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Predation on barnacles of intertidal and subtidal mussel beds in the Wadden Sea

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Abstract Balanids are the numerically dominant epibionts on mussel beds in the Wadden Sea. Near the island of Sylt (German Bight, North Sea), *Semibalanus balanoides* dominated intertidally and *Balanus crenatus* subtidally. Field experiments were conducted to test the effects of predation on the density of barnacle recruits. Subtidally, predator exclusion resulted in significantly increased abundances of *B. crenatus*, while predator exclusion had no significant effects on the density of *S. balanoides* intertidally. It is suggested that recruitment of *B. crenatus* to subtidal mussel beds is strongly affected by adult shore crabs (*Carcinus maenas*) and juvenile starfish (*Asterias rubens*), whereas recruits of *S. balanoides* in the intertidal zone are mainly influenced by grazing and bulldozing of the very abundant periwinkle *Littorina littorea*, which is rare subtidally. Thus, not only do the barnacle species differ between intertidal and subtidal mussel beds, but the biotic control factors do so as well.

Keywords Barnacles · Predation · Tidal zonation · Grazing and bulldozing

Introduction

Ecological patterns may look similar, however, the underlying causes might be different. For instance, after severe winters, massive recruitment of bivalves was recorded in many parts of the Wadden Sea (Beukema et al. 1998; Strasser 1999). This may, on the one hand, be caused by unusually high larvae production of adult mussels (Beukema et al. 1998; Honkoop and van der Meer 1998). Alternatively, a decrease in predation pres-

sure caused by a delayed appearance of shore crabs *Carcinus maenas* (L.) and shrimp *Crangon crangon* (L.) may result in a better survival of juvenile bivalves (Beukema 1991, 1992; Beukema et al. 1998; Strasser 2000). Both processes may generate the same ecological pattern.

This paper deals with the abundance fluctuations of barnacles (*Semibalanus balanoides* (L.), *Balanus crenatus* Bruguière) which are the most frequent epibionts on intertidal and subtidal beds of *Mytilus edulis* L. in the Wadden Sea (Buschbaum and Saier 2001). Barnacle abundances are known to show high interannual and seasonal fluctuations in both the intertidal (Buschbaum 2000) and subtidal (personal observation) parts of the gradient. Field observations indicated that *S. balanoides* dominated on intertidal and *B. crenatus* on subtidal mussel beds. The aim of this study was to test the hypothesis that different biotic factors in the intertidal and subtidal zone cause barnacle fluctuations. Intertidally, previous experiments have demonstrated that variations in barnacle densities are affected by the grazing and bulldozing activity of the very abundant periwinkle *Littorina littorea* (L.) (Buschbaum 2000). On subtidal mussel beds, however, *L. littorea* is rare (Saier 2000) and thus cannot be responsible for barnacle variability there. As there are no other grazers on fouling organisms on the mussel bed, I suspected that predation might be an effective control on barnacle densities. This has been shown to be of importance for macrofauna in the sediments of the study area (Reise 1977, 1978; Scherer and Reise 1981). Field observations on subtidal mussel beds indicated high densities of adult crabs *Carcinus maenas* (L.) and juvenile starfish *Asterias rubens* L. Both species feed on *S. balanoides* and *B. crenatus* (Ropes 1968; Sloan 1980; Rangeley and Thomas 1987; Leonard et al. 1999; personal observation). I hypothesized that predation might affect abundances of barnacles subtidally, while it is expected to be of minor importance on intertidal mussel beds where crab and starfish densities are lower and feeding time is shorter. Thus, field investigations on the density of the benthic predators *C. maenas* and *A. rubens*

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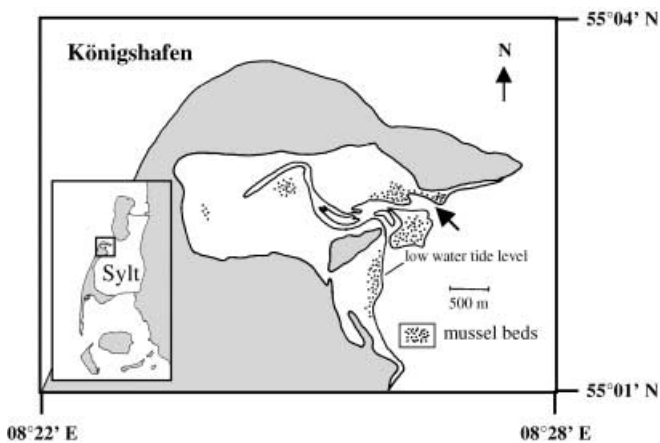


Fig. 1 Tidal flats of Königshafen with mussel beds dotted. Investigations were carried out on a mussel bed north of the main tidal channel (marked by an arrow)

were conducted on intertidal and subtidal mussel beds and predation effects on barnacle abundances were tested by predator exclusion experiments.

