



Direct and indirect effects of *Littorina littorea* (L.) on barnacles growing on mussel beds in the Wadden Sea

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Abstract

On the extensive sedimentary tidal flats of the Wadden Sea, beds of the blue mussel *Mytilus edulis* represent the only major hard substratum and attachment surface for sessile organisms. On this substratum, the barnacle *Semibalanus balanoides* is the most frequent epibiont. In summer 1998, it occurred on over 90% of the large mussels (>45 mm shell length) and the dry weight of barnacles reached 65% of mussel dry weight. However, the extent of barnacle overgrowth is not constant and differs widely between years. Periwinkles (*Littorina littorea*) may reach densities >2000 m⁻² on intertidal mussel beds. Field experiments were conducted to test the effect of periwinkle grazing on barnacle densities. An experimental reduction of grazing and bulldozing pressure by periwinkles resulted in increased recruitment of barnacles, while barnacle numbers decreased with increasing snail density. The highest numbers of barnacles survived in the absence of *L. littorea*. However, a lack of periwinkle grazing activity also facilitated settlement of ephemeral algae which settled later in the year. Field experiments showed that the growth rate of barnacles decreased in the presence of these ephemeral algae. Thus, *L. littorea* may reduce initial barnacle settlement, but later may indirectly increase barnacle growth rate by reducing ephemeral algae. It is suggested that periwinkle density may be a key factor in the population dynamics of *S. balanoides* on intertidal mussel beds in the Wadden Sea.

Introduction

The Wadden Sea is one of the largest coastal soft bottom habitats in the world. In contrast to rocky shores, it is dominated by rather unstable sediments, and primary hard substrata for colonization of sessile epifauna and macroalgae are generally rare. However, epibenthic mussel beds of *Mytilus edulis* L. provide a widely available substratum for epibionts (aggregations of live blue mussels and shell fragments form three-dimensional structures within otherwise macroscopically unstructured mud and sandflats). This secondary hard substratum is utilized by a large number of sessile epifauna and algae (Sebens, 1982; Matsumasa & Nishihira, 1994; Albrecht, 1998).

On rocky shores, herbivorous grazers are very important in structuring patterns of distribution and abundance of algae (e.g. Lubchenco, 1978; Lubchenco & Gaines, 1981; Hawkins & Hartnoll, 1983; Janke,

1990; Vadas, 1992; Anderson & Underwood, 1997; Kim, 1997). Removal of algae by grazing activity causes direct and indirect effects on other sessile organisms (e.g. Petraitis, 1983, 1987; Bertness, 1984; Dungan, 1986, 1987; Vadas, 1992; Anderson & Underwood, 1997; Kim, 1997). For example, Van Tamelen (1987) showed that removal of algae by gastropod grazers indirectly led to higher recruitment of barnacles. On mussel beds in the Wadden Sea, grazing periwinkles, *Littorina littorea* (L.), achieve high densities of hundreds of snails per m² (Wilhelmsen & Reise, 1994). Their grazing pressure limits the distribution of ephemeral macroalgae which are generally rare in this habitat (Albrecht, 1998). Grazing and bulldozing by herbivorous snails was also found to be a mortality factor in young balanids (Connell, 1961; Dayton, 1971; Denley & Underwood, 1979; Hawkins, 1983; Underwood et al., 1983; Petraitis, 1983; Farrell, 1988; Miller & Carefoot, 1989). Nevertheless,

intertidal mussel beds are often strongly overgrown by the barnacle *Semibalanus balanoides* L. The extent of barnacle epigrowth, however, shows strong temporal variation and differs widely between years (pers. obs.).

The aim of this study was to test the hypothesis that these activities of *L. littorea* would reduce survival of recently-settled barnacles on mussel beds in the Wadden Sea. In this case, inter-annual fluctuations in snail densities may be responsible for different barnacle settlement success. However, recently-settled barnacles may grow very fast (Bertness, 1984; Luther, 1987) and, within a short time period, attain a size refuge that protects them from grazing and bulldozing activity (Denley & Underwood, 1979). Then, the snails may actually have positive effects on the barnacles because their grazing activity suppresses algal epigrowth which may have disadvantageous effects for balanids (Crisp, 1960). Therefore, it was hypothesized that exclusion of snails would facilitate the development of ephemeral algae on mussel shell surfaces and that increasing algal epigrowth would reduce barnacle growth rate. Thus, the effect of periwinkle activity would then switch from a direct negative effect on early stages towards an indirect positive effect on the growth rate of balanids that had attained a size refuge from grazing and bulldozing pressure.

Material and methods

Study area

Investigations were carried out in Königshafen, a shallow tidal bay of about 4.5 km², north of the island of Sylt in the North Sea (55° 02' N, 08° 26' E) (Fig. 1). Sandy dunes form the northern and western boundary of the bight while it is limited by dikes in the south. The tidal water enters the bight through a tidal channel in an east-west direction. Due to aerial input of dune sand, the sediment is relatively coarse grained compared with other intertidal areas of the north German Wadden Sea. The area belongs to the cold temperate region with a mean annual water temperature of about 9 °C, a summer average of 15 °C, and a winter average of 4 °C. The tides are semidiurnal and average tidal range is about 1.8 m. Salinity remains close to 30 psu. Further information about hydrography, geology, sediments and biota of the study area is given elsewhere (Reise, 1985; G. Austen, 1994; I. Austen, 1994; Bayerl & Higelke, 1994; Reise et al., 1994).

