

# Dominance of blue mussels versus consumer-mediated enhancement of benthic diversity

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## Abstract

In the shallow subtidal of Kiel Fjord (western Baltic Sea), the blue mussel *Mytilus edulis* is the dominant competitor for space. Vertically suspended settlement substrata in the upper 6 m of the water column almost invariably become dominated by *M. edulis* within a few summer months. However, not all naturally available hard substrata bear mussel monocultures.

In three in situ experiments we investigated the dominance of mussels and the influence of local consumers on establishment and dynamics of a benthic community: (a) the natural course of succession in the absence of benthic consumers was followed on vertically suspended settlement substrata, (b) settling plates were exposed to natural recruitment being either accessible or inaccessible to all benthic consumers, and (c) the three major local consumer species, viz. the shore crab *Carcinus maenas*, the starfish *Asterias rubens* and the periwinkle *Littorina littorea*, were enclosed separately in cages containing a settling panel to assess species-specific consumer effects on recruitment.

The results illustrate that in this region of the Baltic Sea mussels do have the potential to dominate ungrazed substrata within a few weeks and that top-down effects (predation and grazing) may control community structure. While some species - mussels in particular - were suppressed by consumption, others seemed to benefit from the presence of consumers. Thus, barnacles and algae thrived when consumers were present. Blue mussels being the locally dominant competitor, the beneficial effects of consumers on barnacles and algae were presumably indirect ones through consumer-caused release from asymmetrical competition.

The isolated effects of *C. maenas*, *A. rubens* and *L. littorea*, on recruitment differed in quality (positive vs. negative), quantity (strength of effect) and specificity. Barnacle recruitment was significantly reduced in the presence of both starfish and shore crabs. Diatom recruitment was significantly reduced by snails and shore crabs. Scyphozoan recruitment was significantly reduced by crabs only, but was significantly increased by snails. The influence of the shore crabs was most remarkable: recruitment by any potential coloniser species was impeded to a point where in the presence of single individuals of *C. maenas* the plates stayed perfectly clean macroscopically.

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## 1. Introduction

The establishment of a marine hard-bottom community on newly available substrata is governed by pre-settlement (survival and distribution of colonising

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stages; e.g. Gaines and Bertness, 1992), settlement (composition of coloniser pool, competence of settling stages, substratum preferences; e.g. Raimondi, 1991; Bourget and Harvey, 1998; Hills and Thomason, 1998; Rittschof et al., 1998; Andersson et al., 1999) and post-settlement processes (competition, consumption, etc., e.g. Petraitis, 1990; Menge and Sutherland, 1987; Gosselin and Qian, 1997; Jenkins et al., 1999). When, during recruitment, substratum becomes the limiting factor, dominant competitors may drive competitively inferior species to extinction (e.g. Connell, 1978; Menge and Sutherland, 1987) - especially so when productivity is high (Huston, 1979, 1999).

In Kiel Fjord (western Baltic Sea), the blue mussel *Mytilus edulis* with its associated fauna and flora may form a rich and diverse community (Asmus, 1987) and plays an important ecological role by e.g. encompassing the filter-cleaning of the eutrophic water (Brey, 1984) and enhancement of the distribution of eelgrass meadows (Reusch, 1994). The blue mussel, however, seems to be the locally dominant competitor for space in this and many other regions due to its massive recruitment and fast growth in this eutrophic environment (e.g. Suchanek, 1985; Petraitis, 1995; Reusch and Chapman, 1997). When unchecked, blue mussels in the western Baltic have the potential to dominate the community, exclude other species, and reduce diversity (e.g. Reusch, 1994). Thus, within the upper 6 m of the water column most substrata without direct contact with the bottom (pontoons, buoys, etc.) in contrast to benthic substrata become permanently monopolised by mussels (Laudien and Wahl, 1999). On substrata that have contact with the bottom (e.g. pilings), the diversity of the community in the presence of predators is almost twice as higher as in the absence of consumption (Laudien and Wahl, 1999). These observations suggest a control of mussel dominance by benthic predators. An important role of consumption in controlling dominant competitors has repeatedly been demonstrated for different environments and communities (e.g. Day, 1977; Glasser, 1979; Menge and Sutherland, 1987; Petraitis, 1987, 1990; Pacala and Crawley, 1992; Enderlein, 2000; Worm et al., 2002). Possible local candidates for this role are the shore crab *Carcinus maenas*, the common starfish *Asterias rubens* and the periwinkle *Littorina littorea*. The crabs usually feed on mussels of up to 50 mm shell length (Kitching et al., 1959; Elner and

Hughes, 1978), but in the western Baltic preference is low for mussels >40 mm (Enderlein et al., 2003). The starfish prey upon mussels up to a length of 33 mm (Reusch and Chapman, 1997) and the periwinkles may ingest or damage any freshly settled organism (Wahl and Sönnichsen, 1992; Wahl and Hoppe, 2002). All three consumer species may affect a wide spectrum of prey species either by direct ingestion or by 'accidentally' damaging them during feeding-associated activities.

