oregon. Newly recruited barnacles and limpets were significantly more abundant at more dissipative than reflective beaches, and the higher abundance was most likely due to differences in settlement rather than post-settlement mortality. The density and percent cover of barnacles and the density of limpets were significantly higher at more dissipative beaches. In contrast, the density and percent cover of algae were significantly higher at more reflective beaches. The results are consistent with the hypothesis that the surf zone is a semipermeable barrier to the shoreward migration of larvae and that differences in water exchange across the surf zone as function of the beach hydrodynamics result in temporal and spatial variation in larval delivery to the shore.

1. Introduction

Many intertidal invertebrates and fishes produce pelagic larvae that go through their development in the waters over the continental shelf. At the end of this period of development, these larvae must migrate back to the intertidal zone. A variety of mechanisms has been suggested or demonstrated to transport larvae shoreward (reviewed in Shanks, 1995). As these larvae approach shore, the last body of water they must cross is the surf zone, i.e., the region located between the shoreline and seaward extent of wave breaking. The mean breaking location is defined when $H_{mo}/h \geq 0.6$, where H_{mo} is the significant wave height and h is the local water depth (Thornton and Guza, 1983). Field observations of barnacle settlement at different intertidal beach sites are used to test the hypothesis that the hydrodynamics of the surf zone affects the rate of delivery of larvae to the shoreline and was inspired by the patterns of barnacle settlement and observations of the cross-shelf distribution of barnacle larvae in the coastal ocean (see below).

We have observed very large variations in settlement rates of cyprids (barnacle postlarvae) between closely spaced sites. For example, barnacle settlement rates to boulders at Dike Rock beach in southern California (Pineda, 1991; Shanks, 1986) and on boulders in Bastendorff Beach in southern Oregon (Shanks, 2009) were very high (e.g., >10 cm^{-2}days^{-1} at each site), but settlement at nearby rocky intertidal sites was orders of magnitude lower. We assumed that high settlement on boulders in sandy beaches was due to the concentration of settling cyprids on the limited amount of available rocky substrate (Pineda and Caswell, 1997), but settlement rates of cyprids to boulders in beaches in southern Oregon (Shanks, 2009) and central California (S. H. Miller and S. G. Morgan, Bodega Marine Laboratory, unpublished data) were very different despite the similarity in habitat as well as an abundant source of cyprids in the nearshore waters (see below). What might cause such large variations in settlement rates along a shore?

A widely held belief in marine biology is that larvae of intertidal invertebrates are swept offshore during upwelling and onshore during downwelling. We have recently published papers testing this

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hypothesis in three different geographic settings, the mid-Atlantic Bight (Shanks and Brink, 2005; Shanks et al., 2002; Shanks et al., 2003), off southern Oregon (Shanks and Shearman, 2009), and off northern California (Morgan et al., 2009a,b). The results of these studies are very consistent; many types of larvae of intertidal species, including the larvae of intertidal barnacles, the subjects of this study, 1) avoided the surface Ekman layer, 2) were not swept offshore by upwelling nor onshore by downwelling, 3) remained within about 3 or 4 km of shore, and 4), during the summer months, when the sampling for these studies occurred, competent larvae were always abundant within a kilometer of the shoreline. Furthermore, most invertebrate species examined thus far do not appear to be limited to recruiting during upwelling relaxation events (Bennell, 1981; Hawkins and Hartnoll, 1982; Mace and Morgan, 2006; Morgan et al., 2009b; Pineda, 1991; Roegner et al., 2007; Shanks, 1983; Shanks, 1986; Shanks, 1998; Shanks, 2006; Shanks, 2009).

The critical observation from these studies was that, during the summer months, when most intertidal organisms in this part of the world spawn, there was apparently always an abundance of competent larvae in the waters just offshore from coastal habitats yet settlement on the shore, even over short distances (hundreds of meters), can vary by orders of magnitude. During the shoreward migration of larvae from the coastal ocean to the shore, larvae must cross the surf zone and these observations suggest the hypothesis that the surf zone may constitute a semipermeable barrier to this shoreward migration; variation in the permeability of this barrier may affect larval delivery to the shore. Rilov et al. (Rilov et al., 2008) made similar observations on the nearshore distribution of mussel larvae and their settlement in the intertidal zone and arrived at a similar hypothesis.

Spatial variation in larval transport across the surf zone may depend on beach morphology, which in turn supports different surf zone hydrodynamics processes, as described by Wright and Short (1984). Beaches range from dissipative to reflective morphodynamic systems. The relative reflectivity of a beach is a function of the beach slope and the wave steepness, as expressed by the Irribarren number (Battjes, 1974). Fully dissipative beaches are characterized by a wide surf zone, gradual beach slope, fine-grain sand, undertow and alongshore currents (Wright and Short, 1984). In general, most beaches are not fully dissipative and reside in the intermediate morphodynamic beach state (Lippmann and Holman, 1990). Intermediate beaches are characterized by medium surf zones, gradual low tide slopes, steeper high tide slopes, and complex surf zone morphology that generally supports undertow, alongshore currents, and rip currents (Wright and Short, 1984). In contrast, highly reflective beaches are characterized by narrow surf zones, steep beach slopes, coarse-grain sand, and the hydrodynamics are characterized by standing wave motions (Wright and Short, 1984). In general, reflective beaches do not morphodynamically change to intermediate beaches but remain in the reflective state. Rocky shore surf zones are considered to behave like highly reflective beach surf zones. Surf zone hydrodynamics vary with the degree of reflectivity (Neshaei et al., 2009) and variations in reflectivity may translate into different rates of larval delivery to the intertidal zone.

Detailed surf zone field experiments have been performed on dissipative and intermediate beaches (Thornton et al., 2000). Fewer field experiments have been performed on reflective beaches, and, owing to the hazardous nature of deploying instruments at reflective beaches, they generally focused on the swash zone, not the surf zone.

Only a few studies have focused on the rate at which surf zone waters are exchanged with offshore water, i.e., the surf zone flushing rate. These studies found the time needed for half the surf-zone water to be flushed, varied from days when waves were small to only minutes when waves were large (MacMahan et al., 2009; Reniers et al., 2009; Smith and Largier, 1995; Talbot and Bate, 1987). Surf zone currents and flushing rates increase with increasing wave height leading to greater exchange of water within the surf zone with water seaward of the surf zone; this exchange should lead to enhanced delivery of larvae to the shore. Settlement should be lower when the wave height is small and water exchange is less. The exchange of surf zone water and associated delivery of larvae to the shore may also depend upon beach type and the associated variation in surf zone hydrodynamics. Therefore, we hypothesized that larval delivery 1) should increase with increasing wave height and 2) vary with beach type as measured by beach slope.

