Spatio-temporal patterns of larval supply and settlement of intertidal invertebrates reflect a combination of passive transport and larval behavior

V. Hoffmann 1, M.C. Pfaff *,2, G.M. Branch

Marine Biology Research Centre, MA-RE Institute, Zoology Department, University of Cape Town, Rondebosch 7701, South Africa

ABSTRACT

Variability in larval settlement affects marine community dynamics at various spatial and temporal scales. To characterize settlement patterns and potential causes at different spatial scales, we monitored daily settlement rates of intertidal mussels and barnacles at two shore heights (mid, high) at a headland upwelling centre and in a downstream bay. At the bay (where settlement was sufficiently high to warrant more specific analyses), we additionally quantified larval supplies of both taxa at two distances from shore: 0 m (onshore) and 200 m (offshore). The following patterns emerged: (1) settlement in the bay was substantially and significantly greater than at the headland. (2) In the bay, settlement was higher on the midshore than the highshore, mirroring adult mussel zonation but contrasting with adult barnacle zonation. (3) Settlement rates of both taxa were temporally coupled with larval supply, although the strength of this relationship varied spatially among replicate blocks and, for barnacles, also varied between shore heights. (4) Barnacles showed a preference for settling in the midshore vs. the highshore, while this effect was not significant for mussels. (5) The onshore larval pool of both taxa was dominated by late-stage larvae, suggesting that stage-specific behavior facilitated transport of competent larvae to shore. Thus, spatio-temporal settlement patterns were influenced by a combination of passive transport by mesoscale and local currents, and active larval behavior to get to shore and select a preferred settlement zone.

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1. Introduction

Fluctuations in the supply of dispersing larvae to benthic marine systems have long been recognized as a major driver of community structure and dynamics (Thorson, 1950). Larvae from coastal ecosystems face the particular challenge of having to return to the shore after completing their pelagic development, which typically takes weeks to months. In dynamic systems such as coastal upwelling regions, where cross-shelf currents exceed the swimming speeds of larvae by orders of magnitude (Chia et al., 1984), larvae have long been perceived as passive drifters whose fate depends entirely on suitable onshore currents. However, recent reports that larvae are able to maintain their nearshore position despite strong offshore advection of surface waters during upwelling (Morgan et al., 2009; Poulin et al., 2002; Shanks and Shearman, 2009) have emphasized the adaptive role of larval behavior in directing shoreward transport. Upon arrival at the shore, larvae need to settle, and again, selection exists for behavioral adaptations to choose a suitable spot (Crisp, 1985). While our understanding of supply-side ecology has made remarkable progress in the last decades, the relative roles of active larval behavior versus passive larval drift in determining population patterns across a range of spatial scales are still not clear.

Some of the processes that have been proposed as drivers of mesoscale variability of larval supply (over 10s of km) are linked to different legs of the upwelling cycle functioning as means of shoreward transport for larvae. During active upwelling, surface waters are pushed offshore by strong upwelling-favorable winds and are replaced by deep ocean water. Larvae in surface waters may actively position themselves in deeper waters by migrating vertically downwards to be transported to the shore via shoreward movement of the upwelling stream of water. This type of behavior has, for example, been documented in shoreward transport of invertebrate and fish larvae (Field and Shillington, 2004; Garland et al., 2002; Shanks et al., 2000). On the other hand, the ‘downwelling hypothesis’ proposes that larvae concentrated in surface waters are returned shoreward after the relaxation or reversal of upwelling-favorable winds (e.g. Menge et al., 2003). Other mesoscale processes affecting the onshore transport of larvae, such as shoreward-propagating internal tidal waves and bores associated with stratified waters, also act differently in different layers of the water column, thus emphasizing further that active vertical positioning of larvae provides an important strategy.
for reaching suitable settlement sites. Since late-stage larvae are under particular pressure to reach their coastal adult habitat to complete their life cycle, morphological and behavioral adaptations facilitating onshore transport are likely to be stage-specific, as observed for two barnacle species in Southern California (Tapia and Pineda, 2007). Due to their small size, tracking of individual larvae throughout their pelagic development has not been achieved, and indirect evidence from spatio-temporal distributions of larvae is used to infer larval transport. For instance, if transport processes are largely passive, the onshore larval pool should comprise a representative mix of early- and late-stage larvae, whereas if ready-to-settle (competent) larvae regulate their shoreward transport through stage-specific behavior, the onshore larval pool will consist of higher proportions of late-stage larvae than the offshore larval pool (Morgan et al., 2009; Pineda, 2000; Tapia et al., 2010). On arrival at the shore, larval behavior may also influence the vertical zonation patterns typical of intertidal adult populations. Larvae may be mixed evenly throughout the water column at the shore, but selectively choose to settle in a specific zone. Alternatively, larvae could choose a particular depth stratum in the water column and so influence their arrival in a certain zone, as was previously demonstrated for barnacles and mussels (Grosberg, 1982; Porri et al., 2007). However, differences in the intensity of settlement among zones may also simply result from longer submergence times of lower parts of the intertidal zone compared to higher parts, providing greater opportunities for settlement lower on the shore.