Intertidal mussel beds cover 1% of the intertidal area of Königshafen and are partly covered by the

brown algae *Fucus vesiculosus* forma *mytili* (Nienburg), which lacks a holdfast and reproduces only vegetatively (Albrecht, 1998). In general, large mussels (>45 mm shell length) are located in the top layer of the mussel beds and are often heavily overgrown by balanids. Smaller and newly-settled mussels (shell length ≤45 mm) are situated underneath and are attached to the byssus threads of the large mussels. Finally, many small mussels stick in sediment which is finer than in the surrounding tidal flats (Albrecht, 1994; Okun, 1999) due to biodeposit accumulation (Dittmann, 1987).

In the northern Wadden Sea, the periwinkle *L. littorea* achieves high abundance in these mussel beds. Average densities are about 400 m⁻² (Reise et al., 1994) but, in some years, they are far more abundant. Ephemeral algae are dominated by different *Enteromorpha* species. These are restricted to intertidal flats and rarely occur on mussel beds due to high periwinkle grazing pressure (Wilhelmsen & Reise, 1994; Albrecht, 1998). Growth of ephemeral algae starts mostly in the beginning of June after the settlement of *S. balanoides* in April and May (Luther, 1987).

Extent of barnacle overgrowth on intertidal mussel beds

From June 1998 to August 1999, the extent of *Semibalanus balanoides* was examined on an intertidal mussel bed located north of the tidal channel (Fig. 1). Species composition and abundance of mussels in this bed did not differ from other mussel beds in the Königshafen area. Samples were taken in June and September 1998, and in March, May and August 1999 using a box corer of 400 cm² (sampling depth of 25 cm). At each sampling, six replicates were taken. In the laboratory, samples were washed over a 1000 µm sieve, and mussels and *L. littorea* were counted. Afterwards, barnacle epigrowth was removed from the mussels and barnacles, and *M. edulis* were dried separately (3 days, 75 °C) to a constant weight. Dry weight of mussels and barnacle overgrowth was determined to the nearest 0.01 g. However, only *M. edulis* with a shell length >45 mm were examined because smaller mussels were not overgrown by barnacles. The commencement of barnacle settlement on mussels was noted.

Grazing experiments

The influence of periwinkles on the abundance of recently-settled barnacles on mussel shell surfaces was

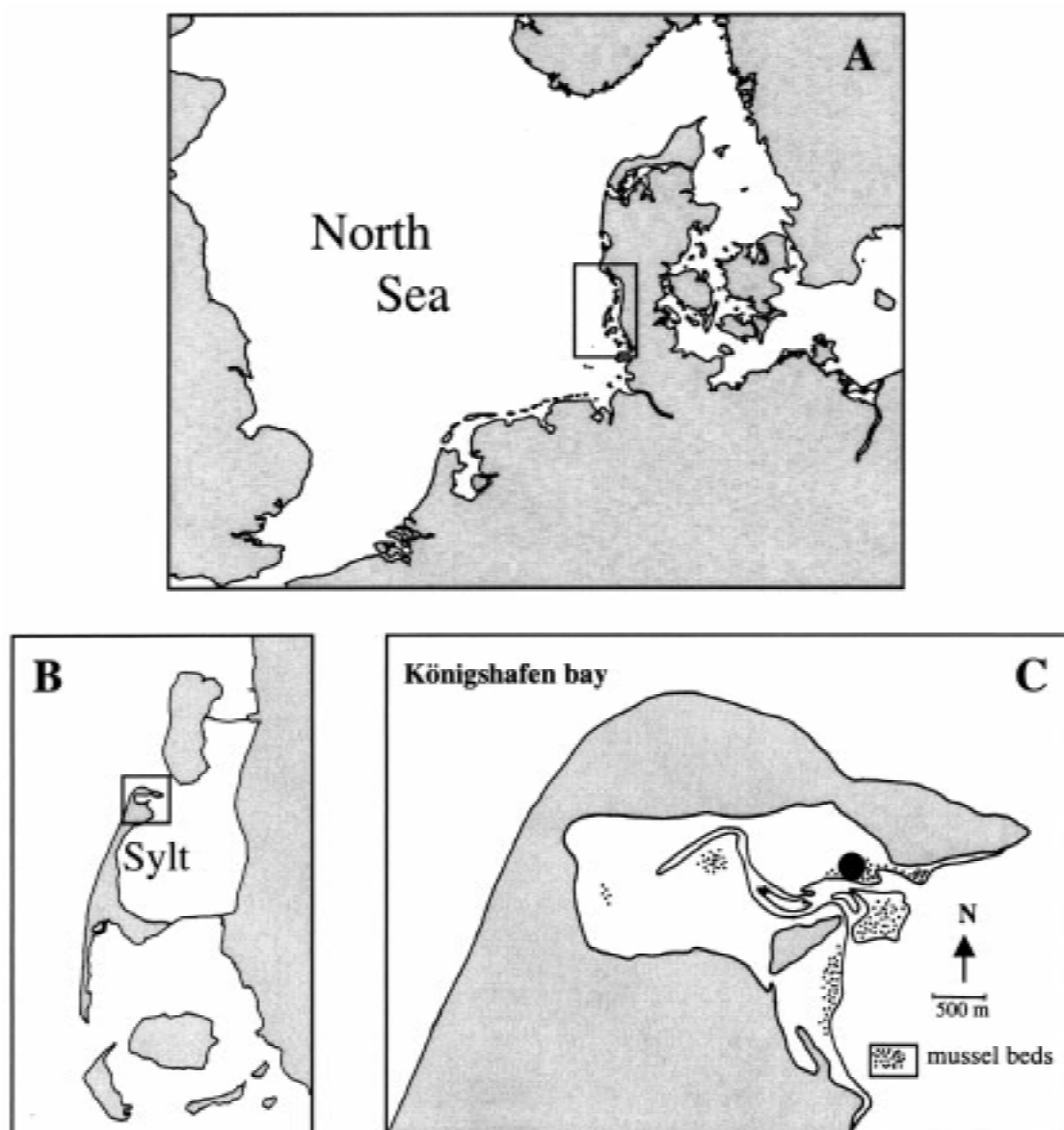


Figure 1. Location of the study area: the Königshafen bay (C) in the north of the island of Sylt (B) in the North Sea (A). Investigation site is marked by a black circle.

