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Selective settlement of the barnacle *Semibalanus balanoides* (L.) facilitates its growth and reproduction on mussel beds in the Wadden Sea

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Abstract On the unstable sedimentary tidal flats of the Wadden Sea, a suitable attachment substrate for sessile organisms is generally lacking. Epibenthic mussel beds (*Mytilus edulis* L.) provide the only and strongly limited settlement sites available for the barnacle, *Semibalanus balanoides* (L.). Field investigations showed that barnacles were non-randomly distributed within a mussel bed. They preferentially occurred near the siphonal apertures of living mussels but rarely grew on dead mussels or shell fragments. Field experiments revealed that this was due to selective settlement of barnacle cyprid larvae. Growth of barnacles was significantly higher upon living mussels than on empty mussel shells. Moreover, a higher reproductive output was obtained by individuals on living mussels which produced twice as many nauplii larvae than barnacles attached to empty shells. This study shows that selective settlement of *S. balanoides* cyprid larvae on living mussels is adaptive with respect to individual fitness.

Keywords Barnacles · Mussel beds · *Semibalanus balanoides* · Selective settlement · Reproductive output

Introduction

Most benthic marine invertebrate species disperse by planktonic larvae which spend between minutes and months in the water column before becoming competent to settle. Mortality and hydrodynamic processes substantially influence the survival and distribution of larvae during this pelagic phase (e.g. Gaines and Roughgarden 1985; Butman 1987). In sessile epibenthic species, the benthic phase is initiated by contact with a substratum

acceptable for attachment and metamorphosis. Therefore, initial recruitment to benthic populations depends on the availability of suitable substrates (Minchinton and Scheibling 1993; Pineda 1994; Pineda and Caswell 1997), while physical disturbance (Bergeron and Bourget 1986; Jenkins et al. 1999), competition for space or food (Zajac et al. 1989; Hurlbut 1991) and mortality caused by predation (Reise 1977, 1978; Gosselin and Qian 1997) are post-settlement processes affecting recruitment success later (Connell 1985; Ólafsson et al. 1994; Hunt and Scheibling 1997; Todd 1998). In mobile species, the location of the initial settlement may be different from the habitat of adults because specimens are capable of migration when living conditions become unfavourable (Chia 1989). Juveniles of the tellinid clam, *Macoma balthica* (L.), for example, migrate from settlement sites to the habitat of older conspecifics because juveniles demand different environmental conditions than adults do (Armonies and Hellwig-Armonies 1992; Beukema 1993). For sessile organisms, however, it is essential to settle on an attachment site where conditions are favourable for the rest of the life span. Therefore, many sessile invertebrate species, including bryozoans (Hurlbut 1991), ascidians (Young and Chia 1984; Svane and Young 1989; Hurlbut 1993), polychaetes (Qian 1999), and barnacles (e.g. Pyefinch 1948; Kühl 1952; Crisp 1961; Crisp and Meadows 1963; Crisp et al. 1985; Le Tourneux and Bourget 1988; Thompson et al. 1998) demonstrate an active larval choice of a suitable habitat.

In soft bottom marine habitats such as the Wadden Sea, settlement and recruitment of sessile organisms is mainly restricted to shells of epibenthic molluscs because natural hard substrate is generally rare (Buschbaum and Reise 1999). Beds of the mussel, *Mytilus edulis* L. provide the only major attachment surface for sessile organisms on tidal flats. This biogenic hard substrate is utilized by a large number of sessile epifauna and algae (Matsumasa and Nishihira 1994; Albrecht 1998) but in the northern Wadden Sea, the most frequent and dominating epibiont is the barnacle, *Semibalanus balanoides* (L.) (Buschbaum and Saier 2001). In the

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north of the island of Sylt (German Bight, North Sea) mussel beds comprise about 1% of the intertidal area (Reise et al. 1994), indicating that this natural attachment surface for barnacles is strongly limited. Nevertheless, epibiont densities varied considerably, both within and between mussel beds.