2. Methods

We tested the hypothesis that increased wave height leads to higher settlement rates by using previously collected time series of daily barnacle settlement. One time series was collected in southern California at Dike Rock (Shanks, 1986), and the other was collected at Bastendorff Beach in southern Oregon (Shanks, 2009). Both Dike Rock and Bastendorff beach are more dissipative beaches. The Dike Rock sample site is located 1.5 km north of the Scripps Institution of Oceanography pier. Settlement was followed on three boulders, which spanned the intertidal zone. The temporal pattern of settlement on these boulders was quite similar and the data presented here are from Rock 2, which was located $+1.0$ m above Mean Lower Lower Water. Settlement plates consisted of pancakes of SpashZone® epoxy into which three circular grooves were pressed (4 cm dia $\times 0.5$ cm wide, surface area per groove 3 cm^2). Using a $10\times$ hand lens, counts of cyprids and recently metamorphosed barnacles were made daily from 9 April through 30 June, 1983 (70 day time series). Cyprids and new barnacles were easily viewed against the olive green of the epoxy. In Oregon, daily observations of barnacle settlement were made from 21 May through 4 August, 2007 (75 day time series). Settlement plates consisted of grey Safety Walk® tape on a 10×10 cm Plexiglas plate (Farrell et al., 1991). Three replicate plates were set within the densely populated barnacle zone and within several meters of each other on the east, west, and north sides of a rock outcrop. Data presented here are from the shadier west-side site. Plates were wetted by breaking waves at tidal elevations $>+1.5$ m. Counts of cyprids and newly metamorphosed barnacles were made daily with a $16\times$ hand lens. At both sites, following the daily counts the plates were cleaned by vigorous brushing with a tooth-brush. Settlers and new-recruits were not identified to species.

Wave data were from NOAA buoy 46025 in the Santa Monica Basin (33.739 N 119.056 W, southern California deployed in 882 m water depth) and buoy 46015 off Port Orford (42.747 N 124.823 W, southern Oregon deployed in 423 m water depth). There were a number of wave gauges in southern California, which were closer to the Dike Rock study site than the Santa Monica Basin buoy we have used (approximately 170 km north). Unfortunately, due to storms generated by the 1983 El Niño, all the wave gauges near the study site were out of service forcing us to use the data from the Santa Monica Basin buoy. The Port Orford buoy is the closest source of wave data to the Bastendorff study site (approximately 80 km south).

Deep-water significant wave heights at the buoys were shoaled to depth-limited (shallow-water) wave breaking using linear wave theory and conserving wave energy flux (Dean and Dalrymple, 1995),

$$H_b = \left(\frac{\gamma}{g}\right)^{1/5} \left(\frac{H_{buoy}^2 C_{buoy} \cos\theta_{buoy}}{2}\right)^{2/5} \tag{2}$$

$$C_{buoy} = \frac{g}{\omega} \tanh\left(k_{buoy} h_{buoy}\right), \tag{3}$$

$$h_b = \frac{H_b}{\gamma}, \tag{4}$$

where H_b is wave height at the onset of wave breaking denoted by the subscript b, γ is the shallow-water, depth-limited breaking criterion set at 0.6 for significant wave heights (Thornton and Guza, 1983), g is the acceleration due to gravity, H_{buoy} is the significant wave height measured at the buoy, C_{buoy} is wave phase speed at the wave buoy, θ_{buoy} is the mean wave direction set to zero owing to lack of directional wave estimates, k_{buoy} is the wave number at the wave buoy, ω is the radian wave frequency, and h_{buoy} is the buoy water depth. The e-folding decorrelation time of the hourly wave height time series for Bastendorff and Dike Rock is approximately 25 and 27 h, respectively. This suggests that averaging the hourly wave height over 1 day is valid.

At each site, the daily settlement of cyprids (corrected for hours of submersion) was strongly cross-correlated with the tidal amplitude (spring-neap) cycle with peak settlement occurring between neap and spring tides. The relationship between the tidal amplitude cycle and daily settlement was apparent in the settlement time series as a significant autocorrelation around a lag of seven days. Prior to running regressions between settlement, and a number of wave height related parameters, the influence of the fortnightly tidal cycle on settlement was minimized by removing the autocorrelation in the settlement time series (Shanks, 1998). In the Dike Rock data set, there was only a significant autocorrelation at 1 day lag in the wave data. The Durban–Watson statistic for the Dike Rock data was 1.9 indicating that the regression did not suffer from an autocorrelation problem (http://hadm.sph.sc.edu/Courses/J716/Dw.html). In the Bastendorff data set, the wave data were significantly autocorrelated at 1 and 2 days lag. The Durban–Watson statistic for the Bastendorff beach data was 1.0, at the cut off between having an autocorrelation problem and not (http://hadm.sph.sc.edu/Courses/J716/Dw.html). To correct this problem we transformed the wave data by removing the autocorrelation using the transformation package in the STATISTICA statistics package. After this transformation, in the autocorrelation of the wave data there were no lags that were significant. The regression analysis at Bastendorff beach was run without modification to the wave data time series and with the autocorrelation removed from the time series.

We tested the hypothesis that differences in beach slope affect the rate of larval delivery to shore by surveying the community composition of large boulders at ten sandy beaches between Coos Bay, Oregon, and Trinidad Head, California, during late summer 2008 (Table 1, Fig. 1). Based on beach slope and surf zone width, four beaches were classified as more dissipative and six as more reflective. We used standard surveying techniques to measure the slope of the beach between the high tide line and the water's edge adjacent to the sampled rocks. As an index of the width of the surf zone, we measured the time waves took to cross the surf zone and assumed that wave transit times were proportional to surf zone width. We made four measurements at each beach, beginning when a wave first started to break at the outer edge of the surf zone and ending when it reached the swash line. Beaches were classified as more dissipative if their slope was relatively flat (<3°) and the surf zone was wide (wave transit time across the surf zone >50 s). They were classified as more reflective if the slope was >4° and the surf zone was narrow (wave transit time across the surf zone <30 s).

At each site, 10 haphazardly positioned digital photographs (roughly 30 by 20 cm) were taken in the barnacle zone. A ruler was placed in each image as a scale reference. To minimize the effects of solar and wave exposure on the data, photographs were taken at several boulders at each site and at locations around each boulder. In this way, we photographed faces of boulders with a diversity of sun and wave exposures. Five of the beaches faced roughly west (Agate, Bandon, Port Orford, Wilson Creek, Freshwater Lagoon, and Stone Lagoon) and three faced roughly north (Bastendorff, Lighthouse, and Humbug). Photographs were taken under natural lighting at a resolution of 12 megapixels with a Canon EOS camera equipped

Table 1

Sample sites in Oregon and California. Beaches were classified as more dissipative (low beach angle, wide beach and wide surf zone) or more reflective (higher beach angle, narrow beach, and narrow surf zone). The time for waves to cross the surf zone (t) was used as an index of surf zone width. Values of t are the mean and standard deviation from four measurements.

Site	Lat., Long.	Beach type	Slope, degrees	Intertidal width, m	Index of surf zone width, t sec
Bastendorff, Oregon	43.34203, 124.35763	Dissipative	1.2	99	100 (12.4)
Lighthouse, Oregon	43.33874, 124.37221	Dissipative	2.7	45	53 (6.1)
Agate Beach, Oregon	43.21688, 124.39674	Dissipative	0.6	141	68 (4.7)
Bandon, Oregon	43.10361, 124.43501	Dissipative	0.7	80	63 (7.1)
Port Orford Head Oregon	42.74407, 124.51411	Reflective	4.3	34	22 (4.6)
Humbug, Oregon	42.68410, 124.44800	Reflective	5.1	29	28 (5.2)
Wilson Creek, California	41.60202, 124.10047	Reflective	5.9	24	17 (2.1)
Freshwater Lagoon, California	41.26432, 124.09882	Reflective	7.2	20	31 (1.6)
Stone Lagoon, California	41.26634, 124.09976	Reflective	6.3	17	ND
Trinidad Beach, California	41.05986, 124.14896	Reflective	4.8	30	29 (1.0)

with a 28–135 mm macro zoom lens. The fine detail provided by this level of resolution was critical for the subsequent analysis of the photographs. From the photographs we determined the density and percent cover of barnacles and algae, the density of limpets, and the size frequency distribution of barnacles and limpets.

