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RESEARCH ARTICLE

Tidal height, rather than habitat selection for conspecifics, controls settlement in mussels

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Abstract Settlement is a major determinant of intertidal populations. However, the energy costs of lost larvae are very high. Accordingly, arrival and attachment on suitable substrata are essential requirements for species' survival. On the intertidal, the presence of cues left by adult or juvenile conspecifics could be vital for the successful establishment of larvae arriving on the shore. Two mussel species, the indigenous *Perna perna* and the invasive *Mytilus galloprovincialis*, co-occur on the lower eulittoral zone on the south coast of South Africa. *P.perna* dominates the low and *M. galloprovincialis* the high mussel zones, with co-existence in the mid mussel zone. This study tested the hypothesis of settlement selectivity for conspecifics in these two mussel species, to understand whether the final adult distribution of mussels on the shores is determined by active behavioural and chemical mechanisms. Preferential selection by larvae for conspecifics was tested in the field during the peak settlement period in 2004 in natural mussel beds across zones and through manipulative experiments in the mid-zone where the species co-exist. On natural beds, settlement was determined by counts of settlers attached over 48 h onto artificial collectors. Collectors were placed on beds of *P. perna* and *M. galloprovincialis* present at both high- and low-adult densities, as well as in mixed beds. On such natural beds, settlers of both species consistently favored low-zone *P. perna* beds. Settlement patterns over 24 h onto experimentally created mussel patches consisting of *P. perna*, *M. galloprovincialis* or the two species combined beds, set in the mixed zone, did not conform with the results of the natural beds study: settlers of both species settled with no discrimination among different patches. The results indicate that mussels, which are sedentary, lack attraction to conspecifics at settlement. This highlights the importance of tidal height in setting settlement rates, and of post-settlement events in shaping populations of these broadcast spawners.

Introduction

In the case of benthic marine animals with planktonic larvae, the processes controlling settlement from the water column into the benthos are critical to population regulation and are presumably under extremely strong selective pressure. For sessile species with internal fertilization, such as barnacles, this is especially true and the larvae of such species exhibit complex behaviour at settlement, including responses to multiple cues and strong chemical attraction to conspecifics (see Burke 1986 for review; Kingsford et al. 2002 for review; Jenkins 2005). The same is true for sessile bivalves with external fertilization, such as oysters (Zimmer-Faust and Tamburri 1994). For sedentary bivalves with external fertilization, such as mussels, selection of behaviour leading to settlement near conspecifics is still important, but presumably not so critical. This may be especially the case as mussels can exhibit primary and secondary settlement (Bayne 1964), giving them a further opportunity to adjust their within-shore distribution. Nevertheless, adult

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mussels show strong aggregative behaviour that can be triggered chemically or by tactile cues (de Vooys 2003; Nicastro et al. 2007). Aggregation has important implications for overall community structure and functioning for several reasons. Mussel beds make an important contribution to habitat complexity allowing the development of an associated infauna (Lintas and Seed 1994); aggregation influences interspecific competition for space (Rius and McQuaid 2006), the concentration of biomass in dense beds affects filtration of the water column (Norén et al. 1999; Davenport et al. 2000) and the behaviour of predators (Nagarajan et al. 2002). There are also trade-offs in depending on chemical cues for settlement as removal of all conspecifics from a habitat may make re-colonization more difficult (Erlandsson et al. 2006).

On South African shores, densities of adult and juvenile mussels are often correlated (Lawrie and McQuaid 2001). It is unclear whether aggregation of larvae with adult mussels is driven chemically or physically, but one line of evidence suggests that physical factors may be more important. A huge proportion of mussel larvae settle onto foliose macroalgae; some may re-locate onto adult mussel beds at a later stage, but it is not clear if this pattern is generally applicable (Erlandsson and McQuaid 2004; McQuaid and Lindsay 2005). The settlement of larvae onto different substrata can be explained in two ways. Settlement may be semi-passive, for example, through physical entanglement of mucous threads (Caceres-Martinez et al. 1994), or through behavioural reactions to small-scale hydrodynamics (Miron et al. 1996). Alternatively, larval behaviour may change when preferred substrata are already occupied and late-comers must occupy non-preferred substrata (Pineda and Caswell 1997; Pineda 2000). Where secondary settlement does occur, we may expect to see chemical attraction of older plantigrades to conspecific adults (de Vooys 2003).