Due to the net of byssus threads produced by the byssus glands of *M. edulis*, mussel beds are conglomerates of living mussels and shell fragments. Personal field observations indicated that most barnacles were attached to living mussels. It seemed intriguing to ask whether barnacle cyprids execute a selection of different attachment surfaces within a mussel bed despite the restricted availability of hard substrate. I hypothesized that larvae of *S. balanoides* prefer settlement on living mussels, where living conditions for balanids after metamorphosis were assumed to be better, as was shown for *Balanus improvisus* Darwin attached to *M. edulis* in the Baltic Sea (Laihonen and Furman 1986). Field investigations were conducted on the distribution and on the recruitment patterns of *S. balanoides* on intertidal mussel beds. Subsequent field experiments tested whether growth and reproductive output of *S. balanoides* attached to living mussels were higher than those of balanids living on dead mussels or shell fragments.

Materials and methods

Study area

Surveys and experiments were carried out in Königshafen, a sheltered bay comprising about 4.5 km² of intertidal flats near the island of Sylt in the North Frisian Wadden Sea (German Bight, 55°02'N, 08°26'E; Fig. 1). The bay is protected from strong on-shore winds by dunes. Tides are semi-diurnal and tidal waters enter the bay from the leeward side. Tidal range is about 1.8 m. Average salinity is 30 psu and mean water temperature is 15°C in summer and 4°C in winter. Detailed descriptions of the hydrography, geology and sediments of the study area are given by G. Austen (1994), I. Austen (1994) and Bayerl and Higelke (1994). The biota have been described by Wohlenberg (1937), Reise (1985) and Reise et al. (1994).

Three species of barnacles frequently occur in the area: *S. balanoides* (L.) is common in the intertidal zone and *Balanus crenatus* Bruguière dominates the subtidal area (Buschbaum and Saier 2001). *Elminius modestus* Darwin was introduced from Australia and colonized the German Bight in 1953, presumably by ship (Kühl 1954). This species is sensitive to winter cold and has become low in density since the severe winter of 1995/1996 (personal observation). Mussel beds (*M. edulis* L.) provide the largest natural available attachment surface for balanids (about 1% of the intertidal area of Königshafen; Reise et al. 1994), while artificial hard substrates such as rocky breakwaters are of minor importance. All investigations were carried out on intertidal mussel beds north of the main tidal channel with a mean emersion time of about 2 h per tide (Fig. 1).

Comparing barnacle overgrowth on shells of living mussels and on empty shells

On 31 May 1999, barnacle overgrowth on living mussels and empty shells was quantified by taking six replicate samples from the mussel bed using a box corer of 315 cm². Contents were washed through a 1,000 µm sieve and living mussels as well as intact emp-

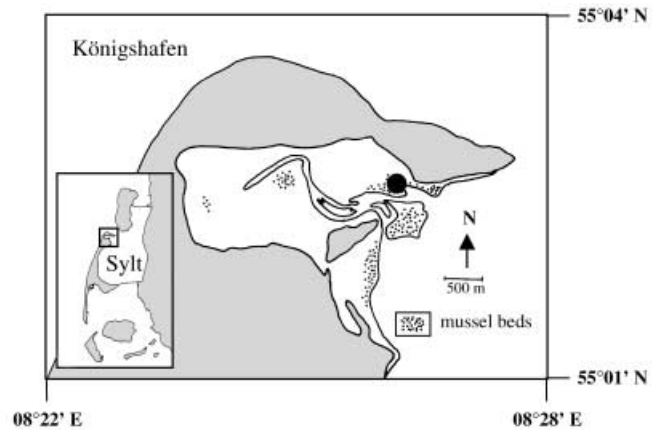


Fig. 1 The intertidal zone of Königshafen with mussel beds (dotted). All surveys and experiments were carried out on mussel beds north of the tidal inlet (●)

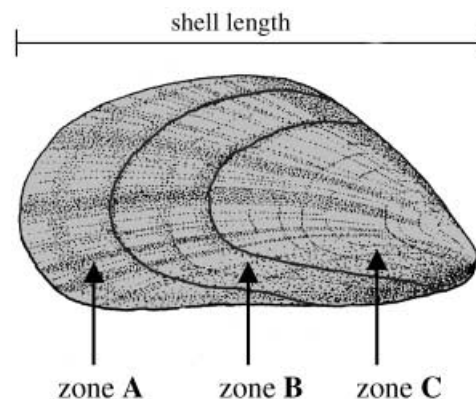


Fig. 2 *Mytilus edulis* shell divided into three zones of about 30% surface area each

ty valves were counted. Barnacle epigrowth of both living mussels and empty shells was then scratched off and dried separately at 75°C for 3 days. Dry weight of balanids was determined to the nearest 0.01 g. For each sample, barnacle dry weight per mussel valve of living and empty mussels, respectively, was calculated. Dry weight per single mussel valve was determined because bi-valve shells usually break into two single valves after the death of the mussel. Therefore, in the field, empty shells occur mostly as single valves. Only *M. edulis* >35 mm shell length (Fig. 2) were considered, because balanids generally occurred from this mussel size upwards.