Barnacle density was determined one of two ways. Where density was low (<250 100 cm^{-2}, more reflective beaches), all the barnacles in the photograph were enumerated. Where density was high (>800 100 cm^{-2}, more dissipative beaches), barnacles in three randomly placed belt transects were counted in each photograph and the overall density within a photograph was the average from the transects. The point–intercept method was used to determine percent cover of barnacles. A clear acetate sheet was placed over the image on the computer screen (image size 35×25 cm), and the presence/absence of barnacles in 25 randomly placed 1-cm^{-2} boxes was noted. To determine the density of algae, all individuals in each photograph were counted. At times it was difficult to differentiate individuals in the photographs, hence, the reported algal densities are somewhat of an underestimate. The percent cover of algae was determined using the ImageJ software package to measure the total area of each photograph and the area in the photograph occupied by algae. Limpet density was generally determined by counting all limpets in the entire photograph. In some of the photographs from the more dissipative beaches, the rock surface was very bumpy due to closely packed barnacles forming hummocks. Due to the narrow depth of field of the photographs, portions of these photographs were out of focus and in these sections of the photographs it was difficult to discern the very small limpets (median size <3 mm) characteristic of the dissipative beach habitats. In this situation, counts were limited to the portions of the photographs that were in focus and the area counted was determined from area measurements using ImageJ. Size frequency distributions of barnacles and limpets were determined in each of five randomly selected photographs per site by enlarging images to 300% and measuring the diameters of individuals using ImageJ software. Approximately 50 haphazardly selected individuals of each species were measured when available, using only individuals, which were both in focus and not at an angle to the camera.
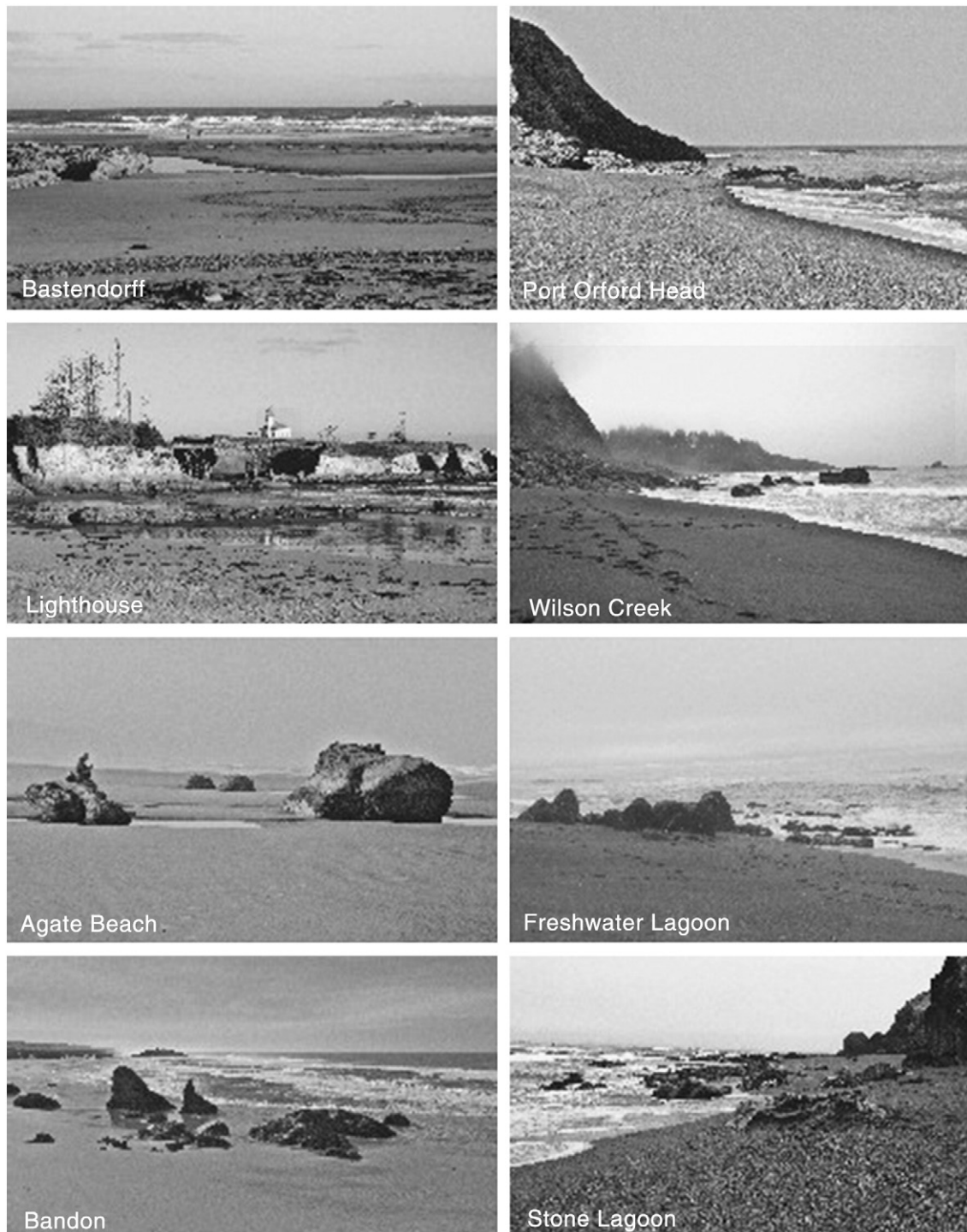
Fig. 1. Photographs of study sites at more dissipative (photographs to the left) and more reflective (photographs to the right) beaches. Photographs of all the more dissipative beaches sampled are presented, but photographs of only four of the six more reflective beaches are.

To investigate the effect of beach type (more dissipative or reflective) on the delivery of larvae to the shore, we would ideally measure daily settlement, but this was logistically impossible. We were able to measure new barnacle recruits after two weeks at six of the 10 sample sites (Bastendorff, Lighthouse, Agate, Bandon, Port Orford Head, and Humbug). At each site, we placed three settlement plates in the barnacle zone where the photographs had been taken. The settlement plates were composed of a pancake of SplashZone® epoxy into which a 10×10 cm plate of SafetyWalk® tape was pressed. This settlement plate design provided an attractive surface for settling cyprids, but, unlike SafetyWalk settlement plates, these settlement plates did not heat up to high temperatures in the sun (Shanks, 2009); in the sun, the surface temperature of the epoxy plates was similar to that of the adjacent rock surface. Settlement plates were photographed under natural lighting using a macro lens on the camera described above.

Recruitment also was estimated using size frequency data gathered at all 10 beaches. Barnacles and limpets <1.5 mm in diameter are no more than about 1 or 2 months old, respectively (Kay, 2002). We estimated the number of new-recruits in the photographs used for the determination of the size frequency distribution by multiplying the percentage of the population in the

photographs <1.5 mm in diameter times the total population in each image.