Materials and methods

Study area

The study was performed at mussel beds (*M. edulis* L.) located in Königshafen (55°02'N; 008°26'E), a sheltered tidal bay in the north of the island of Sylt (German Bight, Northern Wadden Sea) (Fig. 1). The intertidal zone of Königshafen comprises about 4.5 km². Sandy dunes protect the bight against the prevailing westerly winds. Tides are semi-diurnal with a mean amplitude of 1.8 m. Spring and neap tides differ by <0.2 m, but rare strong easterly winds may lower low tide level by 1 m (Reise et al. 1994). Salinity remains close to 30 psu. Mean annual water temperature is about 9°C, with a summer average of 15°C and a winter average of 4°C. Hydrography, geology and biota are described in detail by Reise (1985), G. Austen (1994), I. Austen (1994), Bayerl and Higelke (1994) and Reise et al. (1994).

The balanids *S. balanoides* and *B. crenatus* are the most abundant epibiont species on mussel beds in the area (Albrecht and Reise 1994; Buhs and Reise 1997; Buschbaum and Saier 2001). The barnacle, *Elminius modestus* Darwin, regularly occurred on mussel beds but in very low abundances since the freezing winter in 1995/96 (personal observation). Beds of *M. edulis* comprise about 1% of the intertidal area of Königshafen (Reise et al. 1994). All investigations were conducted on mussel beds near the main tidal channel (Fig. 1). Mean exposure time of the intertidal beds was about 1.5 h. Subtidal mussel beds are referred to as areas below the mean low water line, occasionally emerging during strong offshore winds for about 20–30 min. The vertical difference between the intertidal and subtidal sites of the investigated mussel bed was about 0.5 m. Mussel beds in the study area are partly covered by the brown algae *Fucus vesiculosus* f. *mytili* (Nienburg) (Albrecht 1998) and harbour a specific faunal assemblage (Albrecht and Reise 1994). Since these algae only occur intertidally, surveys and experiments were limited to mussel bed areas free of *Fucus*.

Abundance estimates of *L. littorea*, *C. maenas* and *A. rubens*

Densities of *L. littorea* on intertidal and subtidal mussel beds were estimated from six replicate samples per tidal level. Sampling was

carried out using a box corer of 315 cm² (sampling depth 10 cm). In the laboratory, the contents were washed through 1 mm meshes and periwinkles were counted. Since the grazing and bulldozing effects of *L. littorea* on barnacle recruitment are confined to the period of larval settlement and early stages after metamorphosis (Buschbaum 2000), snail densities were determined in spring 1999 during the phase of barnacle settlement.

Adult *C. maenas* preferentially inhabit the subtidal parts of the Wadden Sea (Klein-Breteler 1976; Reise and Bartsch 1990; Buhs and Reise 1997). This was also true in the study area where most large *C. maenas* were identified on subtidal mussel beds (personal observations). The distribution patterns of juvenile crabs and of *A. rubens*, which are both known to feed on barnacles (Rangeley and Thomas 1987), were estimated as before using six replicate samples from intertidal and subtidal mussel beds in summer, when predators achieve their highest abundances.

Barnacle percentage cover on intertidal and subtidal mussel beds

The density and zonation of balanids on intertidal and subtidal mussel beds were estimated as percentage cover of *S. balanoides* and *B. crenatus* in both tidal zones in June 1999. A clear sheet of PVC pierced by 100 randomly distributed holes of 4 mm in diameter was placed on the mussel beds and the percentage of both barnacle species was determined by counting the holes with *S. balanoides* and *B. crenatus* visible underneath (six replicates per tidal level). The obtained barnacle percentage was a rough estimate for the abundance of both barnacle species on the mussel beds.

Predator exclusion experiments

The effects of predators on the abundance of barnacles attached to mussel shell surfaces were investigated by predator exclusion experiments. Cylindrical cages (25 cm high, 20 cm in diameter) with walls and roofs made of 6×6 mm rust-resistant wire netting were used. The upper and lower ends of the cages were stabilized with a plastic ring (20 cm in diameter). Before barnacle settlement in March 1999, the cages were fixed on intertidal and subtidal mussel beds using three iron rods per cage (50 cm length; 6 mm in diameter). The cages were anchored 5 cm deep in the mussel bed to prevent predators from passing underneath the cages. All mussels within the cages were cleaned of any epigrowth and crabs and starfish were removed. There were three treatments in each tidal zone: (1) closed cages without predators but with the ambient density of *L. littorea*, (2) uncaged areas of the same size as cages, and (3) open cages with walls which left a 10 cm space above the ground so that predators and snails could freely pass into and out of the treated plot. The last treatment was conducted to check for cage artefacts. Each treatment was replicated six times with a random distribution in the mussel bed.

