



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

Alan L. Shanks^{a,*}, Steven G. Morgan^b, Jamie MacMahan^c, Ad J.H.M. Reniers^d

^a University of Oregon, Oregon Institute of Marine Biology, PO Box 5389, Charleston, OR 97420, USA

^b Bodega Marine Laboratory, University of California Davis, 2099 Westside Dr., Bodega Bay, CA 94923-0247, USA

^c Department of Oceanography, Graduate School of Engineering and Applied Sciences, Monterey, CA 93943, USA

^d Rosenstiel School of Marine and Atmospheric Science, University of Miami, 4600 Rickenbacker Causeway, Miami, FL 33149, USA

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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.

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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., $>10 \text{ cm}^{-2} \text{ days}^{-1}$ 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

* Corresponding author.

E-mail address: ashanks@uoregon.edu (A.L. Shanks).

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 × 0.5 cm wide, surface area per groove 3 cm²). Using a 10× 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× 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),

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

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

$$h_b = \frac{H_b}{\gamma}, \quad (4)$$

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