From the model by Huston (1979) and Menge and Sutherland (1987), our observations and the study by Laudien and Wahl (1999) of high blue mussel abundance in predator-free areas with low diversity and vice versa, we predict that benthic predation strongly affects community structure and diversity in the Baltic Sea mainly by controlling the dominance of the blue mussel.

To test this hypothesis we conducted three experiments: In the first experiment we looked for the succession in the total absence of consumers, whereas in the second experiment we investigated the succession in the presence of consumers. Species-specific influences of the three main consumer species were quantified in a third experiment.

## 2. Material and methods

### 2.1. Experimental site

Three in situ experiments were carried out in the Tonnenhof, Kiel Fjord (western Baltic, N: 54°22'E: 10°09'). Kiel Fjord and Bight are situated between the fully marine environment of the Atlantic and the brackish Baltic Proper. Salinity values range between 12 and 18, and water temperatures between 0.7 °C and 20 °C. The study site is sheltered on two sides with an average depth of 6–7 m. It is dominated by sandy to muddy substrata. Hard substrates in the form of small glacial pebbles and small rocks cover approximately 10% of the area. The benthic community in the study area is dominated by blue mussel banks from 2 to 6 m depth. In the shallow water and below 6 m depth blue mussels form patches of 10 to >100 mussel aggregates. All test organisms were collected by SCUBA near the experimental site. Here, the major consumers, viz. the starfish *Asterias rubens* (10–40

animals/m<sup>2</sup>), the shore crab *Carcinus maenas* (1–10 animals/m<sup>2</sup>), and the periwinkle *Littorina littorea* (10–>100 animals/m<sup>2</sup>), are common (Wilhelmy, 1996; pers. obs.).

## 2.2. Succession in the absence of consumers

Forty 5 × 5 cm PVC plates were suspended vertically at a depth of 1.5 m on 16 June 1996. Four randomly chosen plates (replicates) were retrieved after each of the following intervals: 2, 4, 5, 6, 7, 8, 9, 10, 11 and 12 weeks after immersion. The last set of substrata was collected on 4 September 1996. The treatments of plates were coded and kept at minus 20 °C. After the last collection, two collaborators who were unaware of treatment allocation identified all settled individuals to species level and counted them. These raw data were used untransformed to calculate Shannon–Weaver diversity  $H'$  and Simpson's index of dominance.

## 2.3. Multispecies consumption

Twenty PVC-plates (30 × 30 cm, thickness 5 mm) were suspended vertically at the experimental site at a depth of 3 m and 30 cm above ground. Ten of the plates were equipped with a ramp to the seafloor, and thus accessible to motile benthic consumers. The other 10 plates lacked the ramp and were afloat 30 cm above ground inaccessible to shore crabs, starfish and periwinkles. All plates were suspended from a transect line and stabilised by bottom weights. During the regular SCUBA inspections of the experiment we found no predators on the plates without ramps but regular predators on the plates with the ramps as well as on the ramps, which shows that the predators were using the ramps to gain access to the plates.

The experimental set-up was a randomised-block-design with one factor and two levels (with and without ramp, i.e. exposed to vs. sheltered from consumers). Both treatments were replicated ten times and arranged in ten blocks of one accessible and one inaccessible plate each. Arrangement within the blocks was randomised. Distance between blocks was one block-width. Distance between the two plates of each block was one plate-width.

The plates were exposed on 27 April 1995 and retrieved on 31 October 1995. After 4 and 6 months

(on 22 August and 31 October, respectively), the aufwuchs communities were assessed. For that purpose a plexiglas collector with an opening of 10 × 10 cm was pressed with its sharpened edges against the plates, and the portion of aufwuchs within the opening of the collector was scraped off completely with a common spatula slid under the upper side of the collector. In this way, identical areas (first series: upper right quadrant of the plate, second series: upper left quadrant) of all 20 settlement plates were sampled. Samples were refrigerated over night and inventoried the following day (number of individuals per species).

Data were analysed using a 1-way ANOVA with two levels (accessibility, non-accessibility) and block-factor. To obtain homogeneity of variances, data were (log+1) - transformed. Level of significance was 0.05.