investigated by grazer exclusion experiments on the same intertidal bed of *Mytilus edulis* where barnacle overgrowth was determined. To keep snail densities constant, circular cages (25 cm high, 20 cm in diameter) with walls made of $6 \times 6 \text{ mm}^2$ rust resistant wire netting were used. The upper and lower end of the cages were stabilized with a plastic ring (20 cm in diameter). Roofed cages were used to prevent snail migration. On 20 March, 1999 (i.e. before settlement of barnacles), the cages were fixed carefully to the mussel bed using three iron rods per cage (50 cm

length; 6 mm in diameter). Care was taken to prevent periwinkles from passing underneath the cages. Caged mussels were cleaned of any epigrowth using a knife. The experiment included six treatments:

1. no snails in the cages;
2. reduced natural density of *L. littorea* (20 snails per cage corresponding to a density of approximately 650 m^{-2});
3. natural (ambient) snail density of March 1999 (50 snails per cage; $\sim 1500 \text{ snails m}^{-2}$); and

4. three fold natural density (150 *L. littorea* per cage; 4500 snails per m²).

Two treatments served as a control of possible cage artefacts:

5. open cages with walls which left a 10 cm space above the ground so that snails could freely pass into and out of the treated area; and
6. untreated areas of the same size as cages.

Each treatment was replicated 6-fold with a random distribution on the mussel bed. On 13/14 May 1999 (after an experimental period of 8 weeks), when most barnacles had settled, barnacle epigrowth in the cages was determined. This was done using a clear sheet of pvc which was pierced by 100 randomly distributed holes each of 4 mm diameter, resembling the design used by Bertness (1984). The sheet had the same diameter as the cages, and was placed on the top of the cage after removing the roof and enclosed snails. Percent cover of the barnacle epigrowth on caged mussels was obtained by counting the holes with balanids visible underneath. The barnacle percent cover per cage was a rough estimate of barnacle abundance.

Periwinkle grazing effect on different barnacle size classes

A laboratory experiment was performed to test at which size newly-settled *S. balanoides* are protected against grazing pressure of *L. littorea*. Five size classes of barnacles were tested (each 6-fold replicated):

1. attached but not metamorphosed cypris larvae;
2. freshly metamorphosed barnacles with a basal shell diameter of 0.3–0.5 mm;
3. barnacles with basal shell diameter of about 1 mm;
4. barnacles with basal shell diameter of 2–3 mm; and
5. barnacles with a basal shell diameter of 5 mm.

For this experiment, overgrown mussels with a shell size of 50–60 mm were collected in the field and all barnacles were removed except for one size class. The number of the remaining barnacles was counted (10–15 barnacles per mussel) and each mussel was transferred to an aquarium (18 cm length, 12 cm width, 12 cm height) filled with a 2-cm layer of sandy sediment and a 10-cm layer of filtered seawater. Two specimens of *L. littorea* were added to each aquarium (containing a single mussel). A circular fence made of galvanized 6 × 6 mm² wire netting surrounded the mussel and the two periwinkles, preventing escape of the snails because they avoid contact with galvanized

surfaces (Bertness, 1984). As a control, the same experiment was repeated without snails. The experiment started on 13 May, 1999. The number of barnacles remaining per mussel was counted after 24 h.

Exclusion of grazers

The effect of *L. littorea* on algal development and barnacle growth rates was tested by a further field experiment using the same cages as before (25 cm high, 20 cm in diameter). On 24 June, 1999, cages were fixed on a tidal flat with mussel clusters near the investigated mussel bed. Each cage contained seven mussels (shell size: 50–60 mm) with 10–15 barnacles per mussel and no algal epiphytes initially. The number of barnacles per cage was counted and the rostro-carinal length of the barnacle apertures was measured to the nearest 0.01 mm using a stereo microscope with ocular micrometer. At the beginning of the experiment, barnacle apertures had a length of 2.00–3.00 mm. There were three treatments, each replicated 6-fold:

1. cages with barnacle overgrown mussels and 20 snails added;
2. cages with barnacle overgrown mussels but without snails; and
3. cages in which barnacle overgrown mussels were cleaned of algal epiphytes by hand. This was done using a brush and a sponge at weekly intervals. All snails were removed from these cages at the beginning of the experiment.

The last treatment served as a control to test if it was really the cleaning activity of snails that influences algal development and barnacle growth. On 26 September 1999 (after an experimental period of 13 weeks), apertures of barnacles were measured and coverage by ephemeral algae of each mussel shell surface was estimated to the nearest 10%. To determine barnacle mortality, the number of live balanids was counted.