Statistical comparisons of the various parameters (barnacle density and percent cover, limpet density, algal density and percent cover, limpet recruits, and barnacle recruits) between more dissipative and reflective beaches as indicated by beach slope were made using one-way analysis of variance (ANOVA). The percent cover and density data were arcsin and log transformed, respectively, before analysis to meet assumptions of normality and homoscedasticity.

3. Results

In both time series, the transformed daily settlement of cyprids varied significantly with wave steepness (H/T) (Oregon data with autocorrelation removed, $r = 0.31$, $p < 0.05$, $n = 75$, without removing autocorrelation $r = 0.38$, $p < 0.003$, $n = 75$; California data $r = 0.32$, $p < 0.008$, $n = 70$) (Fig. 2). Higher settlement tended to occur on (Oregon data) or a day after (California data) the arrival of steeper waves. Hence, during periods of larger waves and steeper waves when the flushing rates of the surf zone would have been higher, larval delivery to the shore was also higher. While the relationships were

significant, wave steepness explained only a small percentage of the variability in settlement rate (about 14 and 10% for the Oregon and California data, respectively). There was no indication in the data that settlement rate declined when the highest waves were present. However, during the periods of observation, average daily wave height was never greater than 3.5 and 2.5 m in Oregon and California, respectively.

Sample sites that we considered to be more dissipative beaches were characterized by beach slopes between 0.6 and 2.7°, wide beaches (45 to 141 m), and wide surf zones (time for waves to cross the surf zone 53 to 100 s) (Table 1). At sites we considered to be more reflective, the beaches slopes were 4.3 to 7.2°, the beaches were narrower (17 to 30 m), and the surf zones were narrower (time for waves to cross the surf zone 17 to 31 s) (Table 1). The time for waves to cross the surf zone and beach width were both negatively correlated with beach slope (Fig. 3).

On the exposed rocks at more dissipative beaches, barnacles were very densely packed, often forming hummocks (Fig. 4), and within the barnacle zone, the population covered the rock surface almost completely. The only gaps were where waves apparently had dislodged weakly attached hummocks of barnacles. Barnacle densities
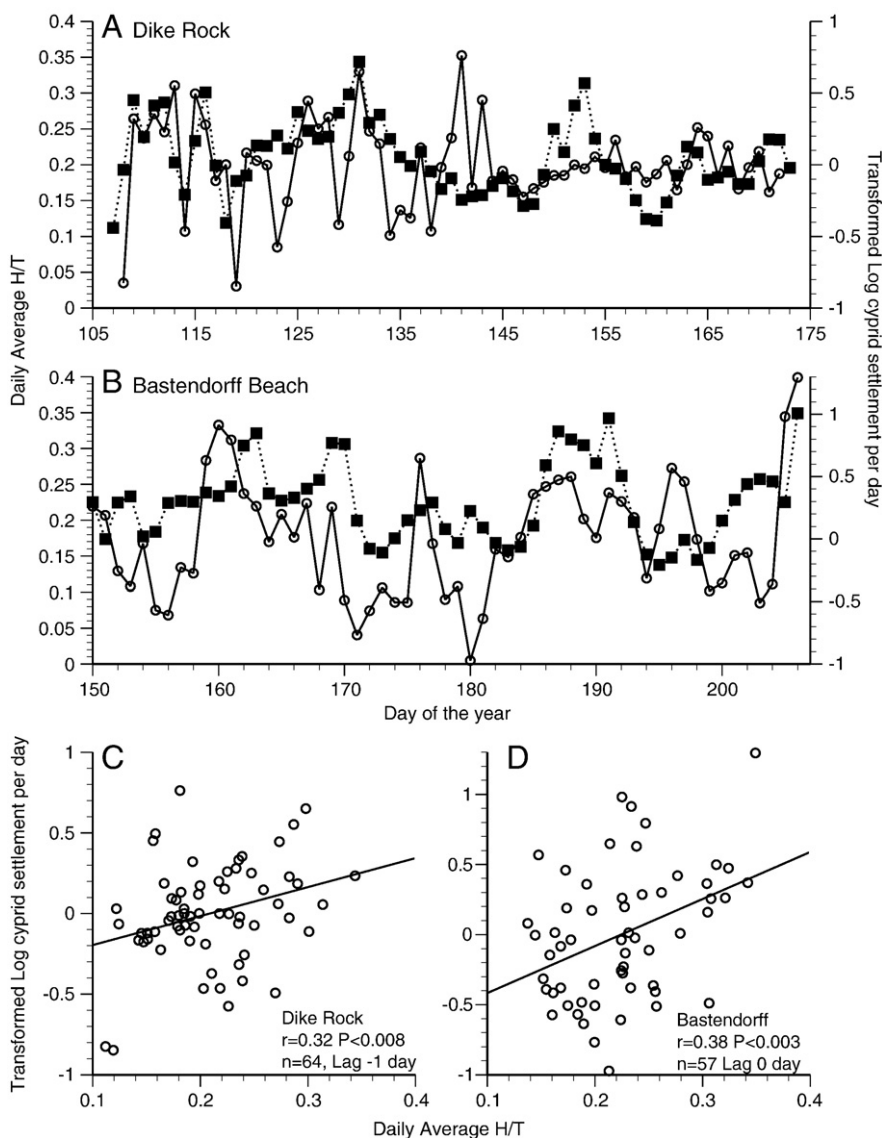

Fig. 2. The average daily ratio of wave height to wave period (wave steepness, *H/T*) (dashed lines and solid squares) at Dike Rock Beach, California (A) and Bastendorff Beach, Oregon (B) plotted with the transformed daily cyprid settlement (solid lines open circles). Scatter plots of the average daily ratio of wave height to wave period (*H/T*) and transformed daily cyprid settlement (see methods for description of the transformation) on rocks in the beach at Dike Rock, California (C) and Bastendorff Beach, Oregon (D).
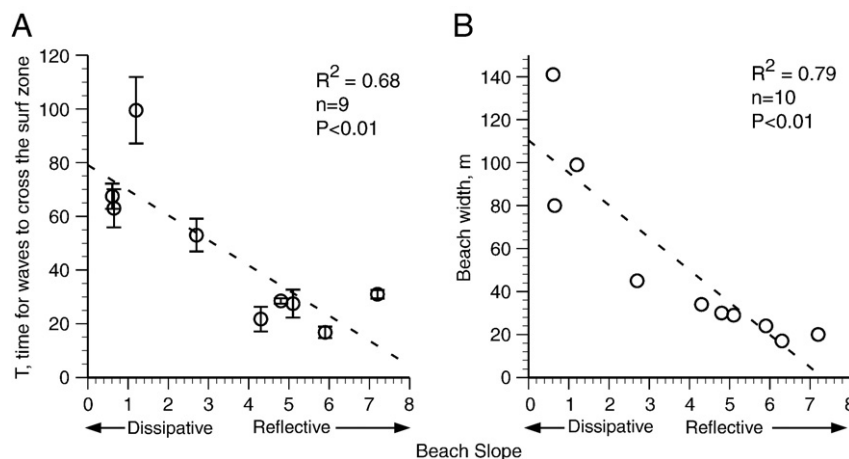
Fig. 3. (A) The relationship between beach slope and the time it took waves to cross the surf zone (mean ± 95% confidence interval, $n = 4$), an index of surf zone width. (B) The relationship between beach slope and beach width.

ranged from 800 to 1700 per 100 cm^{-2} and percent cover ranged from 96 to 100% (Fig. 5). Barnacle populations on rocks at more reflective beaches were much less dense (230 to 29 per 100 cm^{-2}), never formed hummocks (Fig. 4), and covered only a portion of the rock surface (6 to 55%) (Fig. 5). Both the density and percent cover of barnacles at more dissipative beaches were significantly higher than at more reflective beaches (Fig. 5).