In the intertidal zone, a further treatment (six replicates) tested whether small *C. maenas* prey on barnacles. The same sized cages as above were used which contained the ambient snail density and ten enclosed juvenile crabs (carapace width 15–30 mm).

At weekly intervals, cages of all treatments were controlled and cleaned, if necessary. After an experimental period of 4 months (in July 1999) the percentage cover of barnacles on the treated areas was determined by using the 'pierced-sheet-method' described above. After removing the roofs and enclosed periwinkles, the sheet was placed on top of the cages and barnacle percentage cover was determined by counting the holes that had living balanids underneath.

Statistical analysis

Results are given as arithmetic means and standard deviations (SD). Differences in densities of *L. littorea*, *C. maenas*, *A. rubens* and barnacle percentage cover between intertidal and subtidal mussel beds were analysed using Mann-Whitney *U*-tests. Data from predator exclusion experiments were subjected to analysis of

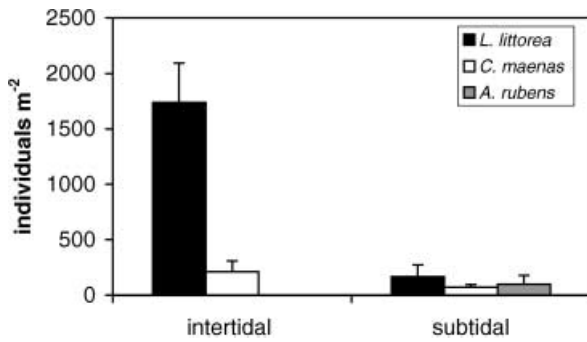


Fig. 2 Average densities (+SD) of *Littorina littorea*, juvenile *Carcinus maenas* (carapace width ≤ 30 mm) and *Asterias rubens* (arm length ≤ 20 mm) on intertidal and subtidal mussel beds

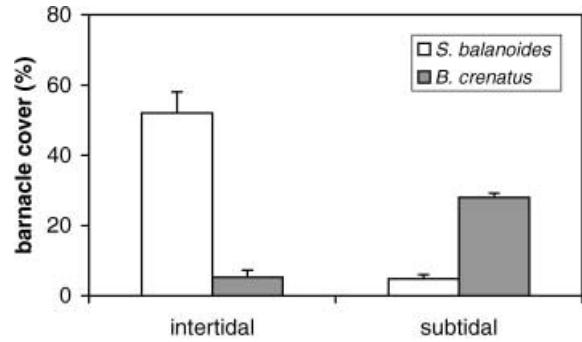


Fig. 3 Mean percentage cover of *Semibalanus balanoides* and *Balanus crenatus* (+SD) on intertidal and subtidal mussel beds

variance (ANOVA). Different levels within a significant experimental factor were analysed using Tukey's honest significant difference (HSD) multiple comparison test. Cochran's test was used to test for homoscedasticity of variances. Data from the cage experiments were heterogeneous in variances and were therefore log-transformed to eliminate heteroscedasticity. Effects were considered to be statistically significant if P was < 0.05 .

Results

Abundances of *L. littorea*, juvenile *C. maenas* and *A. rubens*

In Spring 1999, the density of *L. littorea* was about ten times higher in the intertidal ($1,739 \pm 356$ snails m^{-2}) than the subtidal zone (167 ± 107 snails m^{-2}) (Mann-Whitney U -test, $P < 0.01$) (Fig. 2).

Juvenile *C. maenas* (carapace width ≤ 30 mm) were also significantly more abundant on intertidal (211 ± 98 crabs m^{-2}) than subtidal mussel beds (72 ± 25 crabs m^{-2}) (Mann-Whitney U -test, $P < 0.01$). No *A. rubens* were recorded on intertidal mussel beds while a density of 100 ± 79 starfish m^{-2} was obtained subtidally (Mann-Whitney U -test, $P < 0.01$). Only juvenile starfish with an arm length ≤ 20 mm were recorded.

Tidal zonation of barnacles

Barnacle species composition showed a tidal zonation. On intertidal mussel beds, the percentage cover of *S. balanoides* ($52.0 \pm 6.0\%$) was significantly higher than that of *B. crenatus* ($5.2 \pm 2.1\%$) (Mann-Whitney U -test, $P < 0.01$) while *B. crenatus* ($28.0 \pm 3.9\%$) was more abundant than *S. balanoides* ($4.8 \pm 1.2\%$) in the subtidal zone (Mann-Whitney U -test, $P < 0.01$; Fig. 3). The total barnacle cover was significantly higher on intertidal ($57.2 \pm 7.1\%$) than on subtidal mussel beds ($32.8 \pm 4.7\%$; Mann-Whitney U -test, $P < 0.01$).