Similar to shorelines throughout the world, the rocky shores of the Southern Benguela upwelling region on the west coast of South Africa are characterized by distinct zonation patterns (Stephenson and Stephenson, 1949). The alien invasive mussel *Mytilus galloprovincialis* Lamarck is the dominant mussel on wave-exposed rocky shores and occurs mainly in the low- to midshore. The two most common barnacles are the alien invasive *Balanus glandula* Darwin and the endemic *Notomegabalanus algicola* Plisbysk, which respectively predominate in the highshore and the lowshore. A recent study of their recruitment patterns (Pfaff et al., 2011) showed a strong topographic effect, with consistently much lower mussel and barnacle recruitment (1) at sheltered versus wave-exposed sites, and (2) at prominent headlands, where upwelling is intense and the water column uniformly cold, compared with adjacent downstream bays, where upwelling-generated eddies favor coastal retention of larvae and the water-column is more stratified (Penven et al., 2000). The monthly sampling period of the study by Pfaff et al. (2011) was, however, inadequate to exclude the possibility of post-settlement mortality driving this pattern, as a higher-frequency sampling regime is required to confirm that the striking topographic pattern is indeed driven by pre-settlement factors.

Specific mechanisms for the onshore transport of larvae have been the focus of a parallel study (Pfaff, 2010), but in this paper we explore the coupling of temporal patterns in daily settlement of mussels and barnacles with larval availability in onshore and offshore waters, and the role of larval behavior in determining spatial settlement patterns at two sites, one at a major upwelling centre and the other in an adjacent down-stream bay. Specifically, we addressed the following hypotheses: (1) Settlement rates of mussel and barnacle larvae will be significantly less at the active upwelling site than in the downstream bay. (2) Mussel and barnacle settlement rates on the shore will vary vertically and horizontally in a manner that reflect abundance of post-settlement stages. (3) Settlement intensity will be temporally coupled with larval availability. (4) The age structure of the onshore larval pool will be skewed towards late-stage competent larvae.

## 2. Materials and methods

### 2.1. Study sites

The study was conducted on the west coast of South Africa at Cape Columbine (32°49′39″S; 17°51′23″E) and Elands Bay (32°19′01″S; 18°19′05″E). These sites fall within the Southern Benguela upwelling region, where pulses of upwelling-inducing winds prevail during the austral spring to summer (Sep-Mar), and where upwelling intensity varies spatially, with strong upwelling plumes at major headlands, such as Cape Columbine, and weaker and less frequent upwelling in downstream bays, such as Elands Bay (Pfaff et al., 2011; Shannon and Nelson, 1996). Sampling was performed from 2 December 2006 to 5 February 2007, thus spanning the period when both mussels and barnacles are settling, and that of mussels in particular reaches its peak (Pfaff, 2010). Sampling at both sites was restricted to areas with high wave exposure, as prior work showed that recruitment is most intense there (Pfaff et al., 2011).