Statistical analysis

Results were calculated as mean values with standard deviation ($\bar{x} \pm \text{SD}$). All experiments were analysed by means of analysis of variance (ANOVA). Cochran's test was used to test for homoscedasticity of variances. Different levels within a significant experimental factor were analysed using Tukey's Honest-Significant-Difference (HSD) multiple com-

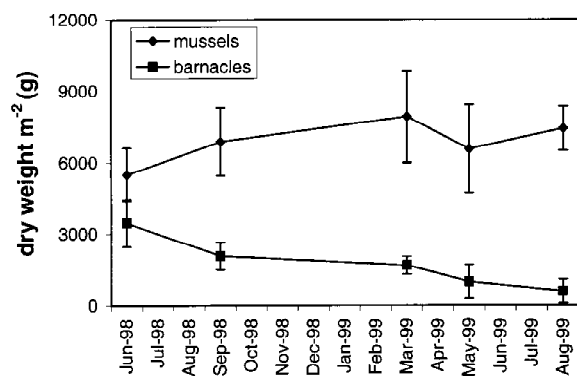


Figure 2. Dry weight of mussels and barnacle overgrowth (means of six replicates \pm SD) over the investigation period from June 1998 to August 1999.

parison test. Data of all experiments were homoscedastic in variance except for the estimation of algae percent cover in the grazing exclusion experiment. The data of this experiment were arcsine transformed to eliminate heterogeneity of variance. Effects were considered to be statistical significant, if p -value was <0.05 .

Results

Extent of barnacle overgrowth

On the investigated mussel bed, overgrowth of *S. balanoides* was present throughout the 14 month investigation period. In June 1998, barnacles occurred on $91.9 (\pm 6.3)\%$ of the large sized mussels (>45 mm) and barnacle dry weight reached $65.2 (\pm 21.5)\%$ of mussel dry weight. However, the extent of barnacle overgrowth strongly decreased from $3445 (\pm 978)$ g m $^{-2}$ dry weight at the beginning of the investigation period (June 1998) to $589 (\pm 496)$ g m $^{-2}$ in August 1999 (Fig. 2). In contrast, mussel dry weight (mean over investigation period 6855 ± 924 g m $^{-2}$) and density [mean $461 (\pm 96)$ m $^{-2}$] did not show this tendency indicating that a fluctuation in available shell surface was not responsible for decreasing barnacle overgrowth. Mean density of *L. littorea* was $1240 (\pm 553)$ m $^{-2}$ with highest densities in spring [$1842 (\pm 362)$ m $^{-2}$ in 1998 and $1739 (\pm 356)$ m $^{-2}$ in 1999] shortly after barnacle settlement.

Grazing effects on newly-settled barnacles

Experimental manipulation of snail density resulted in a significant correlation between snail density and

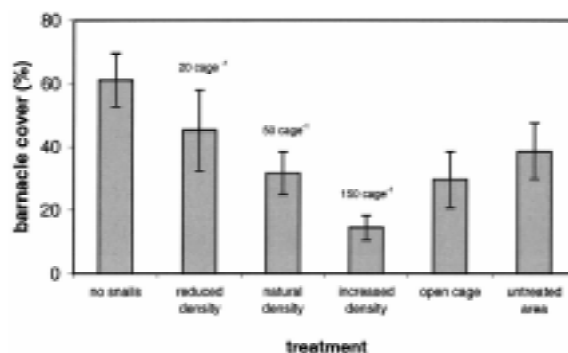


Figure 3. Mean percentage barnacle cover (\pm SD) ($n = 6$ cages) on blue mussels *Mytilus edulis* in treatments with different densities of *Littorina littorea* after an experimental period of 8 weeks.

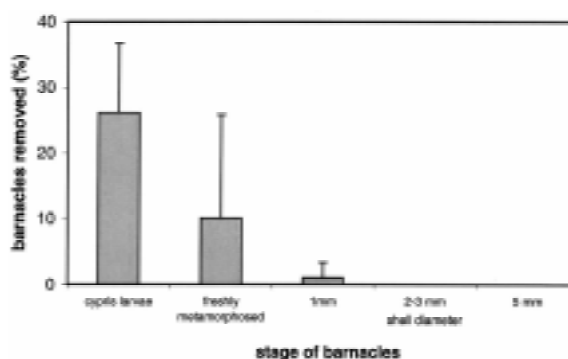


Figure 4. Percentage of barnacles (\pm SD) ($n = 6$ aquaria) of different size classes removed by *Littorina littorea* after 24 hours.

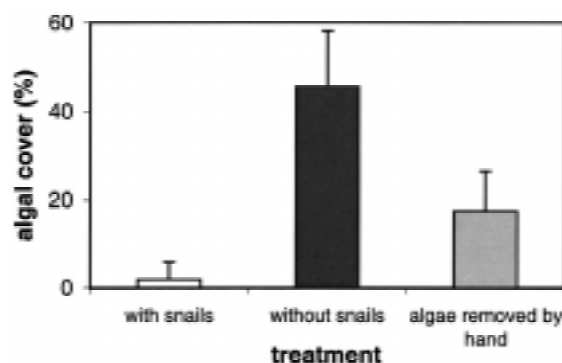


Figure 5. Mean percent of algal cover (\pm SD) ($n = 6$ cages) on blue mussels *Mytilus edulis* in three different treatments.

barnacle percent cover in the cages (one-way ANOVA, $F = 34.027$, $df = 3$, $p < 0.0001$) (Fig. 3). The highest percentage of barnacles became established in the absence of periwinkles, and increasing snail numbers coincided with decreasing barnacle percent cover. The mean percentage of recently-settled barnacles differed significantly between the four ex-

perimental snail density levels (Tukey's test, $p < 0.05$). The barnacle epigrowth in open cages and the untreated areas did not differ from the cages with a natural density (50 snails cage⁻¹) of periwinkles (one-way ANOVA, $F = 1.963$, $df = 2$, $p = 0.175$). Thus, cage artefacts were not detected.