Diversity was analysed using the Shannon–Weaver diversity index. Dominance of mussels was expressed by Simpson's index with a value of 1 representing absolute monopoly by one species (Magurran, 1988). Differences in diversity and in dominance between accessible and inaccessible substrata were compared separately by a t-test.

Assemblages developing in the presence versus absence of consumers were compared by Analysis of Similarity (ANOSIM) and MDS-plotted. The species mainly responsible for significant differences between assemblages were identified by SIMPER.

## 2.4. Species-specific effects of the three consumer species

Thirty cages (15 × 15 × 15 cm) were constructed from PVC netting of 0.6 cm mesh. Using a float and a ground weight, cages were suspended at 1.5 m depth and 50 cm above ground. Within each cage, a PVC panel (15 × 15 cm) was fixed vertically, subdividing the cage chamber into a frontal section with consumers and a consumer-free section at the rear end. The two sides of the panel served as recruitment substrata in the presence (front) or absence of consumers (rear). Through a closable flap at the front of the cage, single individuals of either *Carcinus maenas* (10 cages), *Asteria rubens* (10 cages) or *Littorina littorea* (10 cages) were placed in the frontal compartment of the cages at the start of the experiment. This treatment

represented an increase of consumer density by estimated factors of 10 (*Asterias*, *Littorina*) to 20 (*Carcinus*) as compared to natural conditions. Shore crabs, because of their higher metabolic demand in comparison with *Asterias* and *Littorina*, were fed weekly with blue mussel meat.

Cages were arranged in a randomised-block-design at the experimental site. The experiment ran for three months (5 September to 13 December 1995). At the end of the experiment, barnacles were counted on both faces of the plates, while coverage by diatoms and scyphozoa was estimated to the nearest 10%. Because of extremely low water in September, two cages were lost. Therefore only 9 replicates could be evaluated.

Because accessible and non-accessible substrata were paired (two faces of the same plate in the same cage) the impact of consumption on single colonising species was analysed by a paired t-tests. To compare consumption effects among consumer species and among coloniser species, consumption was quantified as the % -difference in specific abundances between the two sides of a plate and analysed by separate Kruskal–Wallis-ANOVAs followed by an STP post-

hoc procedure (Sokal and Rohlf, 1995) since variances even after transformation were heterogeneous.

### 3. Results

#### 3.1. Succession in the absence of consumers

In the first experiment (Fig. 1), macroscopic colonisation started with barnacles (*Balanus improvisus*) and mussels (*Mytilus edulis*) in week 2 (end of June). The sessile ciliate *Folliculina* sp. and the thecate hydrozoan *Laomedea flexuosa* were found first in week 4 (mid July). A week later, the athecate hydrozoan *Clava multicornis* and the bryozoan *Conopeum reticulum*, appeared in the assemblage as 5th and 6th species. Only in week 10 (end of August) did the last two species recruit, the tube-building polychaete *Polydora ciliata* and the tubicolous amphipod *Corophium volutator*.

While species composition remained fairly stable over the last 7 weeks of succession, proportional abundance, dominance and diversity changed conspicuously, due to a dramatic increase in numbers of

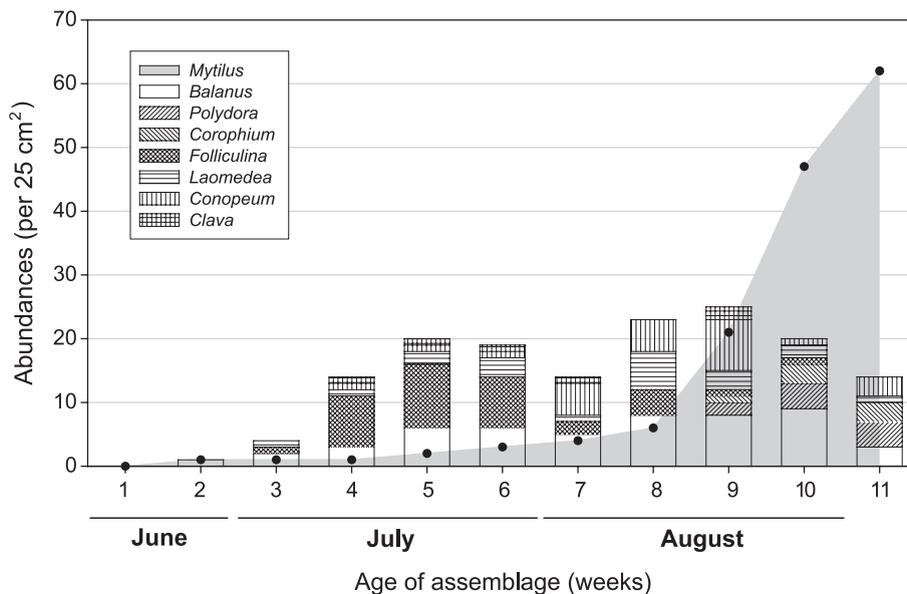


Fig. 1. Succession in the absence of consumers: Establishment and successional changes in species composition of a hard bottom assemblage on artificial substrata exposed at a depth of 1.5 m in Kiel Fjord, western Baltic, between late June and early September 1997 (average % cover, SE's not representable in this type of graphic).