Limpets (mostly *Lottia digitalis*) were common at seven of the 10 sites; few limpets were present in photographs from one dissipative beach (Agate Beach) and two reflective beaches (Humbug and Wilson Creek) (Fig. 5). At more dissipative beaches the population density of limpets ranged from 33 to 37 100 cm^{-2}, significantly higher than at more reflective beaches where the density ranged from 9 to 17 100 cm^{-2} (Fig. 5).

In contrast to the density of barnacles and limpets, densities and percent cover of algae were both significantly higher at more reflective beaches (range 1 to 20 individuals 100 cm^{-2} and 0.5 to 25%) than at more dissipative beaches (range 0.01 to 0.06 100 cm^{-2} and 0 to 0.2%) (Fig. 5). The dominant algae at the reflective sites were "tar spot" forms (unidentified sporophytes) and *Ulva* spp. At the dissipative sites, algae were very uncommon and primarily *Ulva* spp.

At more dissipative beaches, the size frequency distributions of both barnacles and limpets were dominated by small recently recruited individuals with few larger older individuals (Figs. 6 and 7). The reverse was true at the more reflective beach sites (Figs. 6 and 7). The average size of barnacles and limpets at dissipative sites was significantly smaller than at reflective sites (barnacles, $F = 87.62$, $p = 0.000014$; limpets, $F = 100.41$, $p = 0.00017$).

Only one recruit was observed on the six settlement plates that were deployed at the two reflective beaches (Fig. 8). At the more dissipative sites, we lost one settlement plate each at Bastendorff and Agate Beach, and in addition, two of the settlement plates at Bandon were heavily colonized by limpets (about 10 animals per plate), which may have "bulldozed" new settlers. Recruitment to the plates at the more dissipative beaches was highly variable (Fig. 8). Abundance ranged from 20 individuals 100 cm^{-2} (Agate Beach plates and the plates at Bandon colonized by limpets) to 1,500 to 2,000 individuals 100 cm^{-2} on plates at Lighthouse and Bastendorff. Our *a priori* hypothesis was that new-recruits would be more abundant at more dissipative than reflective beaches, and a one-way ANOVA comparing the average recruitment to plates at dissipative and reflective beaches was significant at $p = 0.06$ level (Fig. 8); recruitment was significantly higher at more dissipative beaches. Recruitment estimates from the size frequency data yielded similar results. The number of newly recruited barnacles and limpets at more dissipative beaches was one

to three orders of magnitude higher than at more reflective beaches (Fig. 8).

4. Discussion

While we did not directly test the effect of variable surf zone hydrodynamics on settlement rate, the significant positive correlations between settlement and daily averaged wave steepness (H/T) suggest that larval delivery to shore varied with the rate of exchange of water across the surf zone. The potential surf zone motions that can generate exchange depend on beach type, beach slope, wave period, and wave height. For more dissipative or intermediate beaches, undertow (Garcez Faria et al., 2000; Haines and Sallenger, 1994; Reniers et al., 2004), rip currents systems (MacMahan et al., 2006, 2009; Reniers et al., 2009; Smith and Largier, 1995; Shepard and Inman, 1950; Talbot and Bate, 1987), and alongshore current instabilities (Dodd et al., 1992; Özkan-Haller and Kirby, 1999; Oltman-Shay et al., 1989) cause exchange of water across the surf zone and have the possibility of transporting material (larvae) into the surf zone. The surf zone hydrodynamics at more dissipative or intermediate beaches are conducive to the exchange of surf zone water with the inner shelf and, during this exchange, larvae present in the inner shelf waters appear to be transported shoreward. At more reflective beaches, cross-shore exchange mechanisms have been little studied. More reflective beaches allow for cross-shore standing wave motions, which induce constructive and destructive wave interference (Dean and Dalrymple, 1995). Neshaei et al. (2009) found that cross-shore standing wave motions reduced the magnitude of undertow, which decreases cross-shore transport. Therefore, the hydrodynamics of more reflective surf zones appear to be less conducive to the exchange surf zone waters with inner shelf waters, which should result in lower settlement at more reflective beaches relative to more dissipative beaches; the surf zone may be a barrier to the shoreward migration of larvae.

The effects of the sea breeze on the surf zone might cause diurnal variations in the exchange of water across surf zone. The higher speed onshore winds of the late afternoon/early evening increases wave height at this time, which in turn increases the Stokes drift at a dissipative beach. As a consequence Stokes drift and the sea breeze correlate (Hendrickson and MacMahan, 2009). Because we sampled daily and the effect of the diurnal wind is sub-daily we cannot test for the effect of the sea breeze in our data. In a planned study we should be able to address this hypothesis.

While the cross-correlations between wave steepness (H/T) and barnacle settlement were significant, the relationship explained only
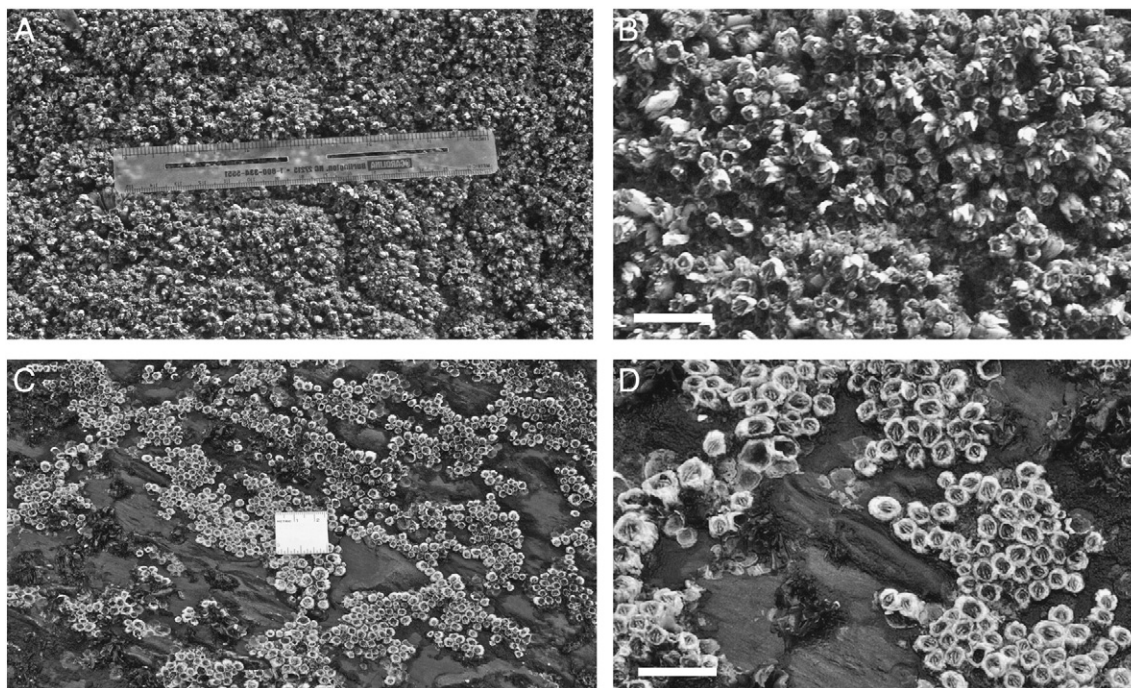
Fig. 4. Photographs of the barnacle cover typically found at more dissipative (A, B) and more reflective (C, D) beaches. The white bar in B and D is 1 cm. Note the abundance of very small barnacles in B and their absence in D.