Predator exclusion experiments

During the experiment in 1999, recruitment of *S. balanoides* was confined to the intertidal mussel bed while *B. crenatus* recruited only into the subtidal zone.

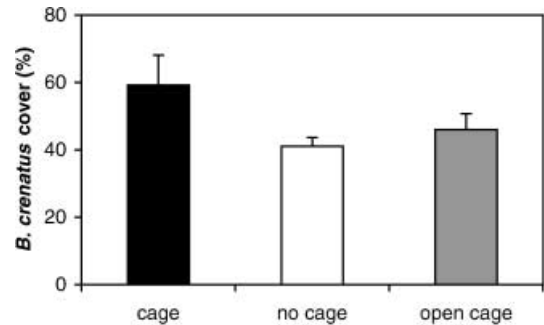


Fig. 4 Mean percentage *Balanus crenatus* cover (+SD) on subtidal mussel beds in three different treatments after an experimental period of 4 months

In the intertidal, predator exclusion had no effect on barnacle recruitment success. No statistical differences in percentage cover of *S. balanoides* were found between closed cages ($35.2 \pm 8.5\%$), uncaged areas ($30.2 \pm 4.7\%$), open cages ($28.8 \pm 7.6\%$) and closed cages with added juvenile *C. maenas* ($26.7 \pm 4.1\%$) (one-way ANOVA, $df=3$, $F=1.4696$, $P=0.2529$).

In the subtidal, by contrast, percentage cover of *B. crenatus* significantly differed between treatments (one-way ANOVA, $df=2$, $F=15.2933$, $P < 0.001$; Fig. 4). The highest percentage of barnacles established in closed cages ($59.2 \pm 8.9\%$). This was significantly higher than in open cages ($46.0 \pm 4.7\%$) and uncaged areas ($41.0 \pm 2.6\%$) (Tukey's test, $P < 0.01$). As in the intertidal zone, there were no significant differences between uncaged areas and open cages (Tukey's test $P > 0.05$). Thus, in both tidal zones no cage artefacts were detected. At the end of the experiments, largest barnacles achieved a basal shell diameter of about 10 mm.

Discussion

The present study illustrates that the relative abundances of the two barnacle species, *S. balanoides* and *B. crenatus*, differ between tidal zones and that different control factors seem to govern barnacle densities in intertidal and subtidal mussel beds.

With respect to balanid distribution pattern, the barnacles showed a distinct tidal zonation despite the small vertical range of about 0.5 m and a mean emergence time of about 1.5 h per tide between the intertidal and subtidal mussel beds investigated. *S. balanoides* dominated the intertidal and *B. crenatus* the subtidal zone. This zonation pattern was also reported from artificial hard substrate in the study area (Luther 1976) and from other shores (Barnes and Powell 1953; Meadows 1969; Gruet 1981; Rainbow 1984). The predominant occurrence of *S. balanoides* in the intertidal zone is considered to result from physiological adaptation to emergence (Grainger and Newell 1965; Newell 1976; Foster 1987). *S. balanoides* is capable of oxygen uptake from air and is tolerant to moderate desiccation stress, while *B. crenatus* is not able to survive long periods of emergence. *B. crenatus* may outcompete *S. balanoides* subtidally due to lower mortality, faster growth rates and a stronger attachment to the substrate (Meadows 1969; Luther 1987). Additionally, the calcareous base of *B. crenatus* may be an advantage when used to lever or push off individuals of *S. balanoides*, which have a membranous base (Meadows 1969). Furthermore, pre-settlement factors may influence the distribution patterns of balanids. For example, Grosberg (1982) found most cyprid larvae of *B. crenatus* occurring in deeper water and suggested that the distribution patterns of adult balanids may be a reflection of a vertical zonation of barnacle cyprids in the water column. However, in the turbid tidal waters of the creek adjacent to the mussel bed studied, this mechanism is unlikely to account for the differential settlement. On the other hand, cyprid larvae show considerable habitat selection behaviour and prefer a substrate where adults of their own species are abundant (Knight-Jones 1953; Larman and Gabbott 1975; Pawlik 1992; Jarrett 1997). In addition to physical factors, this may explain the restricted recruitment of *S. balanoides* intertidally and of *B. crenatus* subtidally, as found in the experiments conducted on mussel beds in the present study.