### 2.2. Adult cover and zonation

To establish adult zonation, the cover and vertical distribution of intertidal adult mussels and barnacles at both study sites was quantified along nine shore-perpendicular transects (of 15–25 m length, 20 m apart), that spanned the vertical distribution of these taxa from low spring tide level up to the top shore. Percentage cover was estimated in 100×50 cm quadrats placed at 1-m intervals along these transects.

### 2.3. Larval settlement rates

Daily intertidal mussel and barnacle settlement rates were quantified using artificial settlement substrata. Plastic-mesh pot scourers ("tuffs") provided a standard 3-dimensional structure for mussel settlers, and 10×10 cm polycarbonate plates coated with indented rubberized “Safety-Walk” (3 M Comp.) were used to quantify barnacle settlement. At each study site, 24 tuffy and 24 plate collectors were attached to the shore substratum, 12 in the centre of the midshore mussel bed and 12 in the highshore barnacle zone. To assess horizontal patchiness, the collectors were arranged in three spatial blocks (A, B, C). Blocks measured ca. 5 m in horizontal extent and were situated 15–50 m apart, each block comprising 4 midshore and 4 highshore collectors. Each collector was situated at least 10 cm from the nearest adult mussel or barnacle to eliminate the effects of gregarious settlement. Collectors were changed daily during the day-time low tide and thus provided an integrated measurement of settlement rate per day.

In the laboratory, the contents of each tuffy were extracted by washing the pads individually in a bucket of water, which was then filtered through a 265-μm sieve and examined under a dissecting microscope to identify and count all newly settled mussels. Settlers of *Mytilus galloprovincialis* and the indigenous *Aulacomya ater* Molina were both likely to be present but due to difficulties in distinguishing mytilids at the early settler stage (Bownes et al., 2008), all mussel species were pooled. Examination of later-stage recruits showed that *M. galloprovincialis* was dominant (>90%). Plates were examined under a dissecting microscope to count newly settled barnacle cyprids and metamorphs. The barnacle species that inhabit the local rocky shores include an alien species, *Balanus glandula*, and an indigenous species, *Notomegabalanus algicola*. Again their settlers were pooled to present counts of daily barnacle settlement, since species identification at the settlement stage is still unresolved; but *B. glandula* was the dominant species recruiting on the shore (~90%).

### 2.4. Onshore larval supply

For the study of onshore larval supply rates we focused on Elands Bay alone because settlement rates at Columbine were too low to distinguish any signal from noise. Daily larval supply of mussels and barnacles to the intertidal zone was quantified from 7 January to 4 February 2007, using larval traps designed after the rocky intertidal plankton trap Ript2 (Castilla et al., 2001; Yan et al., 2004), which were fitted with 80-μm mesh plankton net bags and changed daily at low tide.
Each bag contained chalk soaked in formaldehyde to prevent potential predation of entrapped larvae. Twelve larval traps were installed, six in the midshore and six in the highshore zone, with replicate pairs in close proximity to the corresponding settlement collectors of blocks A–C. After collection, contents of each plankton mesh bag were split using a 265-μm sieve and examined under a dissecting microscope to count barnacle and mussel larvae. Larvae were classified as either pre-competent (mussel pre-settlers: 80 μm–264 μm and all stages of barnacle nauplii) or competent (mussel settlers: 265 μm–470 μm and all barnacle cyprids). As a measure of the volume of water filtered by each trap, the loss-of-mass by erosion of a pre-weighed piece of chalk attached inside each trap was recorded for each period of deployment (Yan et al., 2004). Depending on whether absolute numbers or relative larval densities are addressed, larval supply and settlement rates are henceforth presented either as total numbers collector$^{-1}$ day$^{-1}$ (‘absolute’) or as numbers collector$^{-1}$ day$^{-1}$ g erosion$^{-1}$ (‘adjusted’ by the volume of filtered water).