Grazing effects on barnacle size classes

Barnacle survival in the presence of periwinkles depended significantly on barnacle shell size (one-way ANOVA, $F = 10.404$, $df = 4$, $p < 0.0001$) (Fig. 4). In the laboratory, highest removal of barnacles occurred in attached but not metamorphosed cypris larvae and differed significantly from all other levels of size (Tukey's test, $p < 0.03$). Removal of metamorphosed balanids decreased with increasing shell size but differences were not significant (Tukey's test, $p > 0.05$). The presence of periwinkles did not affect barnacles > 2 mm shell size. In the control experiments without *L. littorea*, no barnacles disappeared.

Exclusion of grazers and cascading effects on algal development and barnacle growth rate

Algal overgrowth

After 13 weeks, the percentage cover of algae on mussels and attached balanids significantly differed over the three treatments (one-way ANOVA, $F = 183.477$, $df = 2$, $p < 0.0001$, followed by Tukey's test, $p < 0.001$) (Fig. 5). Algal development was highest in snail exclusion cages ($45.56 \pm 12.51\%$) and the lowest percentage cover occurred in the treatment with added periwinkles ($1.85 \pm 3.96\%$) (Fig. 6). Mussels cleaned of epigrowth by hand showed an intermediate growth of algae ($17.41 \pm 9.03\%$), indicating that experimental cleaning activity was less effective than that of *L. littorea*.

Growth rate of barnacles

After the experimental period of 13 weeks, mean growth of balanids in the presence of *L. littorea* was $1.62 (\pm 0.23)$ mm. This was significantly higher than growth of barnacles in the absence of snails (1.27 ± 0.19 mm) (one-way ANOVA, $F = 4.9854$, $df = 2$, $p = 0.0218$, followed by Tukey's test, $p = 0.0178$) (Fig. 7). Weekly removal of algae by hand resulted in intermediate barnacle growth of $1.48 (\pm 0.14)$ mm. Differences were not significant compared to the treatments with and without snails (Tukey's test, $p > 0.05$). No differences were found in barnacle mortality (one-way ANOVA, $F = 0.8498$, $df = 2$, $p = 0.4471$). The

mortality rate ranged from 40 to 50% in all three treatments.

Discussion

Seasonal variation of barnacle epigrowth

The barnacle *Semibalanus balanoides* occurs frequently on epibenthic mussel beds in the northern Wadden Sea and, in some years, intertidal mussel beds may be completely covered by barnacle epigrowth (pers. obs.). In June 1998, the extent of barnacle overgrowth reached 65% of mussel dry weight, but decreased to only 8% of mussel dry weight by August 1999. The high density of balanids in 1998 resulted from a strong barnacle settlement in spring 1996 while settlement success was much lower in the following 3 years (pers. obs.). The decreasing abundance of *S. balanoides* from 1998 to 1999 indicates that the barnacle recruitment in these years was not high enough to balance mortality. Such annual variations in recruitment of *S. balanoides* are also reported from other areas (Kendall et al., 1985; Carroll, 1996).

In the present study, the cage experiments demonstrated a strong negative correlation between recruitment of *S. balanoides* on mussel beds and abundance of *L. littorea*. Barnacle percent cover decreased significantly with increasing snail densities in the cages. Abundance of periwinkles on intertidal mussel beds may vary strongly between years (Wilhelmsen & Reise, 1994; Nicolaysen, 1996; Fenske, 1997). This may be a consequence of variations in snail recruitment, varying predation intensity (e.g. by crabs; Scherer & Reise, 1981), or parasitic infestation (Lauckner, 1984). Interestingly, according to Buschbaum & Reise (1999), the barnacle cover on periwinkle shells had a negative effect on snail survival and fecundity, and is, therefore, regarded as a further important factor influencing the population dynamics of *L. littorea*. Although there are no long-term observations on the relationship of snail abundances to the extent of barnacle overgrowth on mussel beds, the strong interaction of snail density and barnacle epigrowth found in this investigation suggests that fluctuating snail densities may be an important factor in interannual variation of *S. balanoides* overgrowth on intertidal mussel beds in the Wadden Sea.

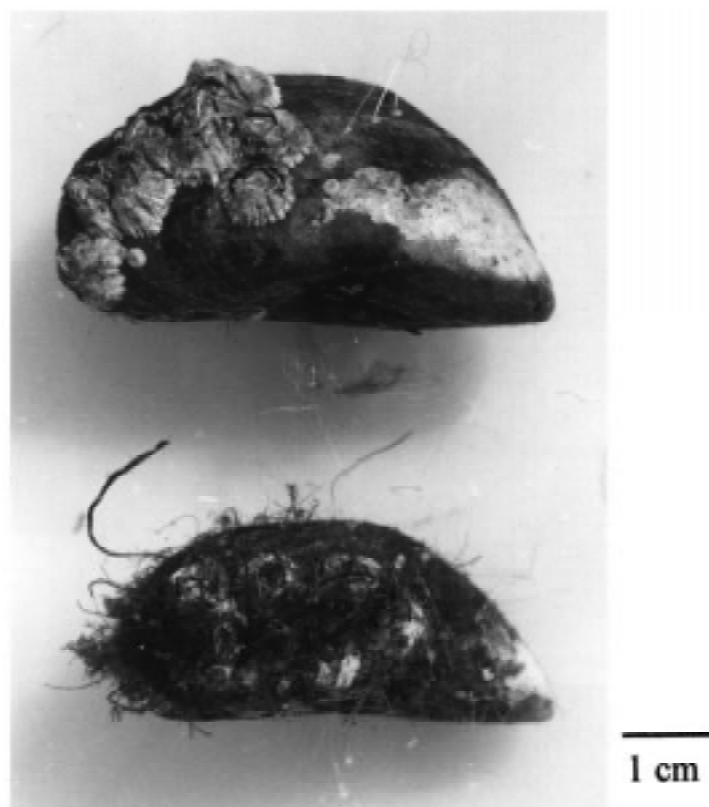


Figure 6. Extent of algal overgrowth on blue mussels *Mytilus edulis* in the cages with *Littorina littorea* (above) and in snail exclusion cages (below) after an experimental period of 13 weeks.