Effects on barnacle density

In contrast to this rather constant zonation pattern, abundances of both barnacle species showed high temporal variations on mussel beds of the study area (Buschbaum 2000). I revealed that fluctuations of *S. balanoides* growing on intertidal mussel beds were strongly influenced by variations in grazing and bulldozing activity of the periwinkle *L. littorea* (Buschbaum 2000). High snail densities reduced barnacle settlement success in field experiments. The assumed dominant role of *L. littorea* for intertidal barnacle recruitment is supported by the results of the cage experiments in this study. These did not reveal any significant predation effects on *S. balanoides* attached to intertidal mussels. On subtidal mussel beds, however, the importance of snail grazing is supposed to be negligible because periwinkle abundance was low. This is presumably caused by snail recruitment restricted



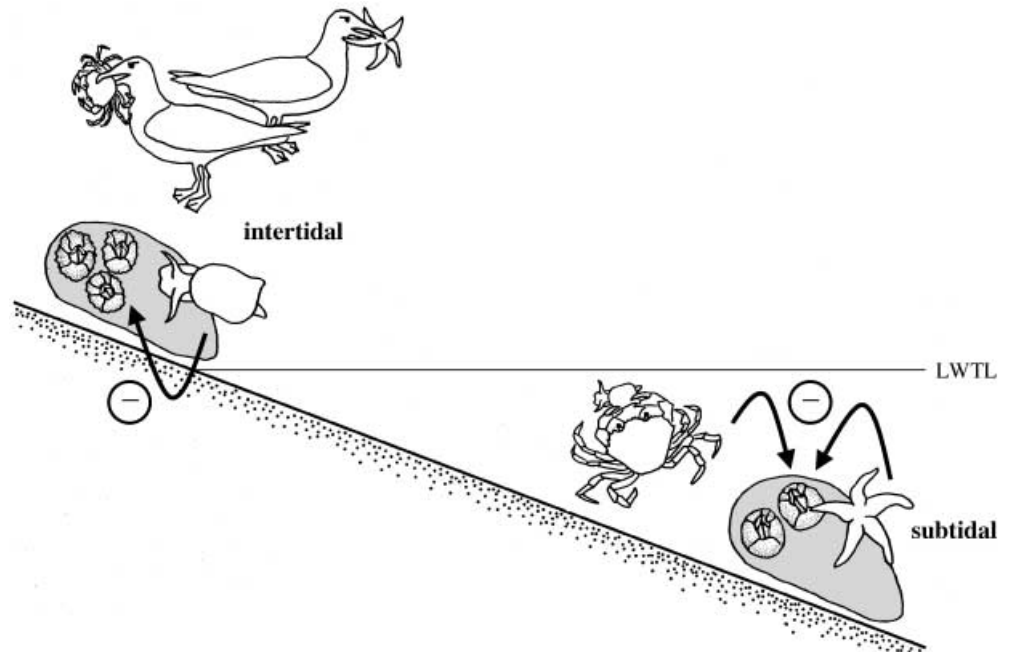
Fig. 5 Feeding marks of adult crabs *Carcinus maenas* (above) and juvenile starfish *Asterias rubens* (below) preying on *Balanus crenatus*. After an attack of adult crabs, only the calcareous bases of the barnacles remain on the mussel shells, while juvenile starfish leave the outer barnacle shell intact

to the intertidal zone in concert with high crab predation pressure subtidally (Saier 2000). Thus, *L. littorea* cannot be responsible for density fluctuations of *B. crenatus*. In contrast to the intertidal zone, an exclusion of predators on subtidal mussel beds resulted in an increased percentage cover of barnacles in the cages. Therefore, I assume that predation may be an important density structuring factor for *B. crenatus* subtidally.

Rangeley and Thomas (1987) reported that balanids are a valuable food source for juvenile *C. maenas* (carapace width 21–29 mm) and pointed out that small crabs may be an important factor for barnacle mortality. Although on intertidal mussel beds the abundance of juvenile *C. maenas* was threefold higher than subtidally, no predation effects were detectable. Thus, it is unlikely that small crabs had an important impact on barnacles in the investigation area. This is supported by the crab enclosure experiments, which did not reveal any effects of juvenile *C. maenas* (carapace width 15–30 mm) on barnacle densities, and these results are in agreement with the findings of Leonard et al. (1999). Presumably, juvenile *C. maenas* used other food sources such as annelids, which are among the preferred prey of small crabs in the Wadden Sea (Reise 1978, 1985; Scherer and Reise 1981) and are very abundant on mussel beds (Dittmann 1990).