2.5. Offshore larval supply

Pelagic mussel and barnacle larvae at Elands Bay were sampled on nine daytime occasions, using oblique 5-min zooplankton tows at a distance of 200 m from shore. Sampling was done with a 200-μm ring net (WP2) with 0.5 m opening, equipped with a mechanical flow meter (General Oceanics, #2030R) to measure the volume of sampled seawater. Pilot studies showed that mesh sizes smaller than 200 μm resulted in unacceptable net clogging. Since the 200-μm mesh size was too large to catch pre-competent mussel larvae, data are presented only for barnacle larvae, all stages of which were captured by this mesh size. Because this sampling method represents instantaneous sampling of the larval pool as opposed to the time-integrated measures of the onshore traps and settlement collectors (for detailed comparison see Dudas et al., 2009), the data were employed only to assess the proportions of pre-competent vs. competent barnacle larvae.

2.6. Data analysis

All analyses were performed with the SPSS Statistics Version 19.0.0.

2.7. Spatial patterns in adult cover and settlement

To test for differences in adult abundance between the two sites, we used unpaired t-tests on transect data of mussel and barnacle cover. To confirm whether the established differences (see Results) were reflected in the mid- and highshores where we measured settlement, we performed ANOVAs with factors Site and Height on the shore as predictors on (square-root-transformed) data of adult mussel (Mytilus galloprovincialis) and barnacle (Balanus glandula) cover, using data for the centers of the mid- and highshore zones (adjacent to where settlement collectors were placed).

To test for differences in (absolute) settlement rates between the mid versus high shores at the two sites, we performed a factorial GLM (negative-binomial, log-link) with factors Site, Height on the shore and Date (nuisance variable) as predictors. As with all equivalent tests below, the pairwise Wald Chi-square test with Sequential Sidak correction was employed as a post-hoc test.

2.8. Coupling between larval supply and settlement

To test for spatial differences (both horizontally and vertically) in the relationship between larval supply on settlement, we performed factorial GLMs (gamma, log-link) for mussel and (separately) barnacle settlement rates with the factors shore Height and Block and the covariate Larval supply as predictors. To assess whether spatial differences in larval supply and settlement occurred due to a preference of larvae for a certain zone rather than differences in submersion times between vertical zones, this analysis was done on adjusted supply and settlement rates, where submergence time was factored out. The analysis of barnacle data required square-root transformation to meet distributional assumptions of the models. Model simplification involved AIC-based model selection, resulting in slightly different model designs for the two taxa (see Table 3). Days of zero supply and settlement were excluded from these analyses, since they would mask potential spatial differences.

2.9. Stage-specific larval onshore transport

As evidence for stage-specific larval onshore transport, we assessed whether the composition of the onshore larval pool was skewed towards late (settling) larval stages relative to the composition of the larval pool 200 m offshore. A full factorial GLM (negative-binomial with log link function) with factors Stage (pre-competent vs. competent) and shore Height (mid vs. high) as predictors was deployed for supply rates from larval traps (excluding days of zero supply).

To test for significant differences in the proportions of pre-competent to competent barnacle larvae between the offshore and the onshore larval pool, a Fisher’s exact test was applied. This analysis was limited to barnacles, for reasons explained above.

3. Results

3.1. Spatial patterns in adult cover and settlement

The adult mussel populations at both sites were dominated by Mytilus galloprovincialis (98%). Adult barnacles comprised Notomeltica balanus algicola in the lowshore, and exclusively Balanus glandula in the mid- to highshore where recruitment and intertidal larval abundance were measured (Fig. 1). Average cover of adult mussels was higher at Elands Bay than at Cape Columbine ($t = 2.064; df = 34; p = 0.047$), but no such difference existed for barnacles ($t = 1.208; df = 20; p = 0.241$). When only considering the mid and highshore zones (where settlement collectors and larval traps were installed), adult cover did not differ between sites, but zonation was confirmed for both taxa at both sites by significant differences between the midshore and highshore and an absence of a Site-Height interaction (Table 1). Whereas mussel (M. galloprovincialis) adults were more abundant in the midshore, barnacle (B. glandula) adults occurred predominantly in the highshore.