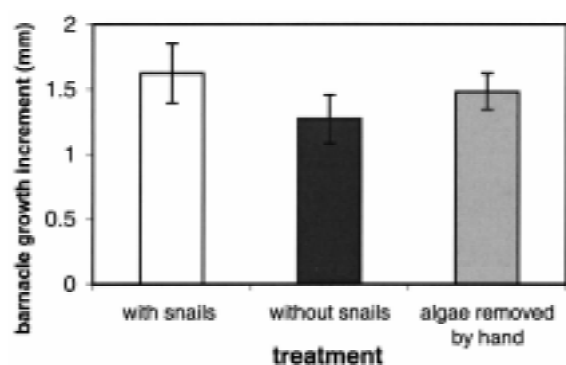


Figure 7. Mean barnacle growth increment \pm SD ($n = 6$ cages) over an experimental period of 13 weeks. Growth rate was highest in the presence of *Littorina littorea*.

Negative effects of *Littorina littorea* on survival of recently-settled barnacles

Littorina littorea is a herbivorous snail, feeding mainly on early successional or ephemeral algae among which different *Enteromorpha* and *Ulva* species are preferred

(Lubchenco, 1978; Watson & Norton, 1985; Imbrie et al., 1989; Norton et al., 1990; Wilhelmsen & Reise, 1994). Thus, periwinkle grazing activity reduces the development of ephemeral algae on intertidal mussel beds (Wilhelmsen & Reise, 1994; Albrecht, 1998). However, herbivorous snails may also have deleterious effects on sessile organisms outside their food spectrum (e.g. Dayton, 1971; Denley & Underwood, 1979; Menge et al., 1986; Petraitis, 1987; Farrell, 1988; Miller & Carefoot, 1989). These include the inadvertent dislodgement and consumption of settled larvae as the snails browse across the mussel shell surface (Denley & Underwood, 1979; Petraitis, 1987; Farrell, 1988; Miller & Carefoot, 1989), and the bulldozing of newly-settled larvae from their substratum by pushing and dislodging them with their foot, mouth, shell or tentacles (Dayton, 1971; Miller & Carefoot, 1989). This may explain how the grazing activity of the periwinkle *L. littorea* on mussel shell surfaces may have reduced survival of recently-settled barnacles in the present study.

Reaching a basal shell diameter of 2 mm, *S. balanoides* were no longer affected by the activity of *L. littorea*. This size is within the range of 2–4 mm estimated by Dayton (1971) to be a minimum size refuge for *Balanus glandula* (Darwin) from bulldozing by limpets, and is similar to the range of 3–4 mm estimated by Denley & Underwood (1979) as a minimum size refuge for *Tesseropora rosea* (Krauss) from mortality caused by *Cellana tramoserica* (Sowerby). Thus, on intertidal mussel beds, direct effects of *L. littorea* on barnacle epigrowth may be confined to the period of larval settlement and early stages after metamorphosis. *Semibalanus balanoides* achieve a shell diameter of 2 mm after approximately two weeks (Bertness, 1984), after which they were no longer vulnerable to the grazing activity of *L. littorea*.

Positive effects of periwinkle grazing on barnacle growth

The grazing activity by periwinkles prevented dense ephemeral algae epigrowth. Indirectly, this increased barnacle growth rate, because barnacle feeding was hindered by the presence of algae epiphytes. Direct observations showed that the opening of barnacle opercula was not hindered by algal epigrowth but that the feeding activity of the setose cirri was hampered. Algal epiphytes may also reduce the water current which may result in a restricted food supply for barnacles (Crisp, 1960). In addition, removal of gastropod grazers may lead to an accumulation of sediment (Bertness, 1984; Anderson & Underwood, 1997) which was also apparent in the treatments within snail-free cages in the present study. This sediment layer may impair living conditions for filter feeders and was supposed to be a mortality factor in balanids (Bertness, 1984). However, barnacles may survive for long periods without feeding (Barnes et al., 1963; Barnes & Barnes, 1967). This may be the reason why, in this study, barnacles covered by algal epigrowth did not show a higher mortality rate than uncovered *S. balanoides*. Nevertheless, the low growth might indicate a reduced fitness and cause a higher mortality in winter and a lower reproductive output in the next spring. Considering the direct negative effects of grazing on barnacle settlement and the indirect positive effects on barnacle growth, best living conditions for barnacles are expected to occur at intermediate periwinkle densities.