between 10 and 15% of the variability in settlement, indicating that other factors affected daily variability of barnacle settlement. One obvious variable that we could not control was the abundance of cyprids in the waters just outside the surf zone that were available for

shoreward transport (Pineda et al., 2006). At both sites, settlement fluctuated over the tidal amplitude cycle. This fortnightly signal is probably due to the shoreward transport of larvae by the internal tides (Shanks, 1986; Pineda, 1991; Pineda, 1999; Shanks, 2002). By
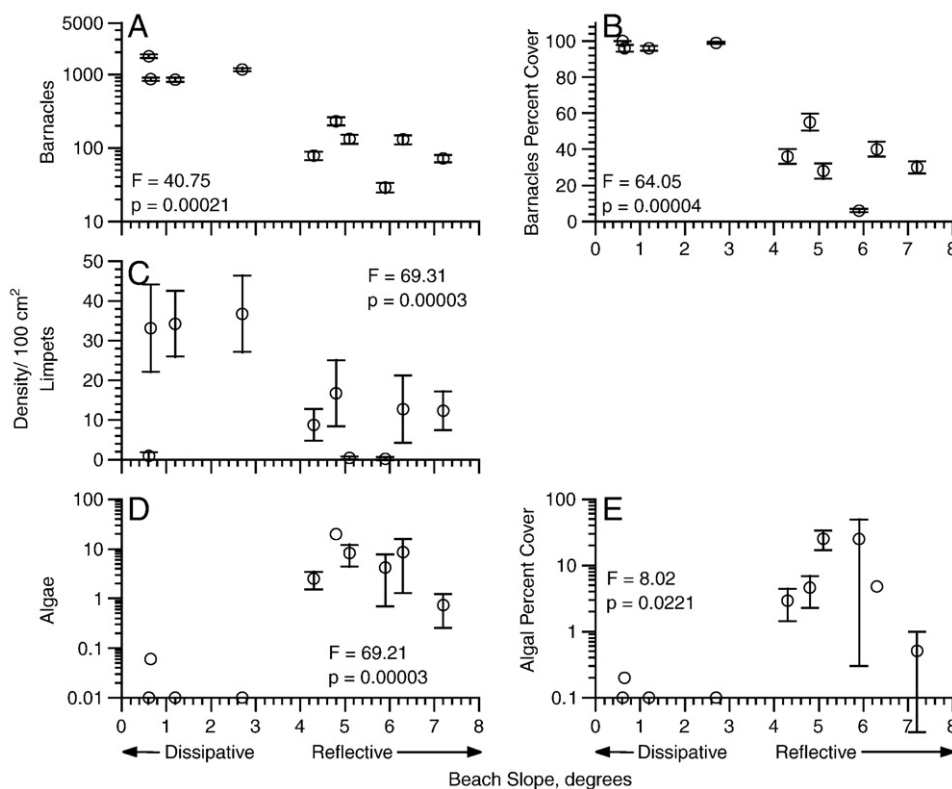
Fig. 5. Mean ($\pm$95% confidence interval, $n = 10$) (A) barnacle density (# 100 cm^{-2}), (B) barnacle percent cover, (C) limpet density (# 100 cm^{-2}), (D) algal density (# 100 cm^{-2}), and (E) algal percent cover plotted against beach slope. Values in each figure are the results of a 1-way ANOVA comparing the density (log transformed) and percent cover (arcsin transformed) at more dissipative and more reflective beaches.
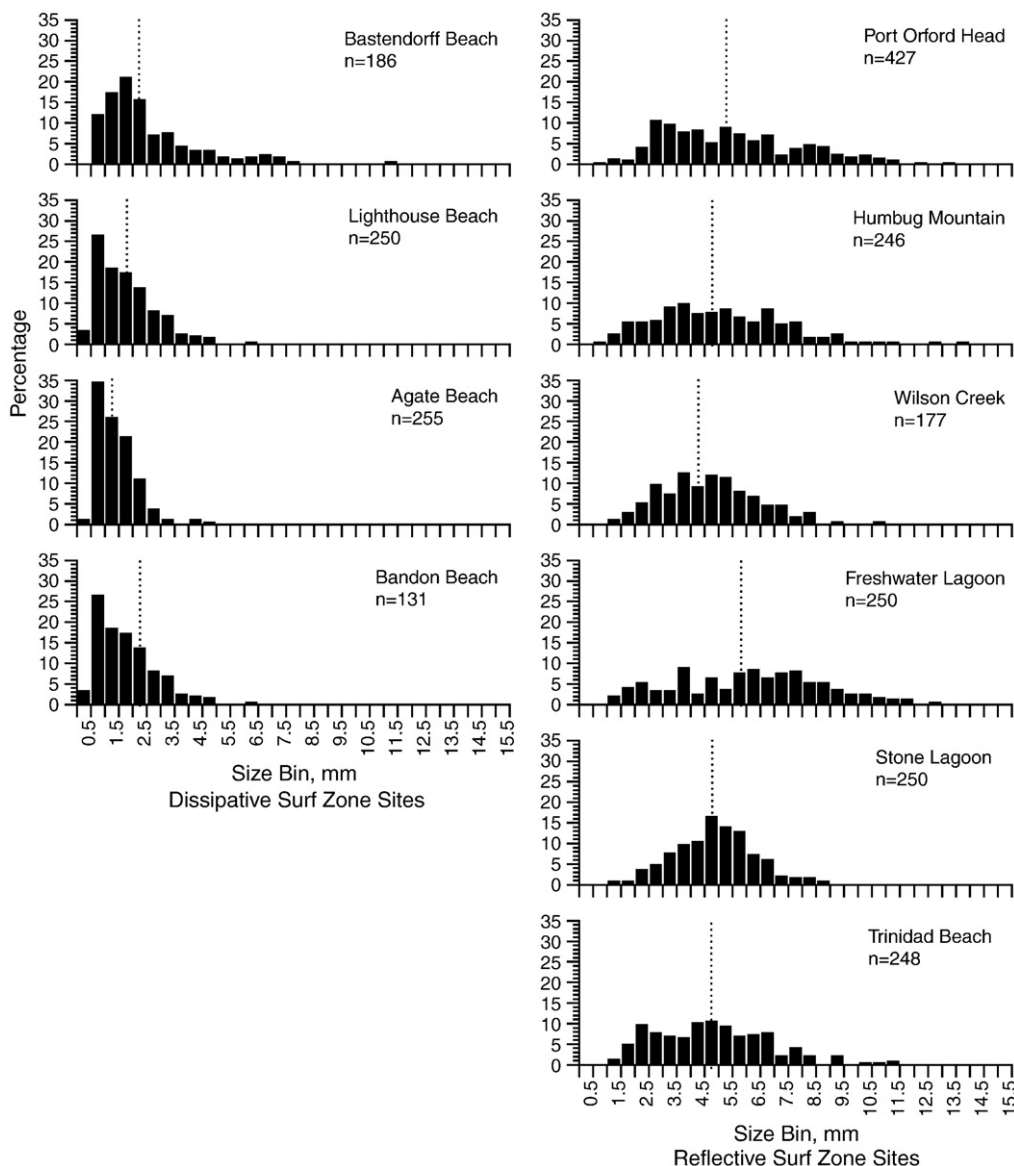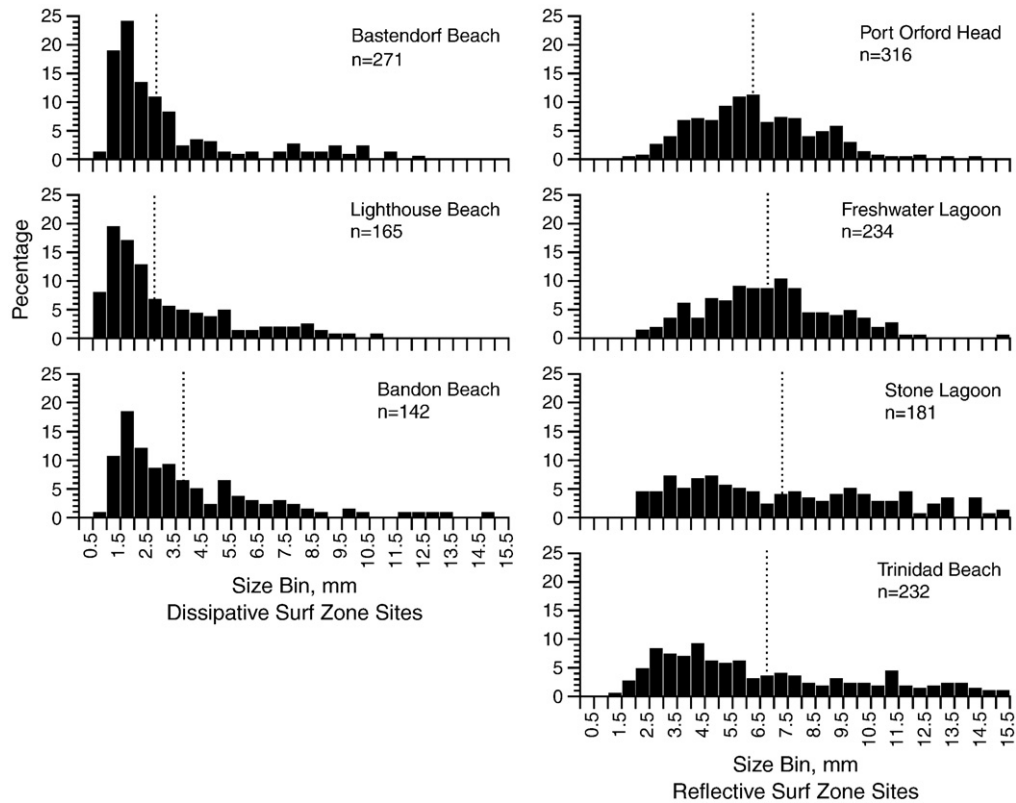
Fig. 6. Size frequency distributions of barnacles at more dissipative (figures to the left) and more reflective (figures to the right) beaches. The distributions were constructed from animals measured in five randomly selected photographs from the ten taken at each study site. Vertical dashed lines indicate the average size at each site. Barnacles <1.5 mm were considered new-recruits and are no more than 1 month old.