Although mussels, as sedentary broadcast spawners, may be less likely to show attraction of settlers to conspecifics than sessile invertebrates, we propose that, attraction to conspecifics would still be a favourable strategy, though perhaps strongest among late plantigrades undergoing secondary settlement. Here we examine settlement patterns of different size classes of two co-occurring and competing mussels in South Africa: the indigenous *Perna perna* and the invasive *Mytilus galloprovincialis*. We test the hypothesis that settlement is driven by cues from conspecifics and that this helps to explain partial habitat partitioning between the two species. However, since *M. galloprovincialis* mainly occurs in the higher level of the mussel zone and *P. perna* in the lower mussel zone (Bownes and McQuaid 2006), a second hypothesis was also considered; that settlement rates depend on zonation rather than attraction to conspecifics.

Materials and methods

Settlement on natural beds

Settlement on natural mussel beds was monitored at one site in Plettenberg Bay, on the south coast of South Africa (34°22′S, 23°22′E), between September and December 2004. Five habitats (regarded as treatments) within the mussel zone were selected as close as possible to each other (maximum distance apart 4 m, minimum 1 m). The habitats had different cover of adult mussels: *P. perna* beds with high cover (P high; >70% adult cover), *P. perna* beds with low cover (P low; <40% adult cover), *M. galloprovincialis* beds with high cover (M high; >70% adult cover), *M. galloprovincialis* beds with low cover (M low; <40% adult cover) and finally beds where *P. perna* and *M. galloprovincialis* coexisted in roughly equal proportions (mix; total cover 70–100%).

Within each habitat, recently settled mussels of *P. perna* and *M. galloprovincialis* were collected five times (2 September, 30 September, 28 October, 27 November and 13 December) at low spring tide using five mussel collectors made of plastic scouring pads (diameter 10–11 cm, thickness 2 cm) as settler collectors (Menge 1992; Porri et al. 2006). Pads were secured to the rocks with screws and plastic cable ties in each habitat. Pads were soaked in seawater prior to deployment, collected after 48 h on the shore, returned to the lab and rinsed in 75-µm filtered water. The contents of each pad were examined under a dissecting microscope. Settlers of *P. perna* and *M. galloprovincialis* were identified and measured to the nearest 0.001 mm using a micrometer scale.

Due to the possibility that species interact as settlers so that their abundances on pads are not independent, separate two-way MANOVAs were run for small (<400 µm) and larger settlers (>400 µm), using each species as a dependent variable and habitat and date as independent parameters. In addition, separate three-way analyses of variance were performed to examine scales of variability for small (<400 µm) and larger settlers (>400 µm). Habitat (five levels) and species (two levels) were considered as fixed factors, while date (five levels) was treated as random (Zar 1996). Prior to analysis, normality and homogeneity of variances of data were examined using Kolmogornov Smirnoff and Cochran's tests, respectively (Zar 1996; Underwood 1997). Heterogeneity of the data was eliminated after logarithmic transformation ($P > 0.05$). Significant effects were further examined using Student Newman-Keuls (SNK) tests (Zar 1996).