Juvenile starfish, *A. rubens*, were absent on intertidal mussel beds, which may be a consequence of high predation pressure by gulls (Dernedde 1993, 1994). Subtidally, however, juvenile *A. rubens* attained a density of about 100 individuals per m². This indicates that they could

Fig. 6 Schematic interactions on intertidal and subtidal mussel beds in the Wadden Sea affecting barnacle densities. Intertidally, grazing and bulldozing by periwinkles (*Littorina littorea*) influence densities of *Semibalanus balanoides*, while adult crabs (*Carcinus maenas*) and juvenile starfish (*Asterias rubens*) affect *Balanus crenatus* on subtidal mussel beds ($\rightarrow \ominus$). The effects of *L. littorea* are restricted to the intertidal zone, presumably due to crab predation pressure subtidally. The effects of large *C. maenas* and *A. rubens* are restricted to the subtidal zone, presumably due to bird predation intertidally (LWTL low water tide level)



have been responsible for predation effects on *B. crenatus* in the cage experiment. Indeed, Sloan (1980) reported that barnacles belong to the preferred diet of small *A. rubens* and laboratory experiments revealed that a single juvenile starfish is capable of consuming up to three barnacles per day (Mertel, personal communication). Juvenile *A. rubens* attack individual balanids by removing the body through the aperture without damaging the outer barnacle shell (personal observation) and the remaining empty barnacle cones are regularly visible on subtidal mussels (Fig. 5). Often, however, groups of barnacles were totally crushed and scraped off from the shells of *M. edulis* and only the calcareous bases of *B. crenatus* remain on the bivalves (Fig. 5). These feeding marks are typical of large *C. maenas* (Rangeley and Thomas 1987). Moreover, direct observations confirmed high numbers of adult crabs preying on barnacles on shallow subtidal mussel beds. Although adult crabs may perform feeding migrations to the intertidal zone (Crothers 1968; Klein-Breteler 1976; Warman et al. 1993), Darnedde (1993) recorded that high numbers of large *C. maenas* were consumed by gulls (especially *Larus argentatus* Pont.) with feeding activity being almost exclusively restricted to the intertidal zones of mussel beds.

Thus, I suggest that the predation effects on *B. crenatus* found in the subtidal zone are mainly caused by the feeding activities of both juvenile starfish and adult *C. maenas*. Other carnivorous species frequently occurring in the area such as shrimps (*Crangon crangon*) and fish (*Pomatoschistus* spp.) appear to be negligible because adult balanids do not belong within their preferred food spectrum (Plagmann 1939; Pihl and Rosenberg 1984; Pihl 1985; Aarnio and Bonsdorff 1993) and there is no evidence that birds feed on barnacles (Darnedde 1993; Hertzler 1995). Further potential predators which are

known to feed on barnacles in other areas, such as the gastropods *Nucella* spp. (Connell 1961, 1970), *Neothais scalaris* and *Lepsiella scobina* (Luckens 1975), or the flatworm *Stylochus ellipticus* (Branscomb 1976) are absent from the Wadden Sea.

Another predator to be considered is the shrimp *Crangon crangon*, preying on barnacle nauplii and cyprid larvae in the water column (Plagmann 1939). This may influence barnacle population dynamics before settlement because variations in shrimp predation may result in decreased barnacle larval supply, which is an important factor in structuring the adult community (Gaines et al. 1985; Bertness et al. 1992). However, long-term data of barnacle cyprid larval abundances in the study area showed no strong interannual variations in the density of cyprid larvae (Buschbaum 2001). This indicates that grazing and predation subsequent to barnacle settlement may be the prevailing processes for barnacle abundance variations on mussel beds.

In summary, the same ecological pattern, i.e. the fluctuations of barnacle densities in intertidal and subtidal mussel beds, is affected by different biotic factors. The restriction of grazing effects to the intertidal zone and predation by crabs and starfish to subtidal mussel beds is governed by higher trophic interactions which are illustrated in Fig. 6. As shown elsewhere (Buschbaum and Saier 2001), the barnacles are key members of the mussel bed community because they affect the growth of the mussels which generate the entire habitat.

