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The surf zone: a semi-permeable barrier to onshore recruitment of invertebrate larvae?

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ABSTRACT

The supply of larvae to the shore is important for population replenishment and intertidal community dynamics but its variability at most scales is not well understood. We tested the relationship between nearshore mussel larval abundance and intertidal settlement rates over several years at multiple spatiotemporal scales in Oregon and New Zealand. Abundance of competent larvae nearshore and intertidal recruitment rates were simultaneously quantified using collectors mounted at different depths on moorings 50–1100 m from shore, and at adjacent rocky intertidal sites. Total mussel larval abundance and oceanographic conditions were also measured in some locations. At all scales, abundance of nearshore mussel larvae was unrelated to intertidal recruitment rates. In the intertidal, patterns of mussel recruitment were persistent in space, with sites of consistently high or low recruitment. In contrast, nearshore competent larval abundance showed generally similar abundances among sites except for a high, and spatially-inconsistent, variability in Oregon during 1998 only. On moorings, recruitment tended to be greater on midwater collectors than shallower or deeper. Finally, on moorings larval abundance in traps and recruitment on collectors was unrelated. These results suggest that (1) among sites, the size of the nearshore larval pool is relatively uniform while onshore recruitment varies and is unrelated to larval abundance, (2) temporal variability in nearshore larval availability is not strongly expressed onshore, (3) vertical stratification of competent larvae nearshore is strong and may influence transport and recruitment, and (4) within-coast variability in onshore recruitment is strongly driven by processes occurring locally within the surf zone that need to be studied to understand coastal recruitment dynamics.

1. Introduction

Most coastal benthic organisms have a complex life cycle that includes a planktonic larval stage and a benthic adult stage (Scheltema, 1986). As a consequence, both pre-settlement (i.e., larval transport, survival and physiological condition in the water column) and post-settlement (i.e. predation, competition, facilitation, thermal and desiccation stress) processes can be important in shaping coastal ecological communities (Connell, 1985). After decades of focusing primarily on the influence of post-settlement factors, in the 1980s ecologists turned their attention towards the influence of propagule inputs on populations and communities (Caley et al., 1996; Gaines and Roughgarden, 1985; Grosberg and Levitan, 1992; and see review, Levin, 2006; Lewin, 1986; Underwood and Denley, 1984; Underwood and Fairweather, 1989). Since then, investigating the role of recruitment relative to other factors in structuring communities (supply-side ecology *sensu* Lewin 1986) has been a central focus of ecological research across multiple spatiotemporal scales (e.g., Connolly and Roughgarden, 1998; Gaines and Bertness, 1992; McQuaid and Lawrie, 2005; Menge et al., 2004; Menge et al., 2003; Navarrete et al., 2005; Petraitis, 1991; Raimondi, 1990; Rilov and Schiel, 2006b; Underwood, 2004; Underwood and Anderson, 1994).

Successful recruits in benthic coastal habitats have to overcome many hurdles (Pineda, 2000). The rate of recruitment to the shore depends on a complex suite of oceanographic and biological factors, including larval production rates, the degree of offshore transport or retention, survival rates in the plankton, onshore transport mechanisms, larval behavior and, once the larvae arrive onshore, substrate availability, settlement cues, environmental stress, predation, competition and micro-hydrodynamics. Despite the dramatic increase in research investigating this issue, and substantial new insights into the patterns and factors influencing recruitment onshore (Connolly and Roughgarden, 1998; Pineda, 2000; e.g., Pineda, 1991; Pineda and Caswell, 1997; Porri et al., 2006; Shanks, 1995; Shanks and Brink,

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2005; Shanks et al., 2003; Tapia and Piñeda, 2007) our understanding of the relative importance of the different factors regulating the supply and delivery of larvae is limited.

Recruitment rates of intertidal organisms can differ in space by orders of magnitude at multiple scales both within and between coasts (e.g., Connolly and Roughgarden, 1998; Harris et al., 1998; Ladah et al., 2005; Lawrie and McQuaid, 2001; Menge et al., 2004; Moreno et al., 1998; Navarrete and Wieters, 2000; Navarrete et al., 2005; Pineda and Lopez, 2002; Todd, 2003). Determination of the factors underlying this variability has been a major challenge. In recent years, ecologists have begun to focus on the role of oceanographic conditions in determining macroscale (>100 km) or mesoscale (10–100 km) variation in recruitment. In particular, effects of the intensity and persistence of seasonal upwelling regimes on nutrient and larval availability in coastal environments have been postulated to be of major importance (Menge et al., 2003). For example, in the persistent upwelling region of central and northern California, recruitment rates can be orders of magnitude lower compared to rates in the intermittent upwelling region of Oregon (Menge et al., 2004). A possible explanation for this large scale difference is that in Oregon north of Cape Blanco, upwelling events are frequently interrupted by "relaxation" events when northerly winds weaken or by reversal events, when winds switch from north to south. This mechanism has been termed the "current reversal hypothesis" (Dudas et al. unpublished manuscript). These interruptions of upwelling-favorable winds are hypothesized to allow larvae that have accumulated near the surface offshore at upwelling fronts to return to shore and settle (Connolly et al., 2001; McCulloch and Shanks, 2003, Dudas et al. unpublished manuscript). In central and northern California, in contrast, upwelling is more persistent, relaxation events are relatively less frequent, and larvae are likely transported farther offshore, the net result of which is postulated to be low recruitment (e.g., Gaines and Roughgarden, 1985). A comparable example comes from a recent study on the Chilean coast (Navarrete et al., 2005).