Settlement on artificial mussel patches

Although the habitats used to study settlement on natural beds were all within the mussel zone, on these shores

M. galloprovincialis primarily occurs in the upper level of the mussel zone, and *P. perna* in the lower mussel zone (Bownes and McQuaid 2006). Therefore, a second hypothesis was that preferential settlement is due to zonation rather than active selection of conspecifics. This hypothesis was tested with a manipulative experiment in the mixed mussel zone, where the two species coexist. Artificial patches of adults were prepared using animals collected from surrounding mussel beds after thorough washing in seawater to remove juveniles; particular attention was paid to the byssus where juveniles often occur (personal observation). Immediately after collection, mussels were placed in bags of loose plastic mesh (mesh size approximately 8 mm). To avoid losses due to wave action, the bags were covered by 28-cm-long PVC pipes of very coarse mesh (1 cm). Pipes were cut longitudinally and half-pipes were placed over each mesh bag with the cut edge down and secured to the shore using eye-bolts and cable ties (Fig. 1). Three treatments were used for this experiment: *Perna* (with 20 *P. perna* adults per bag), *Mytilus* (with 20 *M. galloprovincialis* adults per bag) and mixed (ten adult mussels of each species per bag) (Fig. 1). Each treatment had four replicates, and all bags were collected after 24 h on the shore. Bags covered by half pipes were placed haphazardly on the shore, separated by 0.5–2 m and treatments were assigned randomly. The experiment was repeated four times: two collections were done on a spring tide and two on the following spring tide cycle, 2 weeks later.

Statistical analysis was performed using a four-way nested analysis of variance. The factor date (two levels) was treated as random, nested within tide (random; two levels) and crossed by treatment (two levels), and species (two levels), both considered as fixed (Zar 1996). Separate analyses were performed to assess variability in large and small settlers. For both sets of data homogeneity was achieved after logarithmic transformation of the dependent variable (Cochran's test; $P > 0.05$).

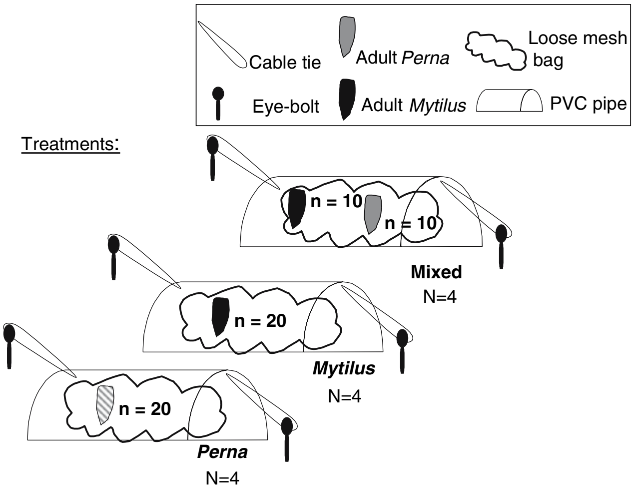

Fig. 1 Experimental design for the manipulated experiment using artificial mussel patches established in the mid-mussel zone. *N* number of replicates per treatment; *n* number of adult mussels in each bag

Results

Settler size and identification

Mussel settlers collected on scouring pads (after 48 h) and on artificial mussel patches (after 24 h) covered a wide range of sizes, from 200 to 3,500 µm (a single individual). However, most individuals (from 65 to 95%) were 200–400 µm in size. The shells of animals of this size were morphologically and dimensionally identical to larvae in the water column (Porri et al. 2006). This size was considered to represent primary settlers and was used for the analysis of "small" settlers. Individuals larger than 400 µm were pooled together and treated as "large" settlers.

Perna perna and *Mytilus galloprovincialis* were separated morphologically. These two species differ substantially at sizes of 850 µm. As primary settlers of 200–400 µm size, differences in morphology are less obvious, but still recognisable and the effectiveness of morphology in identification has been confirmed using DNA sequencing (Bownes 2006).

Settlement on natural beds

Throughout the study on natural mussel beds, there was a general predominance of *P. perna* among both small and large settlers. This was especially obvious on the 27th November, with a difference of one order of magnitude between maximum mean abundance of *P. perna* (314.6 ± 44.5 settlers per pad) and *M. galloprovincialis* (14.4 ± 3.6 settlers per pad), collected from the same beds (Fig. 2).