blue mussels (Fig. 2). Between weeks 7 and 12, mussel abundance grew by a factor of 12 or more. At the same time the numerical dominance of blue mussels increased from 0.12 to 0.85, and diversity of the assemblage decreased by a factor of 3 from almost 0.6 to just over 0.2. Blue mussels increased fastest not only in numbers, but also in individual size. By the end of the experiment most plates showed a mussel ‘monoculture’ with ~ 90% of the individuals,  $\gg 90\%$  of the biomass and about 100% coverage.

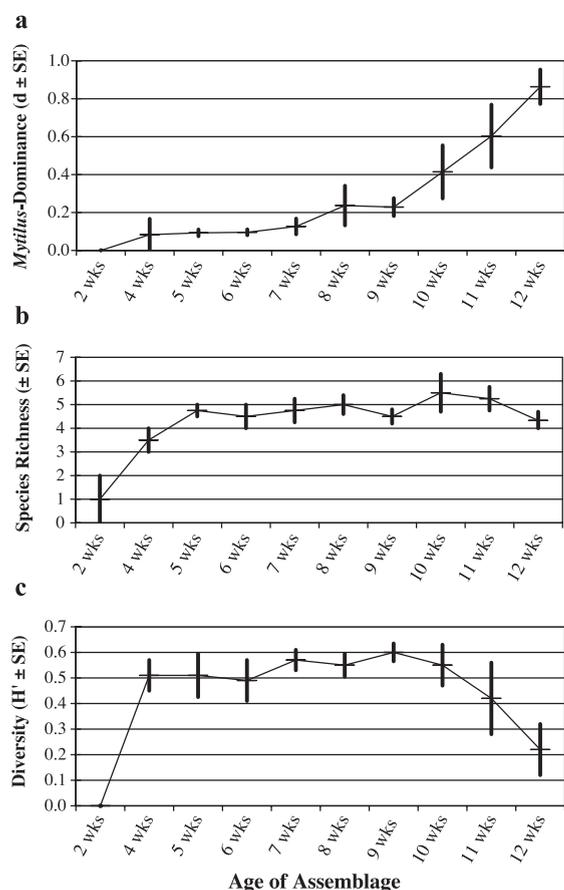


Fig. 2. The rise and fall of diversity during early succession in undisturbed assemblages: The progressive dominance of blue mussels during early succession in a hard bottom assemblage on artificial substrata exposed at a depth of 1.5 m in Kiel Fjord, western Baltic, between late June and early September 1997. (a) mussel dominance as expressed by Simpson's index; (b) species richness; (c) diversity as Shannon  $H'$ . All data are means plus/minus standard error.

### 3.2. Influence of multispecific consumption activity

Within 4 months, the influence of benthic consumers on community structure was conspicuous. The recruitment of all species, with the exception of barnacles, was significantly affected by the presence of *L. littorea*, *C. maenas* and/or *A. rubens*. After 6 months, the abundances of all colonising species assessed differed significantly depending on the absence / presence of consumers.

After 4 months (Fig. 3a), the dominant green alga *Enteromorpha* sp. exhibited significantly higher abundances in the presence of consumers and was completely missing in assemblages sheltered from consumption. The barnacle *Balanus improvisus* appeared to benefit from the presence of consumers although this relationship was statistically just non-significant. In contrast, small and larger blue mussels were significantly more abundant when sheltered from predation.

After 6 months (Fig. 3b), the green alga *Bryopsis plumosa* (which had replaced *Enteromorpha* sp. by then) settled and/ or survived only in the presence of consumers. Barnacles recruited in significantly higher numbers in the presence of consumers as compared to plates sheltered from consumption. In contrast to the first 4 months, newly recruited *Mytilus edulis* (3–6 mm) were more abundant in the presence of consumers than under sheltered conditions. The abundance of mussels larger than 6 mm, however, was drastically reduced in the presence of consumers.

Consumption decreased mussel dominance (Fig. 3a) and increased the diversity of the assemblage. After 4 and 6 months, in the presence of consumers the average diversity was 95% and 51% higher, respectively, and dominance of mussels was 57% and 37% lower (respectively) (t-test  $p < 0.0001$  in all cases).