Absolute settlement rates at Elands Bay were substantially and significantly greater than at Cape Columbine, and—at Elands Bay—significantly greater in the midshore than the highshore, as reflected in a significant Height-Site interaction (Table 2, Fig. 2). These main effects were masked by significant interaction terms with date, which arose because height and site effects were not equally pronounced among different days.

3.2. Coupling between larval supply and settlement

For mussels, larval supply was a significant determinant of (adjusted) settlement (Table 3A, Fig. 3), but this relationship was not equal among horizontal blocks (Block-Larval Supply interaction). The slopes of the supply–settlement relationship were consistently steeper for the midshore vs. the highshore, indicating that at a given supply rate settlement was greater in the midshore than the highshore, but the strength of this effect varied among horizontal blocks (Block-Height interaction, Table 3A, Fig. 3A–C).

For barnacles, the effect of larval supply varied among (horizontal) blocks and (vertical) zones (Block–Larval Supply and Height–Larval Supply interactions; Table 3B, Fig. 3A–C). While consistent and significant differences existed in the slope of the supply–settlement
relationship, the magnitude of this difference also varied among blocks (Block–Height–Larval Supply interaction, Table 3B).

3.3. Stage-specific larval onshore transport

The onshore larval pool of both taxa consisted of significantly higher proportions of competent than pre-competent stages (Table 4, Fig. 4). Late-stage barnacle larvae were more concentrated on the high- than the midshore, whereas mussel larvae were evenly distributed between the shore levels. In the case of barnacles, the proportion of competent larvae (cyprids) was significantly less 200 m offshore than on the shore (Fig. 4; Fisher’s exact test: \( p = 0.023 \)). An equivalent analysis could not be done for mussels, since the mesh size for offshore sampling was ineffective in catching pre-competent stages.

4. Discussion

Four aspects of variability in settlement rates of barnacles and mussels were identified in this study. First, consistent spatial differences in settlement rates existed between the headland upwelling center and the downstream bay for both taxa, corroborating the link between coastal topography, upwelling intensity and recruitment rates previously shown by Pfaff et al. (2011). Second, vertical zonation of settlement, with greater settlement rates of both taxa in the mid vs. the high intertidal zone, was demonstrable at the bay site where settlement was sufficient to explore this question. While this pattern conformed to the adult zonation of mussels, barnacle adults showed the opposite trend, with greater cover in the high- than the midshore. Third, on a temporal day-to-day basis, differences in the intensity of settlement rates in the bay were coupled with fluctuations in the onshore larval pool, but the strength of this supply–settlement relationship varied among blocks (at a scale of 10s of meters) for both taxa and, for barnacles, also between shore heights. Lastly, the concentration of late-stage barnacle larvae in the onshore waters at the intertidal adult habitat (relative to their proportions 200 m offshore) suggests that barnacles develop stage-specific behavior to facilitate the delivery of competent larvae to the shore.

4.1. Spatial patterns in settlement, recruitment and adult cover

Spatial heterogeneity in larval settlement across a number of varying scales has been widely recognized (e.g. Grosberg, 1982; Porri et al., 1987).