A similar theory, the "onshore flow hypothesis" (Grantham, 1997), expands on these ideas. At upwelling fronts off the central California coast, the later (older) developmental stage larvae of some taxa were found deeper in the water column. Under this hypothesis, such larvae would be entrained in the deep onshore flow associated with upwelling and carried shoreward. In this scenario, off Oregon, where upwelling events are relatively short and upwelling fronts rarely move far offshore, greater numbers of larvae would be retained nearshore, than off central California where upwelling events are longer and fronts move correspondingly farther distances offshore. Grantham (1997) postulated that for some taxa it was the onshore movement of deeper waters following the resumption of upwelling that delivered larvae onshore.

Other mechanisms of across-shelf larval transport that may explain variation in recruitment include other types of wind-driven currents (e.g. switching wind directions across an embayment, Bertness et al., 1996), and internal waves and tidal bores (Ladah et al., 2005; Pineda and Lopez, 2002; Shanks and Wright, 1987). Variation in the magnitude, rate or direction of these processes along the shore may explain variation in recruitment on smaller spatial scales. Short and long-term monitoring of recruitment rates shows that order of magnitude differences can occur on small spatial scales of 10s–100s m (Ladah et al., 2005; McCulloch and Shanks, 2003; Porri et al., 2006; Rilov and Schiel, 2006b, Menge, unpublished data). A variety of other factors could underlie such variability including effects of bottom topography or coastal geomorphology, the distribution and behavior of larvae in the water column, and post-settlement variation in mortality tied to environmental stresses during low tides (Caceres-Martinez and Figueras, 1998; Dobretsov and Miron, 2001; Grosberg, 1982; Miron et al., 1995). For example, stratification of larvae in the water column resulting from physical or biological processes may affect onshore delivery and subsequent recruitment (Pineda, 2000) if currents are also stratified (Marta-Almeida et al., 2006; Shanks and Brink, 2005).

Regardless of the across-shelf transport mechanism, hypothetically, recruitment rates should reflect the size of the nearshore larval pool. A recent short-term study on larval distribution of two barnacle species at increasing distances from one intertidal site in southern California revealed a temporal coherence between cyprid abundance nearshore and onshore settlement in one of the species (Tapia and Piñeda, 2007). In contrast, a study from South Africa suggests that on the scale of 100–1000 m, mussel larval availability nearshore is unrelated to onshore recruitment (Porri et al., 2006). Both of these studies used vertical plankton net tows to measure larval abundance. Several limitations arise however when using vertical hauls: (1) they give no information on the vertical distribution of the larvae, which as noted above can affect transport, (2) they are snapshots of larval abundance relevant only to the hours or minutes when they were taken, and (3) in mussels, they capture all sizes including both competent (to settle) and precompetent larvae. Nonetheless, these last two studies represent the first attempts to test the coupling between the larval pool (i.e., the abundance of larvae in the inner shelf region, see Pineda, 2000) and onshore recruitment of intertidal organisms.

Here we integrate data from five studies that were designed to test the relationship between the relative size of the nearshore larval pool of intertidal mussels and onshore recruitment rates. The studies spanned multiple spatial and temporal scales in two biogeographic regions, Oregon and New Zealand. In all cases, we used mussel settlement collectors on moorings instead of plankton nets to assess the relative abundance of competent larvae and we placed them at different depths to evaluate their depth distribution. Mussels are dominant organisms on many rocky shores worldwide and are important ecologically. They serve as ecosystem engineers (i.e., providing habitat for other species), are prey for a multitude of organisms on the shore and are a central component of community structure (e.g., Lawrie and McQuaid, 2001; and see review in, Menge and Branch, 2001; Navarrete and Menge, 1996; Petraitis, 1998). They are also of commercial value in many locations worldwide. For these reasons, they have been a major focus of efforts to understand the relative influence of pre- and post-recruitment factors in determining their abundance (Leonard et al., 1998; McQuaid and Lindsay, 2005; Menge et al., 1994; Menge et al., 2004; Menge et al., 1997a; Menge et al., 2003; Navarrete et al., 2005).

1.1. Hypotheses

To examine the relationship between the relative size of the inner shelf (<30 m water depth, about 0.05–2 km offshore) larval pool and recruitment onshore in the context of local oceanography (where possible), we tested three hypotheses:

H_1. At local (site) scales, the larval pool and onshore recruitment are coupled. Onshore mussel recruitment is proportional to competent larval availability (the larval pool) just beyond the surf zone (50–1000 m offshore). Prediction 1 thus states that onshore recruitment rates and nearshore larval abundance will be positively correlated.

H_2. At coastal (among site) scales, larval pool abundance and onshore recruitment are synchronized. Inner shelf oceanographic events involved in onshore larval transport, such as upwelling relaxations and/or current reversals, are synchronous alongshore at scales of 10–100 km (e.g., Kirincich et al., 2005). Prediction 2 thus states that a) relative larval abundance in the water column will be temporally positively correlated among sites within coasts in the inner shelf at scales of 10–100s of km, and that b) onshore recruitment (or settlement) will be temporally positively correlated among sites at this spatial scale.

H_3. Total larval abundance determines the magnitude of competent larval settlement in nearshore waters. The number of competent mussel larvae at different depths should be proportional to total (competent plus precompetent) mussel larvae abundance at similar depths unless ontogenetic shifts in vertical position exist. Prediction 3 thus states that within the larval pool in the inner shelf area, total