At both ages (4 and 6 months) the structure of consumer-exposed and consumer-sheltered assemblages differed significantly (ANOSIM  $p < 0.0001$  in both cases;  $R = 0.77$  and  $0.97$ , respectively). At 4 months, mussels contributed 68%, *Enteromorpha* 25% and barnacles 8% to the dissimilarity. At 6 months, mussels contributed 54%, *Bryopsis* 32% and barnacles 13% to the difference. The projection of the clustering (MDS, Fig. 4) neatly segregates the

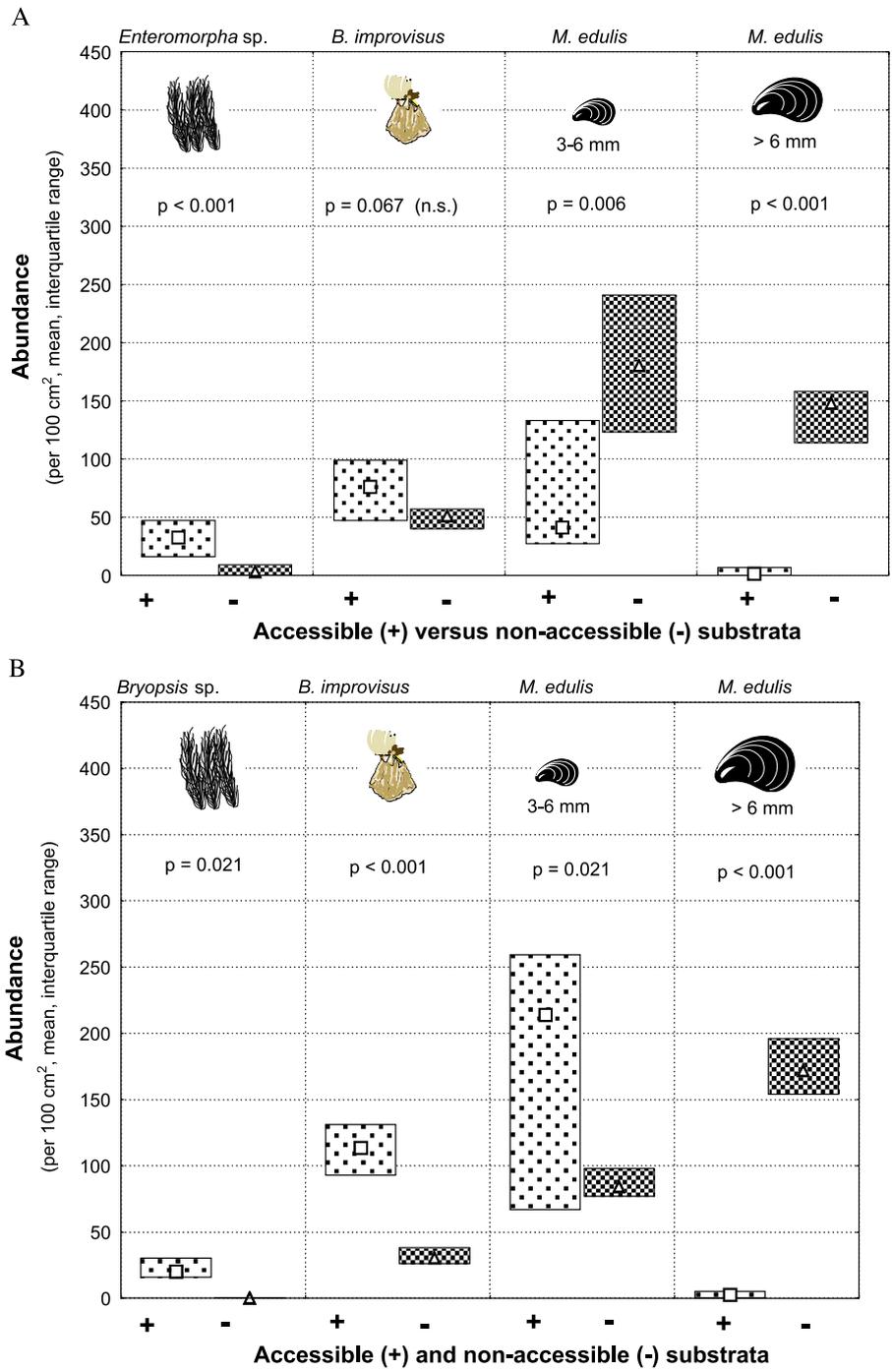


Fig. 3. Effects of natural benthic consumption on different species: Recruitment of different species onto consumer-exposed ('+') and consumer-sheltered ('-') substrata during 4 months (a) and 6 months (b). Numbers of individuals per 100 cm<sup>2</sup> ± SE. Tukey p-values for within-species pairwise comparisons are given.