removing the autocorrelation from these settlement time series, we removed much of this fortnightly signal, however, the remaining portion of this signal could have contributed to unresolved variability in the relationship between waves and settlement. There are additional mechanisms of shoreward transport of cyprids besides the internal tides (e.g., onshore winds, fronts moving onshore, etc.) (reviewed in Shanks, 1995) and daily variability in the strength of these mechanisms could also have contributed to the unresolved portion of the variability between waves and settlement. Despite the 'noise' from these other potential sources of variability, we still found significant positive relationships between the wave steepness and the delivery of cyprids to two different beaches.

During periods of low wave height and hypothesized minimal exchange, weak swimmers, such as cyprids and ciliated larvae, may experience the surf zone as a barrier. There are numerous larval types, particularly fish and decapods, which at the terminal larval or post-larval stage are, however, capable swimmers. For larvae with strong swimming abilities, a stagnant surf zone may not be a barrier; they may simply swim the last tens to hundreds of meters to shore. If these organisms are going to complete their migration by swimming to

shore they must swim in the correct direction. Interestingly, a variety of larval fish and decapods has been found to orient and swim toward the sound of the surf (Kingsford et al., 2002; Leis, 2006), which may be an effective way of swimming in the correct direction across a surf zone.

The abundance of new-recruits was much greater at more dissipative than more reflective beaches. This could be due to differences in larval delivery associated with surf zone hydrodynamics, which we did not measure but infer from the morphology of the beach or to variations in post-settlement mortality. The most likely causes of post-settlement mortality are desiccation/heat stress, predation, and wave-borne rocks. Due to beach orientation, boulders at all but one of the beaches should have experienced significant solar exposure during afternoon low tides. The one exception is the Humbug site where Humbug Mountain, located just south of the site, shaded the boulders for much of the day. If desiccation/heat stress caused significant post-settlement mortality then recruitment should have been high at Humbug. However, there were few new-recruits at this site. Mortality from thermal stress and desiccation was likely not a primary determinant of abundance patterns. If recruitment patterns

Fig. 7. Size frequency distributions of limpets at more dissipative (figures to the left) and more reflective (figures to the right) beaches. Too few limpets were present at one dissipative site (Agate Beach) and two reflective sites (Humbug and Wilson Creek) for the construction of size frequency distributions. The distributions were constructed from animals measured in five randomly selected photographs from the ten taken at each study site. Vertical dashed lines indicate the average size at each site. Limpets <1.5 mm were considered new-recruits and are no more than 2 months old.

were set by post-settlement predation, then we would expect to see higher abundances of barnacle predators at more reflective beaches. However, potential barnacle predators were far more common in photographs from the more dissipative (28 nemertean worms and 15 predatory snails in 40 photos) than the more reflective beaches (1 nemertean worm and 1 predatory snail in 60 photos).