### Table 1

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<tr>
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Fig. 1. Cover (mean ± SE) of adult mussels (black bars) and barnacles (white and grey bars) at horizontal 1-m intervals along shore-perpendicular transects running from low water spring tide (bottom of diagrams) upwards at (A) Cape Columbine, and (B) Elands Bay. The vertical heights of the midshore and highshore, where settlement and larval abundance were measured (as indicated by the grey fields), were equivalent at the two sites, although horizontal distances differed because of shore topography.
al., 2006; Raimondi, 1990) and may be a critical factor in determining adult distribution and abundance, with consequent effects on community structure and dynamics (Gaines and Roughgarden, 1985). At a mesoscale of ~100 km settlement rates of both mussels and barnacles were consistently lower at the prominent headland upwelling centre (Cape Columbine) than in the downstream bay (Elands Bay), supporting our a priori hypothesis to this effect. The abundance of adult mussels (but not barnacles) followed the same pattern. Spatial replication of topographic conditions and their effects on settlement and adult patterns would be necessary to test the generality of this hypothesis. However, in a broader-scale study comparing three headland-bay pairs in the Southern Benguela, Pfaff et al. (2011) showed that this headland-bay pattern is consistent for later-stage mussel and barnacle recruits at a number of sites: strong relationships exist between the temporal and spatial variability in upwelling intensity and recruitment of both taxa, with recruitment being greatest in the shoreward-moving water column, potentially leading to the settlement of larvae in particular zones (Grosberg, 1982). While this process is likely to occur only in relatively calm conditions where wave-induced turbulence will not mix larvae, our findings from shores that are wave-exposed also show vertical zonation in settlement of both taxa, with higher settlement rates on the midshore than the highshore. Two alternative explanations exist for this pattern. Firstly, the more prolonged submergence time experienced in the midshore would increase the probability of settlement there. This process appears to explain the zonation of mussel settlers. However, when its influence was removed by adjusting settlement rates to allow for differential submergence times between vertical zones, the zonation in barnacle settlement (but not that of mussels) remained a significant pattern. We suggest that a second explanation, that larvae actively select settlement zones, holds for barnacles. Preferential habitat selection has been documented previously for barnacles (Grosberg, 1981; Jenkins, 2005; Raimondi, 1988) and is a likely cause of the vertical settlement patterns we observed. The highshore is less hospitable for settlers because of greater desiccation and temperature stress there (Blanchette and Gaines, 2007). Active avoidance of the highshore by barnacle cyprid settlers has been recorded and attributed to the benefits of settling in zones where survival is greatest (Minchinton and Scheibling, 1991). Substratum selection by mussel larvae has also been shown in several studies, which have reported the influence of biofilms on settlement and metamorphosis of Mytilus galloprovincialis hydrodynamics (Pineda, 2000). For example, larvae reaching the shore may be stratified in the shoreward-moving water column, potentially leading to the settlement of larvae in particular zones. During active upwelling, coastal waters experience strong offshore advection at headland upwelling centers, while cyclonic eddies in their lee entrain waters shoreward (Penven et al., 2000), thereby concentrating suspended particles and larvae in down-stream bays (Pfaff, 2010). Since our study of earlier-stage settlers corroborates the second explanation, that larvae actively select settlement zones, post-settlement mortality appears to play a limited role in altering recruitment patterns at our sites.

Larval settlement patterns on a smaller scale of meters can be influenced by other pre-settlement factors, such as larval supply, larval behavior and local micro-scale topographic influences on settlement. Unique letters above bars indicate significant differences between zones (p < 0.05), and horizontal lines with asterisks (**p < 0.001) indicate significant differences between the two sites.

Table 3
Results from GLMs for (A) mussels and (B) barnacles, testing for the effects of Block, Height and Larval Supply on relative settlement rates (after factoring out submergence times of collectors and traps) at Elands Bay. The models differed between taxa due to model simplification according to AIC-based model selection.

<table>
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and *Perna perna* (Bao et al., 2007; Satuito et al., 1995; von der Meden et al., 2010). Our findings did not, however, support this notion. Since mussels (unlike barnacles) are able to detach from an unsuitable settlement site and re-attach again at a different place (Bayne, 1964), larval selection of a settlement site will be less critical for their survival than it is for barnacles.

On a small horizontal scale (between blocks that were 10s of meters apart), we found significant differences in settlement of both taxa. This may reflect local hydrodynamic effects that concentrate or diffuse larvae in crevices or other small topographic features of the rocky shore (Jeffery and Underwood, 2000; Wethey, 1986). Several authors have noted that patterns at large spatial scales often break down at small spatial scales, and that variability at small scales generally exceeds that at larger scales (Porri et al., 2006; Reaugh-Flower et al., 2011; Underwood and Chapman, 1996).