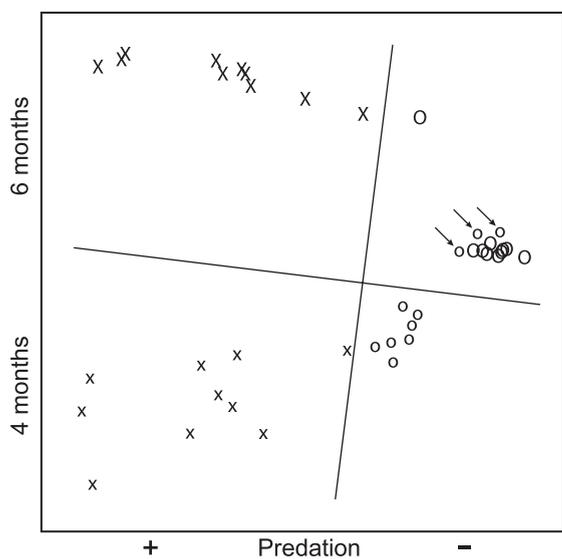


Fig. 4. Successional stage and consumer effects determine the nature of assemblages: MDS-plotting of the 20 assemblages exposed to (crosses) vs sheltered from (circles) natural benthic consumption at 4 months (small symbols) and 6 months of age (large symbols). The horizontal line separates younger from older assemblages (with 3 exceptions: arrows) and represents successional change. The vertical line separates consumer-exposed (left) from consumer-sheltered assemblages (right). Both factors Age and Consumption affect assemblage structure.

data sets according to age ('y-axis') and consumption level ('x-axis').

### 3.3. Consumption effects by single consumer species

During the experimental phase, which was performed later in the year than the previous experiment, no mussels recruited and only four other taxa occurred in substantial numbers: an un-identified diatom assemblage, the hydrozoan *Laomedea flexuosa* (on about one third of the plates), the scyphopolyp *Aurelia aurita* and the barnacle *Balanus improvisus*. Consumption by single species significantly affected recruitment on the accessible faces of settlement plates as compared to their sheltered faces (paired t-test  $p < 0.001$ ; Fig. 5). Consumption effects differed by consumer species and by coloniser species.

#### 3.3.1. *Carcinus maenas*

The effects of consumption by the shore crab *Carcinus maenas* were most remarkable. On plate sides accessible to crabs, virtually no macroscopic species recruited. After 3 months, the plates exposed to crab consumption were still absolutely clean. Diatoms,

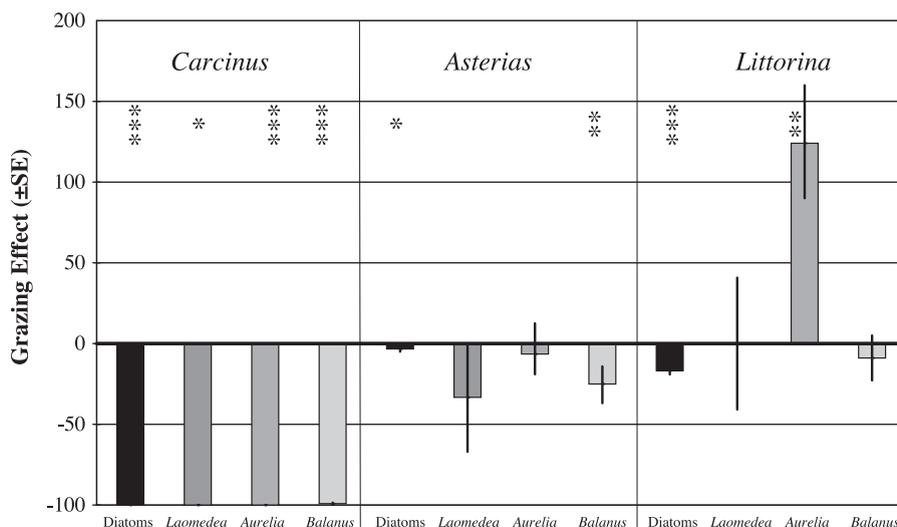


Fig. 5. Species-specific consumer effect on recruitment split by consumer species (*Carcinus maenas*, *Littorina littorea* and *Asterias rubens*) and coloniser taxa (diatoms, the hydrozoan *Laomedea flexuosa*, the scyphopolyp *Aurelia aurita*, and the barnacle *Balanus improvisus*). 'Grazing effect' ( $\pm$  SE) expressed as the  $\ln(\text{grazing}/\text{control})$  difference between the consumer-sheltered and the consumer-exposed side of each plate. Significance of grazing effects (i.e. its difference from zero): \*\*\*= $p < 0.001$ , \*\*= $p < 0.01$ , \*= $p < 0.05$ .