Barnacle settlement and recruitment on shells of living and dead mussels

The term settlement includes attachment to the substrate and metamorphosis, while recruitment refers to survival until the organism is counted by an observer (Keough and Downes 1982). In this study, settlers are defined as attached cyprids and freshly metamorphosed barnacles, whereas recruits are the surviving organisms after a period of 7 weeks.

To test the hypothesis that barnacle cyprid larvae prefer settlement on shells of living *M. edulis* over empty shells, the number of newly settled and recently metamorphosed larvae attached to 40 living mussels and 40 empty valves was counted in the field on 22 May 2000 using a magnifying glass (magnification 8×). Only mussels without adult *S. balanoides* were selected because the oc-

currence of adult conspecifics and their chemical attractants may influence larval settlement (Knight-Jones 1953; Crisp 1955; Larman and Gabbott 1975; Wetthey 1984). To ensure that living and empty shells were equally available to larvae and that settlement was not affected by sediment or mussel aggregations, only mussels and valves from the top layer of the mussel bed were sampled.

An additional field experiment tested barnacle recruitment on shells of living and dead mussels. Eighty naturally clean *M. edulis* (shell length 50–65 mm) were collected from a mussel bed and 40 of them were killed by cutting the adductor muscles. After removing the mussel tissue, the empty shells of killed bivalves were filled with mortar. During this preparation both living and killed mussels were exposed to air for the same period of time (about 4 h). This was done to prevent differences in biofilm conditions between the treatments. Each living and artificial *M. edulis* was glued by one valve onto a circular piece of PVC netting (15 cm diameter, mesh size 5×5 mm). On 25 April 1999, mussels were randomly distributed on the mussel bed where they had been collected, and were fixed using three iron rods (50 cm in length; 6 mm in diameter). After an experimental period of 7 weeks (when most barnacles had settled) barnacle number of the upper mussel valves was counted on 14 June 1999.

Barnacle zonation on *M. edulis* shells

To determine the occurrence of barnacles in different zones of a mussel shell, 238 *M. edulis* (>35 mm shell length) with barnacle overgrowth were randomly sampled in September 1998. Each mussel shell was divided into three roughly equal zones of about 30% each (according to Laihonon and Furman 1986; Fig. 2) and the presence/absence of barnacles in each of the zones was noted.

The settlement of barnacle cyprid larvae on these different shell zones of living mussels and empty mussel shells was tested on 20 May 2000. Thirty living *M. edulis* and 30 empty valves (shell length 50–65 mm) with macroscopically visible barnacle larvae were randomly collected from the mussel bed. Valves with a comparatively high number of barnacles were chosen to detect a larval preference for a distinct mussel shell zone. Therefore, the number of barnacles per valve did not represent the natural density of cyprids and freshly metamorphosed barnacles. The number of attached cyprids and freshly metamorphosed balanids in each shell zone was counted using a magnifying glass (magnification 8×). Again, only mussels and valves from the top layer of the mussel bed and without adult *S. balanoides* were considered, in order to ensure that all shell zones could be reached equally easily by the cyprid larvae.

Experiments on barnacle growth and reproduction

A field experiment was performed to test whether the growth rates of barnacles attached to living mussels differed from those of balanids growing on empty shells of dead *M. edulis*. For this experiment, 60 mussels (shell size 50–65 mm) with barnacles were collected in the field and all barnacles were removed except for one size class in shell zone A near the siphonal apertures. The number of balanids per mussel was counted (5–10 mussel⁻¹) and the rostro-carinal length of the barnacle apertures was measured to the nearest 0.01 mm using a stereomicroscope with ocular micrometer (Fig. 3). At the beginning of the experiment, barnacle apertures had a length of 2.0–3.5 mm. After barnacle size measurement, 30 of the 60 collected mussels were killed by cutting the adductor muscles and the mussel tissue was removed. One living and one killed mussel were glued onto a piece of circular PVC netting (20 cm diameter, mesh size 5×5 mm) and marked with a number ($n=30$ replicates). On 11 June 1999, the experimental devices were fixed to the mussel bed using three iron rods (50 cm length; 6 mm diameter). After an experimental period of 9 weeks (on 13 August 1999) apertures of barnacles were measured again and the growth increment was calculated. Barnacle mortality was determined by