Two-way MANOVA provided no indication of an influence of species on settler abundance on pads, and since the results did not differ from those of three-way ANOVA, only the latter are presented. Analysis of variance of the abundance of small settlers showed a significant three-way interaction between habitat, date and species. There was a preference for *P. perna* adult beds on specific dates (27th November and 13th December 2004), with more small settlers arriving onto *P. perna* beds, but no discrimination among adult densities (Fig. 2a, b). Although the effect of habitat was significant for settlers of both *P. perna* and *M. galloprovincialis*, there were differences in abundance between the two species that resulted in the three-way interaction ($P < 0.0035$, Table 1).

Large settlers also showed a significant interaction between habitat, date and species (Table 1). More large settlers appeared on *P. perna* adult beds on some dates. On the

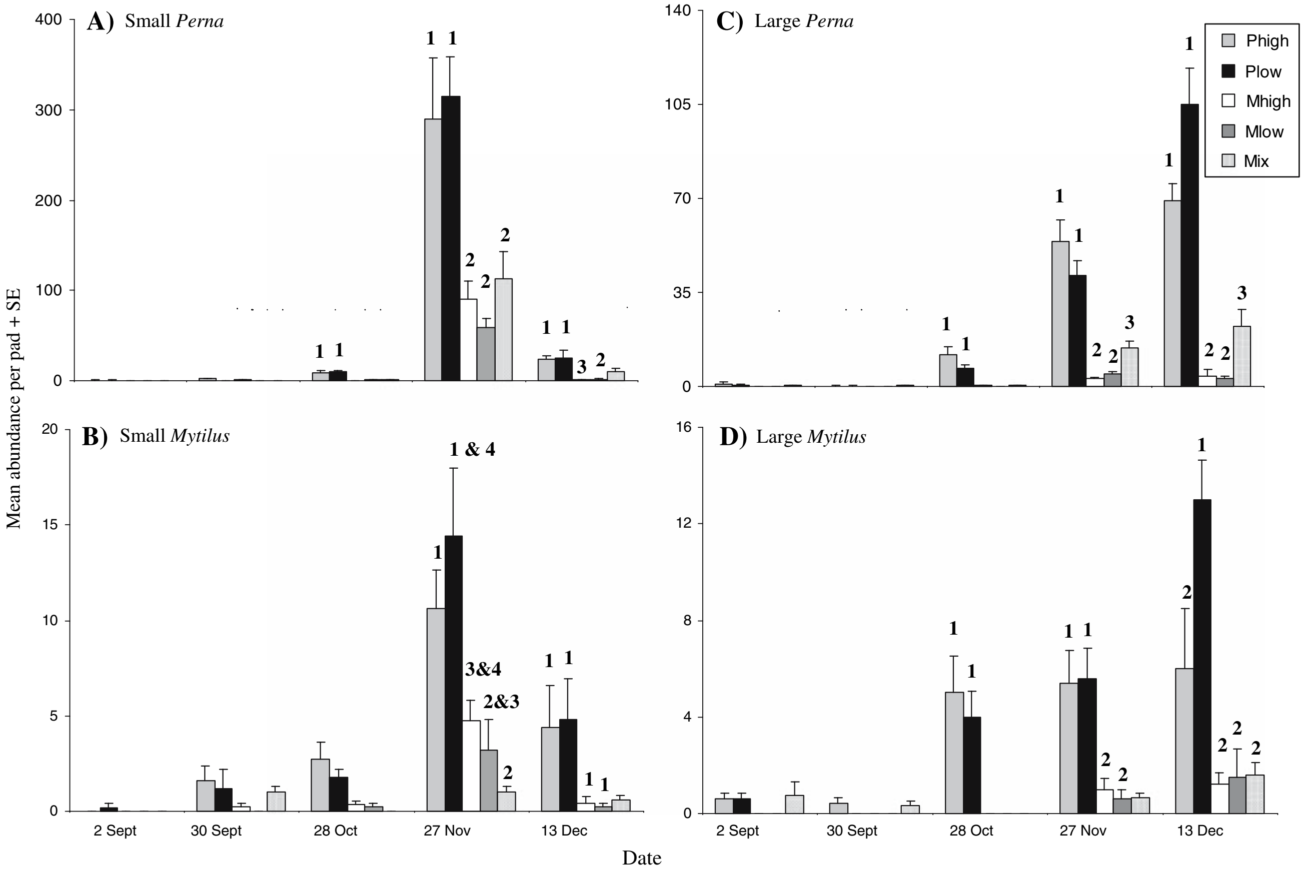

Fig. 2 Settlement on natural mussel beds with different adult cover (*P. perna* high *P high*, *P. perna* low *P low*, *M. galloprovincialis* high *M high*, *M. galloprovincialis* low *M low*, and mixed *mix*). *Error bars* indicate standard errors. *Numbers* on histogram bars refer to post-hoc homogenous groups within each sampling date. Scales on the four axes are different to accentuate the treatment effect within each sampling date

27th November and 13th December, the relative abundance of large settlers of both species was higher on *P. perna* beds, even though the abundances were much greater for *P. perna* (maximum abundance on 13th December: 105 ± 13.5 settlers per pad) than for *M. galloprovincialis* (maximum abundance on 13th December: 13 ± 1.6 settlers per pad).

While small settlers of neither species discriminated between beds with different adult densities, on the 13th December, large settlers of both species were found in greater numbers on “P low” beds. However, SNK post-hoc tests confirmed the significance of this tendency only for *M. galloprovincialis* (Fig. 2d).