hydrozoa and scyphozoa were completely suppressed (minus 100%,  $p < 0.0001$ , 0.001, and 0.05, respectively), barnacles were reduced by  $99\% \pm 0.63\%$  ( $p < 0.0001$ ). Only on two plates was a single barnacle found. Both had settled in the least accessible centre of the vertical plates. The impact of crab consumption did not differ among coloniser species (Kruskal Wallis ANOVA  $p = 1$ ) being almost 100% in all cases.

### 3.3.2. *Asterias rubens*

Hydrozoans and scyphozoans were not affected by the presence of the starfish *Asterias rubens* ( $p = 0.173$  and 0.133, respectively). Starfish consumption reduced barnacle recruitment by minus  $25\% \pm 12\%$  ( $p = 0.007$ ) and to a lesser extent that of diatoms (minus  $3.3\% \pm 1.67\%$ ,  $p = 0.04$ ). The presence of numerous calcareous bases on the accessible plate face testified of the predatory activity of *Asterias* on *Balanus improvisus*. The impact of starfish consumption did not differ significantly among coloniser species (KW  $p = 0.24$ ).

### 3.3.3. *Littorina littorea*

Plates exposed to consumption by the snail *Littorina littorea* showed a significantly lower diatom density than control plates (minus  $17\% \pm 2.3\%$ ,  $p < 0.0001$ ) while scyphozoa density was significantly higher (plus  $124\% \pm 35\%$ ,  $p = 0.007$ ). Recruitment of barnacles and hydrozoans was largely unaffected by the presence of snails ( $p = 0.417$  and 0.5, respectively). The impact of *Littorina* grazing differed significantly between diatoms (decrease) and scyphopolyps (increase) (KW  $p < 0.01$ , STP posthoc  $p < 0.05$ ).

### 3.3.4. Consumer-specific sensitivity of coloniser species

The susceptibility of diatoms to grazing differed with regard to consumer species (KW  $p < 0.0001$ ). Diatoms were affected more by *Carcinus* than by *Littorina* and least by *Asterias* (STP  $p < 0.01$  in all cases). The consumer-specific sensitivity of *Laomedea* could not be compared since it occurred too irregularly. The scyphopolyp *Aurelia aurita* was very differently affected by the three consumer species (KW  $p < 0.001$ ). It was more heavily reduced by *Carcinus* than by *Asterias* (STP  $p < 0.01$ ) while it was enhanced by *Littorina* (STP  $p < 0.05$ ). Barnacles were significantly more reduced by crabs than by the other two consumers (STP  $p < 0.01$ ).

## 4. Discussion

In Kiel Fjord, early primary succession (*sensu* Hawkins and Hartnoll, 1983; Raffaelli and Hawkins, 1996) on vertical artificial hard substrata showed a clear pattern: species numbers increased progressively during the first weeks accompanied by a steadily rising diversity of the assemblage. Subsequently the competitively dominant species *Mytilus edulis* increased exponentially leading to a proportional decrease of the inferior species and of assemblage diversity. The dominance of mussels is a product of dense spat fall and fast individual growth (Petraitis, 1995; this study). This monopolising capacity of the blue mussel is wide-spread (e.g. Seed, 1969a,b; Suchanek, 1985; Petraitis, 1990; Reusch and Chapman, 1997; Dürr and Wahl, in press).

Ten weeks after the start of the colonisation process, the new fouling community could be considered a mussel monoculture (species dominance  $> 0.9$ , estimated biomass dominance  $> 0.99$ ) featuring low numbers of associated sessile fauna. At this stage, the assemblage seems to correspond to the scenario of the Menge and Sutherland (1987) model and Huston's (1979) model which under high recruitment, low stress and low predation predicts intense competition and low diversity. The correspondence is, however, not perfect: in the present study diversity decline was brought about mainly by numerical dominance of mussels and less by competitive exclusion of inferior competitors. The ciliate *Folliculina* and the bryozoan *Conopeum* disappeared from the assemblage before the explosive increase of mussel numbers. On the other hand, the recruitment of the tubicolous *Polydora* and *Corophium* coincided with the progressing mussel dominance. This could represent a case of facilitation or just seasonality of recruitment. Indeed, in a parallel study (Dürr and Wahl, in press) where mussel recruitment was inhibited *Polydora* and *Corophium* occupied similar successional positions and recruited in similar seasons (July and August, respectively). Thus, overall species numbers stay more or less constant across successional changes despite increasing mussel dominance.