Conclusions

Many factors affect the population dynamics of *Semibalanus balanoides*. Barnacle settlement may be limited by planktonic larval supply (Bertness et al., 1992), while bioorganic films developed on the attachment surface influence settlement of barnacle cypris larvae (Maki et al., 1988; Keough & Raimondi, 1995). On rocky shores, Jernakoff (1985) and Jenkins et al. (1999) showed that newly-settled barnacles are hindered in early recruitment by algal epigrowth. As the barnacles grow, predation and competition for space become increasingly important. On intertidal mussel beds, however, these two factors may be of minor importance for barnacle density, because predation by epibenthic predators such as shore crabs *Carcinus maenas* (L.) and starfish *Asterias rubens* L. seem to be important only in the adjacent subtidal zone (Buschbaum, unpublished). Since *S. balanoides* settle earlier in the year than ephemeral algae, and other sessile invertebrates are not common, interspecific competition for space can be disregarded. Therefore, the negative relationship between *L. littorea* density and barnacle percent cover on mussel shell surfaces found in this investigation indicates that grazing activity of periwinkles is a very important factor in settlement and post-settlement processes structuring barnacle distribution on intertidal mussel beds in the Wadden Sea.

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References

- Albrecht, A. S., 1994. Effects of *Fucus vesiculosus* covering intertidal mussel beds in the Wadden Sea. *Helgoländer Meeresunters.* 48: 243–256.
- Albrecht, A. S., 1998. Soft bottom versus hard rock: community ecology of macroalgae on intertidal mussel beds in the Wadden Sea. *J. exp. mar. Biol. Ecol.* 229: 85–109.

- Anderson, M. J. & A. J. Underwood, 1997. Effects of gastropod grazers on recruitment and succession of an estuarine assemblage: a multivariate and univariate approach. *Oecologia* 109: 442–453.
- Austen, G., 1994. Hydrodynamics and particulate matter budget of Königshafen, southeastern North Sea. *Helgoländer Meeresunters.* 48: 183–200.
- Austen, I., 1994. The surficial sediments of Königshafen variations over the past 50 years. *Helgoländer Meeresunters.* 48: 163–171.
- Barnes, H. & M. Barnes, 1967. The effect of starvation and feeding on the production of egg masses in the boreo-arctic cirripede *Balanus balanoides* (L.). *J. exp. mar. Biol. Ecol.* 1: 1–6.
- Barnes, H., M. Barnes & D.M. Finlayson, 1963. The metabolism during starvation of *Balanus balanoides*. *J. mar. biol. Ass. U.K.* 43: 213–223.
- Bayerl, K. A. & B. Higelke, 1994. The development of northern Sylt during the last Holocene. *Helgoländer Meeresunters.* 48: 145–162.
- Bertness, M. D., 1984. Habitat and community modification by an introduced herbivorous snail. *Ecology* 65: 370–381.
- Bertness, M. D., S. D. Gaines, E. G. Stephens & P. O. Yund, 1992. Components of recruitment in populations of the acorn barnacle *Semibalanus balanoides* (Linnaeus). *J. exp. mar. Biol. Ecol.* 156: 199–215.
- Buschbaum, C. & K. Reise, 1999. Effects of barnacle epibionts on the periwinkle *Littorina littorea* (L.). *Helgol. Mar. Res.* 53: 56–61.
- Carroll, M. L., 1996. Barnacle population dynamics and recruitment regulation in southcentral Alaska. *J. exp. mar. Biol. Ecol.* 199: 285–302.
- Connell, J. H., 1961. Effects of competition, predation by *Thais lapillus*, and other factors on natural populations of the barnacle *Balanus balanoides*. *Ecol. Monogr.* 31: 61–104.
- Crisp, D. J., 1960. Factors influencing growth-rate in *Balanus balanoides*. *J. anim. Ecol.* 29: 95–116.
- Dayton, P. K., 1971. Competition, disturbance and community organizations: the provision and subsequent utilization of space in a rocky intertidal community. *Ecol. Monogr.* 41: 351–389.
- Denley, E. J. & A. J. Underwood, 1979. Experiments on factors influencing settlement, survival and growth of two species of barnacles in New South Wales. *J. exp. mar. Biol. Ecol.* 36: 269–293.
- Dittmann, S., 1987. Die Bedeutung der Biodeposite für die Benthosgemeinschaft der Wattsedimente. Unter besonderer Berücksichtigung der Miesmuschel *Mytilus edulis* L. PhD thesis, University of Göttingen, Germany, 182 pp.
- Dungan, M. L., 1986. Three-way interactions: barnacles, limpets and algae in a sonoran desert rocky intertidal zone. *Am. Nat.* 127: 292–316.
- Dungan, M. L., 1987. Indirect mutualism: complementary effects of grazing and predation in a rocky intertidal community. In Kerfoot, W. C. & A. Sih (eds), *Predation: Direct and Indirect Impacts on Aquatic Communities*. University Press of New England, Hanover, NH: 188–200.
- Farrell, T. M., 1988. Community stability: effects of limpet removal and reintroduction in a rocky intertidal community. *Oecologia* 75: 190–197.
- Fenske, C., 1997. The importance of intraspecific competition in a *Littorina littorea* population in the Wadden Sea. *Hydrobiologia* 355: 29–39.
- Hawkins, S. J., 1983. Interactions of *Patella* and macroalgae with settling *Semibalanus balanoides*. *J. exp. mar. Biol. Ecol.* 71: 55–72.
- Hawkins, S. J. & R. G. Hartnoll, 1983. Grazing of intertidal algae by marine invertebrates. *Oceanogr. Mar. Biol. Annu. Rev.* 21: 195–282.
- Imbrie, D. W., S. J. Hawkins & C. R. McCrohan, 1989. The olfactory-gustatory basis of food preference in the herbivorous prosobranch, *Littorina littorea* (Linnaeus). *J. Moll. Stud.* 55: 217–225.
- Janke, K., 1990. Biological interactions and their role in community structure in the rocky intertidal of Helgoland (German Bight, North Sea). *Helgoländer Meeresunters.* 44: 219–263.
- Jenkins, S. R., T. A. Norton & S. J. Hawkins, 1999. Settlement and post-settlement interactions between *Semibalanus balanoides* (L.) (Crustacea: Cirripedia) and three species of furoid canopy algae. *J. exp. mar. Biol. Ecol.* 236: 49–67.
- Jernakoff, P., 1985. The effect of overgrowth by algae on the survival of the intertidal barnacle *Tesseropora rosea* Krauss. *J. exp. mar. Biol. Ecol.* 94: 89–97.
- Kendall, M. A., R. S. Bowman, P. Williamson & J. R. Lewis, 1985. Annual variation in the recruitment of *Semibalanus balanoides* on the North Yorkshire coast. *J. mar. biol. Ass. U.K.* 65 (4): 1009–1030.
- Keough, M. J. & P. T. Raimondi, 1995. Responses of settling invertebrate larvae to bioorganic films: effects of different types of films. *J. exp. mar. Biol. Ecol.* 185: 235–253.
- Kim, J. H., 1997. The role of herbivory, and direct and indirect interactions, in algal succession. *J. exp. mar. Biol. Ecol.* 217: 119–135.
- Lauckner, G., 1984. Impact of trematode parasitism on the fauna of a North Sea tidal flat. *Helgoländer Meeresunters.* 37: 185–199.
- Lubchenco, J., 1978. Plant species diversity in a marine intertidal community: Importance of herbivore food preference and algal competitive abilities. *Am. Nat.* 112: 23–39.
- Lubchenco, J. & S. D. Gaines, 1981. A unified approach to marine plant-herbivore interactions. I. Populations and communities. *Ann. Rev. Ecol. Syst.* 12: 405–437.
- Luther, G., 1987. Seepocken der deutschen Küstengewässer. *Helgoländer Meeresunters.* 41: 1–43.
- Maki, J. S., D. Ritschoff, J. D. Costlow & R. Mitchell, 1988. Inhibition of attachment of larval barnacles, *Balanus amphitrite*, by bacterial surface films. *Mar. Biol.* 97: 199–206.
- Matsumasa, M. & M. Nishihira, 1994. Habitat structure provided by *Mytilus edulis* and the modification by sessile inhabitants. *Bull. Mar. Biol. Stn. Asamushi* 19: 51–63.
- Menge, B. A., J. Lubchenco & L. R. Ashkenas, 1986. Experimental separation of effects of consumers on sessile prey in the low zone of a rocky shore in the Bay of Panama: direct and indirect consequences of food web complexity. *J. exp. mar. Biol. Ecol.* 100: 225–269.
- Miller, K. M. & T. H. Carefoot, 1989. The role of spatial and size refuges in the interaction between juvenile barnacles and grazing limpets. *J. exp. mar. Biol. Ecol.* 134: 157–174.
- Nicolaysen, M., 1996. Die Bedeutung von Seegraswiesen (*Zostera noltii*) für die Strandschnecke (*Littorina littorea* L.) im Nordsylter Wattenmeer. MSc thesis, University of Kiel, Germany, 67 pp.
- Norton, T. A., S. J. Hawkins, N. L. Manley, G. A. Williams & D. C. Watson, 1990. Scraping a living: a review of littorinid grazing. *Hydrobiologia* 193: 117–138.
- Okun, N., 1999. Einfluß der Sedimentation auf die Miesmuschel (*Mytilus edulis* L.). MSc thesis, University of Hamburg, Germany, 68 pp.
- Petraitis, P. S., 1983. Grazing patterns of the periwinkle and their effect on sessile intertidal organisms. *Ecology* 64: 522–533.