The zonation pattern of adult mussels, which were more abundant in the midshore than the highshore, corresponded with the same pattern in larval settlement at Elands Bay. However, a study spanning multiple sites in the Southern Benguela, including our sites, failed to find any correlation between mussel recruitment and various other measures of adult abundance at multiple sites (Xavier et al., 2007), suggesting that there is no causal link between the corresponding patterns we observed. Adult barnacles were more abundant in the highshore, despite predominant larval settlement in the midshore. Thus, vertical differences in larval barnacle settlement clearly do not determine adult zonation.

### 4.2. Spatial differences in the coupling between larval supply and settlement

While our data show a positive relationship between larval supply and settlement for both mussels and barnacles at Elands Bay, the strength of this coupling varied among horizontal blocks for both taxa, and also among shore heights for barnacles. Although the nearshore larval pool and onshore settlement appear to be more often decoupled than correlated (Pineda et al., 2010; Porri et al., 2006; Rilov et al., 2008), our study indicates that fluctuations in larval supply determine variability in settlement (see also Dudas et al., 2009). Therefore, our findings support the notion that surf-zone processes underlie the potential decoupling between the nearshore and the onshore, as suggested by above-mentioned and other recent studies (Shanks et al., 2010).

Differences among vertical zones in the strength of the relationship between larval supply and settlement existed for barnacles, but not for mussels. At any given rate of larval supply, barnacle settlement was greater in the midshore than the highshore, which provides further evidence that *Balanus glandula* cyprids actively select the midshore as a preferred settlement zone, as has been previously demonstrated for other species of barnacles (Jenkins, 2005). As indicated before, barnacles are capable of selecting their settlement site in response to a number of environmental cues such as presence of conspecifics, predators, competitors or other intertidal indicator species (Grosberg, 1981; Raimondi, 1988), as well as algal films.

### 4.3. Stage-specific larval onshore transport

Settlement rates differed on a day-to-day basis, suggesting that the availability of larvae onshore is governed by processes such as advective delivery events that act as shoreward transport mechanisms (Pineda, 2000; Shanks and Brink, 2005), which may differ substantially over time, as well as in space. The oceanographic processes that may facilitate larval onshore transport have been the subject of a parallel study (Pfaff, 2010), and here we focused on the question of whether larvae are passive drifters reliant on favorable currents, or employ behavioral mechanisms to facilitate their onshore delivery. Our data showed that the onshore larval pool of both mussels and barnacles predominantly comprised competent settling-stage larvae. Two possible explanations for this exist. Competent larvae in the offshore larval pool are known to be able to delay metamorphosis when they enter a 'competency window' (Pineda, 2000). This allows larvae to 'wait' for the right conditions for shoreward transport. If metamorphosis is delayed, this larval pool will eventually largely comprise competent larvae, which can be advected shoreward when conditions are favorable. Alternatively, larvae residing in offshore waters may use behavioral mechanisms to exploit shoreward transport
mechanisms once they become competent. For example, as larvae near the end of their larval stage, vertical migration in the water column could allow them to use currents at particular depths as transport mechanisms to return to the shore. Empirical evidence has shown that many larvae residing in the pelagic zone are capable of migrating vertically in the water column to control their horizontal distribution and, hence, their dispersal (Field and Shillington, 2004; Minchinton, T.E., Scheibling, R.E., 1991. The influence of wind-driven cross-shelf currents and diel vertical migrations. Limnol. Oceanogr. 36, 394–409).

The pronounced mesoscale pattern of greater larval settlement at the downstream bay than the headland upwelling centre appeared to be driven by topographically-induced variability in upwelling and coastal currents. However, we found multiple lines of indirect evidence indicating that smaller-scale variability in settlement rates are largely due to larval behavior facilitating the onshore transport of larvae (as shown for barnacles) and/or the active selection of settlement sites (as shown for both mussels and barnacles).

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References


Fig. 4. Average daily supply rates of pre-competent and competent larvae of (A) mussels and (B) barnacles at two different shore heights (left panels) and—for barnacles—at 200 m offshore (right panel) at Elands Bay. Unique letters above bars indicate significant differences between larval stages (**p<0.0001; ns= not significant) indicate significant differences between shore heights.

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