Wave-borne rocks can crush and dislodge barnacles and other invertebrates (Shanks and Wright, 1986), but this cause of mortality is also unlikely to explain the observed differences in abundance at the two types of beaches. Waves at more reflective beaches break very close to shore and these beaches were composed of coarser sand and pea sized gravel, which could contribute to increased wave-borne rock damage and mortality at these sites. In the close up photographs at the more reflective sites, we saw evidence for rock damage; in some photographs the peaks of barnacle shells were truncated as if they had been broken off and we occasionally observed limpets with shell damage. Cyprids and new limpet and barnacle recruits are very small and would be easily killed by the impact of even small wave-borne
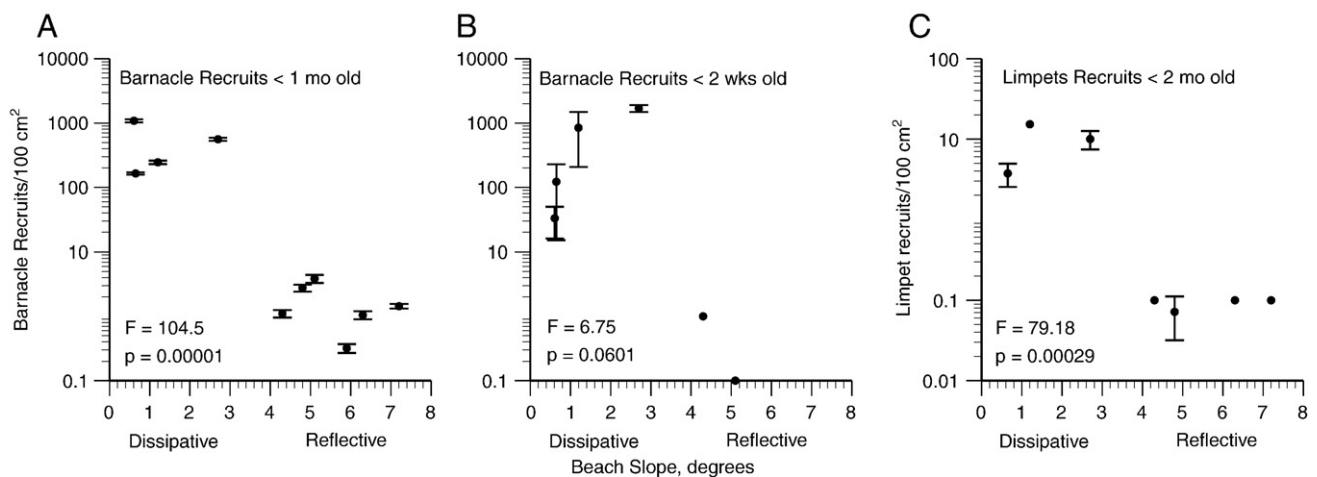
Fig. 8. (A) Mean (±95% confidence interval, $n=5$) new barnacle recruits (<1 month old) determined from the size frequency data (see Methods). (B) Mean (±SE) new barnacle recruits after two weeks on settlement plates. (C) Mean (±95% confidence interval, $n=5$) new limpet recruits (<2 month old) determined from the size frequency data (see Methods). Values in each figure are the results of a 1-way ANOVA comparing the number of new-recruits at more dissipative to more reflective beaches. The a priori hypothesis in each case was that new-recruits would be more abundant at the more dissipative beaches, hence, in all case, the ANOVA results are significant.

rocks, however, their small size should allow them to be protected from rock damage by even small depressions, cracks and relief on the rocks. Hence, if settlement was occurring at the more reflective beaches, but exposed recruits were killed by rock damage then we should have observed new-recruits in sheltered sites on the rocks or amongst adult barnacles and limpets. For example, Shanks and Wright (1986) observed extensive wave-borne rock damage to barnacle populations on boulders in the Dike Rock beach and, at this same site at the same time, Shanks (1986) observed very high settlement of cyprids to grooved settlement plates; the grooves protected the settlers from rock damage. In the photographs from the more reflective beach sites, there were always many locations in each photograph where cyprids and newly recruited limpets and barnacles could have found shelter from wave-borne rocks, but new-recruits, even in sheltered microhabitats were extremely uncommon. Thus, the difference in the abundance of new-recruits at the different types of beaches is most likely due to higher delivery and settlement of their larvae at the more dissipative beaches rather than differences in post-settlement mortality.

In contrast to larval settlement, algal density and percent cover were both significantly higher at more reflective than more dissipative beaches. There are two possible explanations for these differences and, with the available data, we cannot eliminate either. The first possibility, and a likely one, is that at the more dissipative beaches, algal recruits lose in the competition for space to the very abundant barnacles. The second possibility is more interesting; settlement of algal spores may be higher at more reflective than at more dissipative beaches. Due to hydrodynamics, the residence-time of water in a reflective beach surf zone may be generally longer than at a more dissipative beach. The pelagic phase of algal propagules is generally quite short. Perhaps at more dissipative beaches, algal spores are washed offshore by the exchange of surf zone-water with offshore water leading to lower settlement rates while longer residence-times of water at more reflective beaches allows algal propagules to remain near potential settlement sites leading to higher settlement rates and, ultimately, higher adult populations densities. The slow exchange of water within surf zones at reflective beaches may favor the retention and settlement of organisms with short propagule pelagic durations.

At the more reflective beaches we sampled, large barnacles and limpets comprised a much larger percentage of the community than at the more dissipative beaches. This was in part due to the very high abundance of new-recruits at the latter beaches, but it was also due to the absence of large individuals at these beaches. There are a couple of likely explanations. At the more dissipative beaches, barnacles settled so densely that they formed hummocks (Bertness et al., 1998). The hummock growth form in barnacles leads to smaller diameter individuals; individuals are so densely packed that they cannot grow by increasing their diameter and must grow upward. Individuals in hummocks are not attached to the rock well and during winter storms they are washed away. By the end of winter, rocks at the sampled more dissipative beaches were largely free of *Balanus glandula*. This regular seasonal die back of the barnacle population would tend to remove larger individuals. In addition, because at the more dissipative beaches so much of the substrate was occupied by hummocks of barnacles, limpets living in this community run the risk of being washed off the rocks as the barnacle substrate is washed away leading to the removal of larger limpets. The data suggest that while settlement at more reflective beaches is likely lower than at more dissipative beaches, longevity of barnacles and limpets at the reflective beaches is longer.

Rilov et al. (2008) found no correlation between the abundance of mussel larvae in the nearshore waters and settlement on the shore suggesting to them that the surf zone, the water between the nearshore and the settlement site, was acting as a barrier to the shoreward movement of the larvae. We found large differences in the recruitment of barnacles to rocks in dissipative and reflective beaches. Recruitment was significantly higher at dissipative beaches, where surf zone hydrodynamics should cause greater exchange of surf zone water with near shore water, than at reflective beaches where surf zone hydrodynamics apparently leads to less exchange. Our results and those of Rilov et al. (2008) suggest that the surf zone may act as a barrier to the shoreward migration of larvae developing in the coastal ocean. The very large differences we found between recruitment at dissipative and reflective beaches suggests that larvae transported shoreward by a variety of transport mechanisms (e.g., internal waves, internal bores, upwelling fronts relaxing to shore etc.) may not actually reach the shore if the surf zone acts as a barrier.

Most research in intertidal ecology is focused on rocky shores and most rocky shores appear to be reflective. The slope of intertidal rocky shores generally is similar or greater than that of typical reflective beaches, and the shallow subtidal topography adjacent to the typical rocky shore is generally much more reflective than the bottom adjacent to a reflective beach. The surf zone at rocky shores appears to be much narrower than that of more dissipative beaches and even narrower than that of more reflective beaches. For example, the time it took waves to cross the surf zone (an index of surf zone width) at the more dissipative and reflective beaches was around 65 and 25 s, respectively, while the time for waves to cross the surf zone at rocky shores around Cape Arago, Oregon ranged from 0 (no surf zone) to 6 s ($n = 10$). We hypothesize that the exchange of water in reflective surf zones on rocky shores is slower than that across both reflective and dissipative sand beach surf zones. Indeed, dye released into the surf zone of rocky shores was observed to rapidly mix vertically and spread, but was only slowly transported away from shore (Koehl et al., 1988). Thus, the surf zone along rocky shores may, due to slow exchange of water within the surf zone with offshore water, act as a barrier to the shoreward migration of larvae and larval delivery to rocky shores may be at least partly driven by the hydrodynamics of the surf zone.

Acknowledgments

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