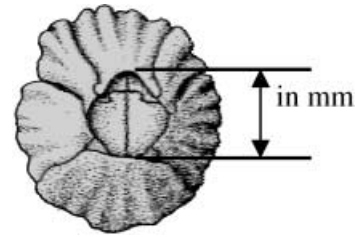


Fig. 3 Measurement of barnacle size (mm) as rostro-carinal length of the barnacle apertures

counting the number of living balanids per mussel at the end of the experiment.

To examine the reproductive output of *S. balanoides*, the number of nauplii larvae per balanid was measured. The species *S. balanoides* is hermaphroditic and viviparous, and breeds once a year (Barnes 1989, 1992). In the study area breeding occurs from March to May (Luther 1987). Larval release has been shown to be synchronized with a diatom bloom in the water column (Barnes 1962). Nauplii larvae develop outside the body within the mantle cavity of the adults (H. Barnes 1962; M. Barnes 1989) and are visible from below after removing the balanids from the substrate. In the field, *S. balanoides* attached to (1) shells of living mussels, (2) empty shells, and (3) stones within the mussel bed, were carefully removed from the substrate on 28–30 March 2000. Stones seldom occur within intertidal mussel beds but were nevertheless sampled in order to test barnacle reproductive output on another non-living substrate. While still alive, barnacles were observed under a magnifying glass (magnification 8×). When individuals were found bearing ripe eggs with nauplii, the eggs were carefully separated from the calciferous cones in the laboratory and transferred to Petri dishes containing seawater where the nauplii hatched. Larvae of individual barnacles were then fixed in 2% formaldehyde solution and kept in 100-ml Kautex bottles. Since larvae numbers per sample were very high, samples were diluted with seawater to 300 ml. Starting from this solution, 5-ml aliquots were removed with a Hensen-Stemple plankton pipette and nauplii counted with a stereomicroscope. Nauplii numbers were calculated back to 300 ml. For each of the three treatments, the larvae number of 30 *S. balanoides* of the same size class (aperture length 4.5–6.0 mm) was determined.

Statistical analysis

Results were calculated as arithmetic means with standard deviation ($\bar{x}\pm SD$). Barnacle dry weight and settlement on living and dead mussels was analysed using analysis of variance (ANOVA). Data of dependent variables were tested for homoscedasticity using Cochran's test. Data for barnacle settlement in different shell zones, recruitment and reproduction were subjected to non-parametric tests because of the heterogeneity of variances despite transformation. Growth and mortality of *S. balanoides* attached to living and killed *M. edulis* was analysed using Wilcoxon's matched pairs signed rank test. Barnacle occurrence on different mussel shell zones was analysed by a chi-squared test. Effects were considered to be statistically significant, if P was <0.05.

Results

Density of barnacles on shells of living mussels and on empty shells

The field surveys revealed that dry weight of barnacle overgrowth was significantly higher on shells of living

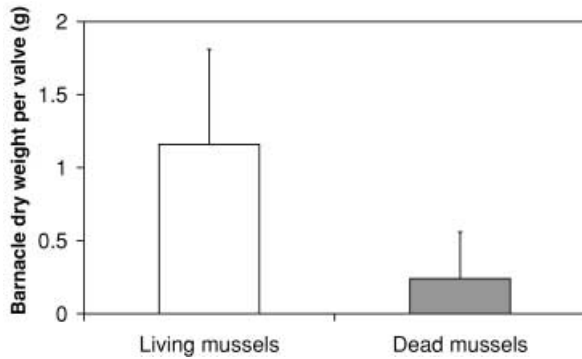


Fig. 4 Mean (+SD) barnacle dry weight (g) on mussel valves of living and dead *Mytilus edulis*. Dry weight of *Semibalanus balanoides* was significantly higher on living mussels