Overall, post-hoc tests revealed that, when densities of settlers were generally low, there was no habitat effect. When numbers of settlers were generally large, more of both size classes were found on *P. perna* than *M. galloprovincialis* beds. Generally, the post-hoc tests also showed that, for both size classes, the habitats “P high” and “P low” grouped together, while the habitats “M high” and “M low” formed a separate homogenous group, often including the mixed habitat (see Fig. 2 for homogenous groups).

Settlement on artificial mussel patches

Again there was a prevalence of *P. perna* among settlers, with differences of an order of magnitude in abundances of the two species.

The only significant effect in the four-way nested ANOVA of the small settlers was date, nested within tide ($P < 0.022$), with no significant effect of treatment ($P > 0.05$). On the first day of each tide, November 12 and 27, respectively, more small settlers were collected from the artificially created beds than on the second day (Fig. 3).

The results of the four-way nested ANOVA for large settlers showed no significant effects for any factor or interaction.

Discussion

We hypothesised that, although selection for attraction to conspecifics may not be very strong among sedentary broadcast species, it would nevertheless be advantageous. To test this, and examine whether habitat selection by

Table 1 Factorial analysis of variance for settlement study on natural beds, for small and large settlers

	df	MS	*F*	*P*
Small settlers				
H	4	12.70	6.44	<0.003
D	4	75.51	3.57	NS
S	1	70.30	3.56	NS
H × D	16	1.97	3.35	<0.01
H × S	4	0.98	1.67	NS
D × S	4	19.75	33.56	<0.0001
H × S × D	16	0.59	2.33	<0.003
Error	200	0.25		
Large settlers				
H	4	22.27	7.81	<0.001
D	4	40.65	3.77	NS
S	1	30.53	3.617	NS
H × D	16	2.85	5.56	<0.0007
H × S	4	1.66	3.23	0.04
D × S	4	8.45	16.46	<0.00001
H × S × D	16	0.51	2.69	<0.0007
Error	200	0.19		

H habitat, *D* date, *S* species

mussel larvae is primarily active and driven by behaviour or passive and controlled by physical factors, we used the distinctive zonation pattern of *Perna perna* and *Mytilus galloprovincialis* on the South African coast. The results demonstrated clearly that grown-up zonation of the two species is not driven by active habitat selection by either primary settlers or late plantigrades.