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References

- Aarnio K, Bonsdorff E (1993) Seasonal variation in abundance and diet of the sand goby *Pomatoschistus minutus* (Pallas) in a northern Baltic Archipelago. *Ophelia* 37:19–30
- Albrecht AS (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
- Albrecht A, Reise K (1994) Effects of *Fucus vesiculosus* covering intertidal mussel beds in the Wadden Sea. *Helgol Meeresunters* 48:243–256
- Austen G (1994) Hydrodynamics and particulate matter budget of Königshafen, southeastern North Sea. *Helgol Meeresunters* 48:183–200
- Austen I (1994) The surficial sediments of Königshafen variations over the past 50 years. *Helgol Meeresunters* 48:163–171
- Barnes H, Powell HAT (1953) The growth of *Balanus balanoides* (L.) and *B. crenatus* Brug. under varying conditions of submersion. *J Mar Biol Assoc* 32:107–128
- Bayerl KA, Higelke B (1994) The development of northern Sylt during the last Holocene. *Helgol Meeresunters* 48:145–162
- Bertness MD, Gaines SD, Stephens EG, Yund PO (1992) Components of recruitment in populations of the acorn barnacle *Semibalanus balanoides* (Linnaeus). *J Exp Mar Biol Ecol* 156:199–215
- Beukema JJ (1991) The abundance of shore crabs *Carcinus maenas* (L.) on a tidal flat in the Wadden Sea after cold and mild winters. *J Exp Mar Biol Ecol* 153:97–113
- Beukema JJ (1992) Dynamics of juvenile shrimp *Crangon crangon* in a tidal-flat nursery of the Wadden Sea after mild and cold winters. *Mar Ecol Prog Ser* 83:157–165
- Beukema JJ, Honkoop PJC, Dekker R (1998) Recruitment in *Macoma balthica* after mild and cold winters and its possible control by egg production and shrimp predation. *Hydrobiologia* 375/376:23–34
- Branscomb ES (1976) Proximate causes of mortality determining the distribution and abundance of the barnacle *Balanus improvisus* Darwin in Chesapeake Bay. *Chesapeake Sci* 17:281–288
- Buhs F, Reise K (1997) Epibenthic fauna dredged from tidal channels in the Wadden Sea of Schleswig Holstein: spatial patterns and a long-term decline. *Helgol Meeresunters* 51:343–359
- Buschbaum C (2000) Direct and indirect effects of *Littorina littorea* (L.) on barnacles growing on mussel beds in the Wadden Sea. *Hydrobiologia* 440:119–128
- Buschbaum C (2001) Siedlungsmuster und Wechselbeziehungen von Seepocken (Cirripedia) auf Muschelbänken (*Mytilus edulis* L.) im Wattenmeer. PhD thesis, University of Hamburg, Germany
- Buschbaum C, Saier B (2001) Growth of the mussel *Mytilus edulis* L. in the Wadden Sea affected by tidal emergence and barnacle epibionts. *J Sea Res* 45:27–36
- Connell JH (1961) Effects of competition, predation by *Thais lapillus*, and other factors on natural populations of the barnacle *Balanus balanoides*. *Ecol Monogr* 31:61–104
- Connell JH (1970) A predator–prey system in the marine intertidal region. I. *Balanus glandula* and several predatory species of *Thais*. *Ecol Monogr* 40:49–78
- Crothers JH (1968) The biology of the shore crab *Carcinus maenas* (L.). 2. The life of the adult crab. *Field Stud* 2:579–614
- Dernedde T (1993) Vergleichende Untersuchungen zur Nahrungszusammensetzung von Silbermöwe (*Larus argentatus*), Stormmöwe (*L. canus*) und Lachmöwe (*L. ridibundus*) im Königshafen/Sylt. *Corax* 15:222–240
- Dernedde T (1994) Foraging overlap of three gull species (*Larus* spp.) on tidal flats in the Wadden Sea. *Ophelia* 6 [Suppl]:225–238
- Dittmann S (1990) Mussel beds – amensalism or amelioration for intertidal fauna? *Helgol Meeresunters* 44:335–352
- Foster BA (1987) Barnacle ecology and adaptation. In: Southward AJ (ed) *Barnacle biology*. Balkema, Rotterdam, pp 113–133
- Gaines S, Brown S, Roughgarden J (1985) Spatial variation in larval concentrations as a cause of spatial variation in settlement for the barnacle, *Balanus glandula*. *Oecologia* 67:267–272
- Grainger F, Newell GE (1965) Aerial respiration in *Balanus balanoides*. *J Mar Biol Assoc UK* 45:469–479
- Grosberg RK (1982) Intertidal zonation of barnacles: the influence of planktonic zonation of larvae on vertical distribution of adults. *Ecology* 63:894–899
- Gruet Y (1981) Peuplements de l'estran rocheux sur la côte normande de la baie Du Mont Saint-Michel à Champeux (Manche): situation et conditions generales. *Bull Soc Linn Normandie* 109:21–32
- Hertzler I (1995) Nahrungsökologische Bedeutung von Miesmuschelbänken für Vögel (Laro-Limikolen) im Nordfriesischen Wattenmeer. MSc thesis, University of Göttingen, Germany
- Honkoop PJC, Meer J van der (1998) Experimentally induced effects of water temperature and immersion time on reproductive output of bivalves in the Wadden Sea. *J Exp Mar Biol Ecol* 220:227–246
- Jarrett JN (1997) Temporal variation in substratum specificity of *Semibalanus balanoides* (Linnaeus) cyprids. *J Exp Mar Biol Ecol* 211:103–114
- Klein-Breteler WCM (1976) Migration of the shore crab, *Carcinus maenas*, in the Dutch Wadden Sea. *Neth J Sea Res* 10:338–353
- Knight-Jones EW (1953) Laboratory experiments on gregariousness during settling in *Balanus balanoides* and other barnacles. *J Exp Biol* 30:584–598
- Larman VN, Gabbott PA (1975) Settlement of cyprid larvae of *Balanus balanoides* and *Elminius modestus* induced by extracts of adult barnacles and other marine animals. *J Mar Biol Assoc UK* 55:183–190
- Leonard GH, Ewanchuk PJ, Bertness MD (1999) How recruitment, intraspecific interactions, and predation control species borders in a tidal estuary. *Oecologia* 118:492–502
- Luckens PA (1975) Predation and intertidal zonation of barnacles at Leigh, New Zealand. *N Z J Mar Freshw Res* 9:355–378
- Luther G (1976) Bewuchsuntersuchungen auf Natursteinsubstraten im Gezeitenbereich des Nordsylter Wattenmeeres. *Helgol Wiss Meeresunters* 28:145–166
- Luther G (1987) Seepocken der deutschen Küstengewässer. *Helgol Meeresunters* 41:1–43
- Meadows PS (1969) Settlement, growth and competition in sublittoral populations of barnacles. *Hydrobiologia* 33:65–92
- Newell RC (1976) Adaptations to intertidal life. In: Newell RC (ed) *Adaptations to environment: essays on the physiology of marine animals*. Butterworth, Sydney, pp 1–82
- Pawlik JR (1992) Chemical ecology of the settlement of benthic marine invertebrates. *Oceanogr Mar Biol Annu Rev* 30: 273–335
- Pihl L (1985) Food selection and consumption of mobile epibenthic fauna in shallow marine areas. *Mar Ecol Prog Ser* 22: 169–179
- Pihl L, Rosenberg R (1984) Food selection and consumption of the shrimp *Crangon crangon* in some shallow marine areas in western Sweden. *J Exp Mar Biol Ecol* 57:273–301
- Plagmann J (1939) Ernährungsbiologie der Garnele (*Crangon vulgaris* Fabr.). *Helgol Wiss Meeresunters* 2:113–162
- Rainbow PS (1984) An introduction to the biology of British littoral barnacles. *Field Stud* 6:1–51
- Rangeley RW, Thomas MLH (1987) Predatory behaviour of juvenile shore crab *Carcinus maenas* (L.). *J Exp Mar Biol Ecol* 108:191–197
- Reise K (1977) Predator exclusion experiments in an intertidal mud flat. *Helgol Wiss Meeresunters* 30:263–271
- Reise K (1978) Experiments on epibenthic predation in the Wadden Sea. *Helgol Wiss Meeresunters* 31:55–101