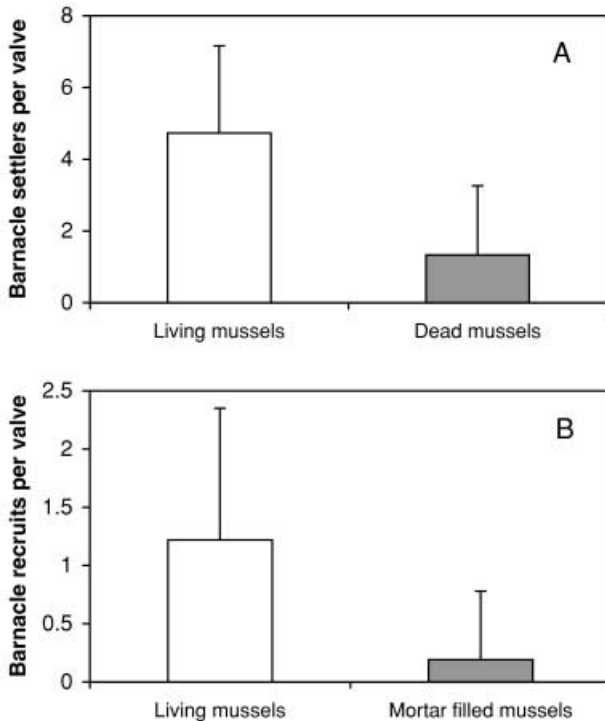


Fig. 5 Mean number (+SD, $n=40$) of barnacle settlers on living and dead *Mytilus edulis* on 22 May 2000 (A). Mean number (+SD; $n=40$) of barnacle recruits on living and mortar filled mussels after an experimental period of 7 weeks in 1999 (B). Numbers of settlers and recruits were significantly higher on living mussels

mussels (1.16 ± 0.65 g valve⁻¹) than on empty shells (0.24 ± 0.32 g valve⁻¹) (one-way ANOVA, $F=9.735$, $df=1$, $P<0.02$; Fig. 4). Similarly, initial barnacle settlement was also significantly higher on living mussels (4.7 ± 2.4 valve⁻¹) than on empty valves (1.3 ± 1.9 valve⁻¹) (one-way ANOVA, $F=48.122$, $df=1$, $P<0.0001$; Fig. 5A).

After an experimental period of 7 weeks, the number of barnacle recruits on living mussels (1.2 ± 1.1 recruits valve⁻¹) was significantly higher than on mussels which had been filled with mortar at the beginning of the experiment (0.2 ± 0.6 recruits valve⁻¹) (Mann-Whitney U -test, $P<0.001$; Fig. 5B).

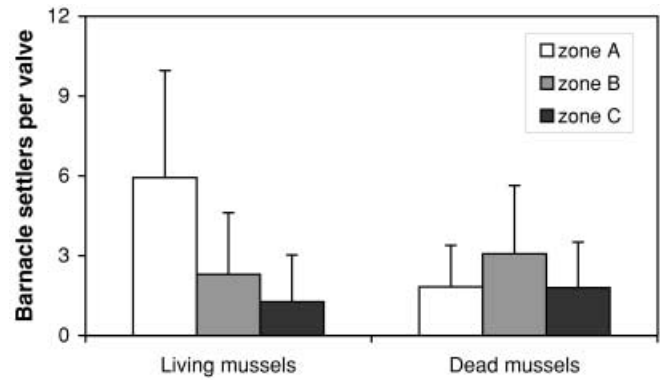


Fig. 6 Mean number (+SD, $n=30$ mussel valves) of barnacle settlers in three distinct mussel shell zones from outer edge (A) to middle (B) and inner portion (C) of the shell (see Fig. 2). On living mussels, barnacle settlement on the shell zones was significantly different

Barnacle distribution on mussel shells

Barnacle occurrence differed significantly over the three distinct shell zones ($\chi^2=69.199$, $df=2$, $P<0.0001$). 79% of mussels with barnacles had barnacles in shell zone A, 67% in shell zone B, and 24% in zone C (see Fig. 2). Only seven out of the 238 *M. edulis* investigated had barnacles in shell zone C without having them in shell zone A as well. This indicates that *S. balanoides* tend to settle in zone C only when zone A is already occupied.

On living mussels collected during the period of barnacle settlement, barnacle larvae showed a preference for the shell zone near the siphonal apertures. Settlement of cypriids in shell zone A (5.9 ± 4.0 valve⁻¹) was significantly higher than in shell zone B (2.3 ± 2.3 valve⁻¹) and shell zone C (1.3 ± 1.8 valve⁻¹) (Kruskal-Wallis H -test, $P<0.0001$, followed by Mann-Whitney U -tests, $P<0.0001$; Fig. 6). The number of recently settled larvae in shell zone B was also significantly higher than in zone C (Mann-Whitney U -test, $P<0.05$). In contrast, larval settlement on empty shells was more even and no significant differences over the shell zones were detectable (Kruskal-Wallis H -test, $P>0.05$).