While there is evidence that settlement in barnacles, sessile polychaetes and oysters (Zimmer-Faust and Tamburri 1994; Toonen and Pawlik 2001; Jenkins 2005) is mainly driven by larval choices, with larvae attaching close to adult and juvenile conspecifics, the pattern is not so obvious when considering mussel habitat selection at settlement (Petersen 1984; Caceres-Martinez et al. 1994; Gilg and Hilbish 2000; Bierne et al. 2003; Coughlan and Gosling 2007). Aggregational behaviour for adult mussels has been shown to have biochemical characteristics (de Vooys 2003), while juveniles of *M. galloprovincialis* and *P. perna*, 4–10 mm in size, show immediate clumping behaviour if within a distance ≤ triple the shell length (personal observation). Thus, it seems likely that active selection of adult beds and the ability to respond to conspecific chemical cues could exist at earlier developmental stages, during settlement. In addition, recent findings have shown that algal chemical cues, GABA, epinephrine and L-DOPA promote metamorphosis and settlement in mussels (Dobretsov and Qian 2003; García-Lavandeira et al. 2005; Alfaro et al. 2006). However, all of these studies have been performed in the laboratory, testing settlement induction under unnatural concentrations. In fact, Dobretsov and Qian (2003) state that it is unlikely that many of these chemicals will be found to be natural

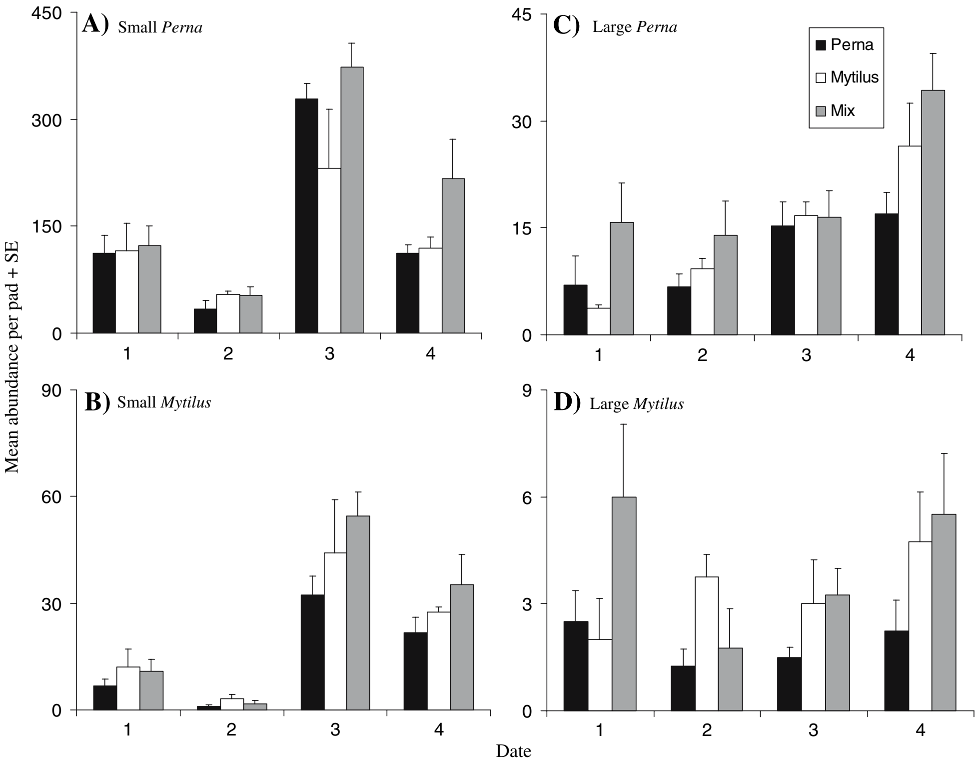

Fig. 3 Settlement on artificial mussel patches, *P. perna* (*Perna*), *M. galloprovincialis* (*Mytilus*) and mixed species (*mix*). *Error bars* indicate standard errors. Scales on the four axes are different to accentuate the treatment effect in each group

settlement inducers, so that their ecological role remains uncertain. Here we tested the hypothesis of attraction of settling larvae to adult conspecifics under field conditions.