- Petraitis, P. S., 1987. Factors organizing rocky intertidal communities of New England: herbivory and predation in sheltered bays. *J. exp. mar. Biol. Ecol.* 109: 117–136.
- Reise, K., 1985. Tidal flat ecology. Springer, Berlin, 191 pp.
- Reise, K., E. Herre & M. Sturm, 1994. Biomass and abundance of macrofauna in intertidal sediments of Königshafen in the northern Wadden Sea. *Helgoländer Meeresunters.* 48: 201–215.
- Scherer, B. & K. Reise, 1981. Significant predation on micro- and macrobenthos by the crab *Carcinus maenas* L. in the Wadden Sea. *Kieler Meeresforsch., Sonderh.* 5: 490–500.
- Sebens, K. P., 1982. Competition for space: growth rate, reproductive output, and escape in size. *Am. Nat.* 120: 189–197.
- Underwood, A. J., E. J. Denley & M. J. Moran, 1983. Experimental analyses of the structure and dynamics of mid-shore rocky intertidal communities in New South Wales. *Oecologia* 56: 202–219.
- Vadas, R. L., 1992. Littorinid grazing and algal patch dynamics. In Grahame, J., Mill, P. J., Reid, D. G. (eds), *Proceedings of the Third International Symposium on Littorinid Biology* 197–209.
- Van Tamelen, P. G., 1987. Early successional mechanisms in the rocky intertidal: the role of direct and indirect interactions. *J. exp. mar. Biol. Ecol.* 112: 39–48.
- Watson, D. C. & T. A. Norton, 1985. Dietary preferences of the common periwinkle *Littorina littorea* (L.). *J. exp. mar. Biol. Ecol.* 88: 193–211.
- Wilhelmsen, U. & K. Reise, 1994. Grazing on green algae by the periwinkle *Littorina littorea* in the Wadden Sea. *Helgoländer Meeresunters.* 48: 233–242.