Growth and reproductive output of *S. balanoides*

After the investigation period of 9 weeks, growth increment of barnacles attached to shells of living mussels (1.64 ± 0.34 mm) was significantly higher than of barnacles grown on mussels which were killed at the beginning of the experiment (1.24 ± 0.42 mm) (Wilcoxon's matched pairs signed rank test, $P<0.01$, $n=22$; eight experimental devices were lost during the experiment; Fig. 7). Mean barnacle mortality was about 35% without any significant difference between treatments (Wilcoxon's matched pairs signed rank test, $P=0.50$).

The reproductive output of *S. balanoides* varied with the type of substrate. In March 2000, average number of larvae of barnacles attached to living *M. edulis* was

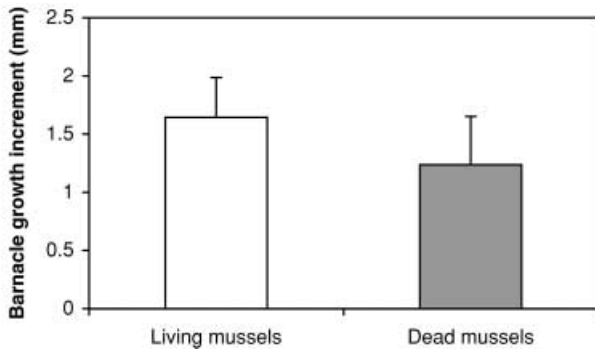


Fig. 7 Mean (+SD) barnacle growth increment (mm) after an experimental period of 9 weeks. Growth of *Semibalanus balanoides* was significantly higher on living mussels

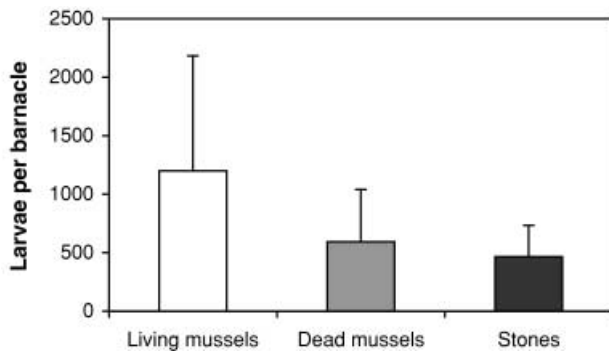


Fig. 8 Mean (+SD; $n=30$) number of nauplii per barnacle in each test group of *Semibalanus balanoides*. Larval numbers of balanids attached to living mussels were significantly higher than those of barnacles on dead mussels or stones

1,200±984 nauplii per barnacle, and was significantly higher than that of balanids on empty shells (593±446 nauplii per barnacle) and stones (465±268 nauplii per barnacle) (Kruskal-Wallis H -test, $P<0.001$, following Mann-Whitney U -test, $P<0.01$; Fig. 8).

Discussion

Selective settlement of barnacles within mussel beds

On the unstable sediments of the Wadden Sea, sessile organisms generally profit from a biogenic substrate which constitutes a limiting resource. Nevertheless, in the study area, *S. balanoides* barnacles did not settle and recruit equally on any available substrate within a mussel bed, but showed a non-random distribution, with most balanids attached to the shells of living mussels particularly near the siphonal apertures. Basically the same pattern was found by Laihonon and Furman (1986) for *Balanus improvisus* Darwin attached to *M. edulis* in the Baltic Sea. The recruitment pattern depends on three components: (1) larval supply to the specific substrate, (2) site selection by competent larvae, and (3) the survival of settlers (Bertness et al. 1992). Therefore, the non-

random distribution of *S. balanoides* within mussel beds might be a result of a higher planktonic larval supply to living mussels and/or a higher post-settlement mortality of barnacles attached to empty shells. Results of this study, however, indicate that active habitat selection by barnacle cyprid larvae was the major cause for a higher abundance of barnacles on the shells of living *M. edulis*.