Regardless of species and size, settlers did not discriminate for conspecifics, but attached non-selectively onto beds of different mussel species. The results also showed that settlement is dictated by vertical zonation. In general, settlers of both species settled among *P. perna* beds, at the lowest levels of the mussel zone, with no preferences among treatments with different densities. Since most *M. galloprovincialis* settlers arrived on the low shore while few adults occur there, we can assume that the final adult zonation of this species is driven by post-settlement mechanisms.

The significant preference of settlers of both species for natural *P. perna* beds, but not for artificial *P. perna* patches placed in mixed beds higher on the shore, where both mussel species naturally coexist, indicates that apparent selection in favour of *P. perna* was an artefact. Selection was actually for lower shore mussel beds. During incoming tides, larvae pass across the low shore first while this zone is also submerged for longer time during each tidal cycle, giving more opportunities for settlement onto suitable substrata in the low shore. In this way, the low shore may act as a screen, filtering out and retaining larvae before the water reaches the higher zones so that settlement rates decrease with tidal height (c.f. Bertness and Grosholz 1985 for soft sediments; Minchinton and Scheibling 1991 for barnacles on rocky shores). Differences in bacterial community composition of biofilms can also account for differential settlement of invertebrates (c.f. Lau et al. 2005 for differential barnacle and polychaete settlement induced by different biofilms; Qian et al. 2003 for differential settlement of barnacles at high-, mid-, and low intertidal levels). However, in the present study, the use of identical settler collectors ensured homogeneity of settlement substrata so that zone and biofilm were not confounded. The fact that both size classes of both species responded similarly to natural and artificial beds, clearly indicates that mussels up to about 3 mm in size do not show attraction to conspecifics, or if they do, it is overwhelmed and masked in the field by water movement.

Johnson and Geller (2006) studied the role of settlement in adult mussel distribution in California and came to similar conclusions, emphasising that physical mechanisms drive settlement, while final adult distribution is shaped by a combination of physical processes and biological post-settlement mechanisms (Johnson and Geller 2006). However, their study plates were deployed for about 12 days and settlers and recruits were considered as a single group. We have data that indicate ontogenetic changes in the responses of recently settled mussels as they age (Erlandsson, unpublished. data). This strongly implies differences in behaviour towards conspecifics between settlers and larger recruits that may be crucial in determining final zonation, so that different size classes must be analysed separately.

The present study suggests that chemical attraction in the intertidal could be driven by different evolutionary cues depending on the organisms' life histories. For sessile species such as barnacles, oysters and some polychaetes (Zimmer-Faust and Tamburri 1994; Toonen and Pawlik 2001; Jenkins 2005) the first attachment on a suitable substratum is crucial for survival, resulting in strong selection of behavioural patterns leading to settlement among conspecifics. For sedentary broadcast spawners such as mussels, attachment within conspecific beds is important, but not critical because they can change their position through detachment and re-attachment (secondary settlement) or aggregate through small-scale crawling.

Differential spatial delivery of competent mussel larvae from nearshore waters to the intertidal explains variability in distribution of mussels among locations separated on scales of 100 m (Porri et al. 2006), while the results of the present study indicate that physical mechanisms, through the effect of tidal height on larval delivery, affect within-shore zonation. We suggest that, at least for *M. galloprovincialis*, early post-settlement mechanisms are the primary determinant of adult distribution, and thus of the vertical zonation of these two mussel species.

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