- Reise K (1985) Tidal flat ecology. Springer, Berlin Heidelberg New York
- Reise K, Bartsch I (1990) Inshore and offshore diversity of epibenthos dredged in the North Sea. *Neth J Sea Res* 25:175–179
- Reise K, Herre E, Sturm M (1994) Biomass and abundance of macrofauna in intertidal sediments of Königshafen in the northern Wadden Sea. *Helgol Meeresunters* 48:201–215
- Ropes JW (1968) The feeding habits of the green crab, *Carcinus maenas* (L.). *Fish Bull* 67:183–203
- Saier B (2000) Age dependent zonation pattern of the periwinkle *Littorina littorea* (L.) in the Wadden Sea. *Helgol Mar Res* 54:224–229
- Scherer B, Reise K (1981) Significant predation on micro- and macrobenthos by the crab *Carcinus maenas* L. in the Wadden Sea. *Kiel Meeresforsch Sonderh* 5:490–500
- Sloan NA (1980) Aspects of the feeding biology of Asteroids. *Oceanogr Mar Biol Annu Rev* 18:57–124
- Strasser M (1999) Rekrutierungsmuster ausgewählter Wattfauna nach unterschiedlich strengen Wintern. PhD thesis, University of Hamburg; Germany
- Strasser M (2000) Recolonization patterns of benthic fauna in the intertidal Wadden Sea after severe winter of 1995/96. *Wadden Sea Newsl* 2000(1):9–11
- Warman CG, Reid DG, Naylor E (1993) Variation in the tidal migratory behaviour and rhythmic light-responsiveness in the shore crab, *Carcinus maenas*. *J Mar Biol Assoc UK* 73 355–364