Larval habitat selection was reported to be influenced by many factors including physical cues such as surface contours (Crisp and Barnes 1954; Wethey 1984; Raimondi 1988) as well as chemical cues such as biofilms developed on the settlement substrate (Crisp and Meadows 1963; Crisp et al. 1985; Keough and Raimondi 1995; Thompson et al. 1998). Presumably these factors differed between living and dead mussels because living mussels, for example, wipe their shells with their foot (Theisen 1972) which may influence shell surface properties (S. Holmes, personal communication). Crisp (1955), however, showed that currents encourage barnacle settlement, which may particularly be the case near the siphonal apertures of living mussels due to their filter activity. The currents produced by the mussel siphons may also enhance the feeding conditions for balanids after metamorphosis (Laihonon and Furman 1986; Bertness et al. 1991; Sanford et al. 1994). Food availability may be enhanced by an increased amount of water passing the balanids, and the costs of foraging might be reduced because balanids may keep the cirral net out in the current instead of actively swiftng it (LaBarbera 1984; Trager et al. 1990). These factors may result in a better nutritional level of *S. balanoides* on living mussels, and this may have resulted in an improved growth and reproductive output compared with individuals attached to empty shells or stones as has been shown by Crisp (1960) and Barnes and Barnes (1967, 1975). During periods of unfavourable conditions, selective settlement of *S. balanoides* on living mussels may become important for successful recruitment. Then, the doubled larvae production of balanids on living mussels may be essential for a sufficient larval supply which can guarantee a genotype's representation in the next generation.

In the particular case of mussel beds in the Wadden Sea, the accumulation of biodeposits through mussel filtration is an important aspect (Dittmann 1987). To escape sediment burial, mussels vertically migrate to the top of the mussel bed (Okun 1999). Barnacle epifauna may profit from these upward migrations because they are protected against sediment accumulation, which hampers feeding activity and is assumed to be a mortality factor in balanids (Bertness 1984).

Barnacle settlement in relation to available substrate

Settlement of larvae depend on the amount of suitable habitat, and settlement may be proportional to the available substrate, i.e. the more available substrate, the higher total settlement (Gaines and Roughgarden 1985;

Minchinton and Scheibling 1993). Other studies, however, suggest that settlement per unit area intensifies as suitable substrate becomes rare (Bertness et al. 1992; Pineda 1994; Pineda and Caswell 1997) because barnacle larvae become less selective in habitat choice when suitable attachment sites are limited (Bertness et al. 1992). As a consequence, the settlement behaviour of barnacle cyprid larvae may be masked because the cyprids arriving early in the settlement period select the most suitable attachment sites, while larvae arriving later are restricted to less favourable locations (Gaines and Roughgarden 1985; Raimondi 1990; Bertness et al. 1992; Minchinton and Scheibling 1993; Jarrett 1997). This is in agreement with the findings of this study; barnacles occurred in the least favourable shell zone C when zone A near the siphonal apertures was occupied. Accordingly, the high interannual variations of barnacle settlement (e.g. Hawkins and Hartnoll 1982; Connell 1985; Gaines and Roughgarden 1985; Raimondi 1990; Buschbaum 2000) should be accompanied by variations in the kind of substrate actually used. Indeed, when barnacle recruitment was very strong in spring 1996, mussels as well as shell fragments were evenly overgrown by *S. balanoides* (personal observation). However, this strong recruitment was not due to a high larval supply in the water column, as had been shown by Gaines et al. (1985) and Bertness et al. (1992). Instead, long-term data for planktonic larval abundance in the study area (P. Martens and M. Strasser, unpublished) revealed that in 1996 cyprid abundance was no higher than in other years and, therefore, was unlikely to be responsible for the high recruitment success. This indicates that processes subsequent to larval attachment may be stronger determinants of barnacle recruitment success on intertidal mussel beds. As an example, the grazing activity of periwinkles, *Littorina littorea* (L.), on mussel beds proved to be a significant mortality factor in recently settled barnacles (Buschbaum 2000). In spring 1996, during the period of barnacle settlement, snail densities were comparatively low, suggesting that reduced grazing pressure was the reason for the high recruitment success of *S. balanoides*. Thus, interannual variations in barnacle recruitment on mussel beds are assumed to be predominantly controlled by post-settlement factors, while the relationship between available settlement surface area and the number of competent larvae may be responsible for the site selectivity observed within the mussel bed. Without mussel beds, *S. balanoides* would be a rare species in the Wadden Sea.

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