In the presence of benthic consumption, very different fouling assemblages established. The blue mussel dominance was reduced by predatory activities of *Carcinus maenas*, *Asterias rubens* and/or *Littorina*

*littorea*, while other species persisted only in the presence of consumers. Thus, two species of algae which themselves are potential prey of one of the consumer species (*Littorina littorea*) occurred almost exclusively in the presence of grazers. Apparently, these species were excluded on the no-consumer, mussel-dominated substrata either because their settling stages were eliminated by mussel filtration or because there was not enough plate surface that was not occupied or shaded by mussels. Recruitment onto mussel shells does not occur at this stage because young mussels are protected against fouling by foot-wiping, periostracum chemistry and surface microtopography (Wahl et al., 1998). Under consumption pressure the community's diversity is twice as high as when mussel dominance stays unchecked.

The combined activities of all three consumer species (experiment 2) affected recruitment and community structure in ways whose nature (direct vs. indirect) remains a matter of speculation: The reduced mussel abundance was probably due to direct consumption by shore crabs and starfish. The moderation of the massive *Mytilus* recruitment by natural *Carcinus* and *Asterias* predation allowed the persistence of inferior competitors such as barnacles and algae. Grazing by periwinkles was not sufficient to inhibit the recruitment by algae. The snails were either not numerous enough or their grazing efficiency was hampered by the presence of barnacle-created surface rugosity (Petraitis, 1987; Wahl and Hoppe, 2002). The high abundance of new *Mytilus* recruits on consumer-exposed substrates illustrates how an existing top-down control may be swamped by extreme settlement rates (Menge and Sutherland, 1987; Reusch and Chapman, 1997). On the other hand, their relatively low recruitment on the consumer-sheltered substrates, which at that time were already dominated by mussels, could have been caused by the fouling-reducing cumulative filtration effect described for mussel aggregations (Wahl et al., 1998).

When splitting by consumer species (at enhanced consumer densities) in the last experiment, periwinkles suppressed diatoms and favoured scyphozoan polyps, starfish reduced barnacle and diatom abundances, and in the presence of the shore crab not one species recruited to any extent. This experiment was run in late summer after mussel spatfall. At present, we are unable to explain how *Carcinus* inhibited the

recruitment of diatoms and *Aurelia* polyps, the first being too small to handle and the second (as yet) unknown as a prey item of shore crabs. In a comparable study, Turner and Todd (1991) found similarly drastic effects on recruitment by the snail *Gibbula cineraria*, whereas in their experiment *Nucella lapillus* and, in contrast to our results, *Asterias rubens* did not affect recruitment.

Consumers may either affect a recruiting species directly by consumption or indirectly by preying on a species competing or otherwise interacting with the species under consideration. Additionally, non-lethal direct (Nakaoka, 2000) and indirect consumer effects (Peacor and Werner, 2000) through interaction modification have been reported. All three consumer species tested here may be classified as generalists with wide diets but not without dietary preferences. While *Littorina littorea* is known to prefer microalgae, juvenile macroalgae and ephemeral algae over red and brown adult algae (e.g. Watson and Norton, 1985), the snail may feed on other recruits and/or damage or remove them by pedal mucus secretion and bulldozing. In earlier studies in the same area, this snail's presence reduced recruitment of all algae, of sessile ciliata, of the sedentary polychaete *Polydora ciliata* and of the barnacles *Balanus crenatus* and *B. improvisus* (Wahl and Sönnichsen, 1992). Of all species recruiting in that study, only blue mussels were unaffected by the presence of the periwinkle. The starfish *Asterias rubens* preys preferentially on the blue mussel, but also feeds on endobenthic bivalves, small crustaceans, polychaetes, periwinkles, barnacles and any kind of carcass (Reusch and Chapman, 1997; own obs.). Especially small organisms such as young recruits may be unselectively ingested when the starfish are 'suction-feeding' with everted stomach. Stomach analyses of *Carcinus maenas* showed that they feed on local bivalves and gastropods but also on brown and green algae (Ropes, 1968; Adelung and Ponat, 1977; Elner, 1981). In a more extensive study in the wadden flats of the North Sea, Scherer and Reise (1981) report that the shore crab is an extremely general predator selecting mainly by prey abundance. We could observe that Baltic *Carcinus* feed on mussels and endobenthic bivalves, the mud snail *Hydrobia ulvae* and small periwinkles, the bryozoan *Electra pilosa* and barnacles (Wahl et al., 1997, and unpubl. obs.).

The effects of generalist consumers on a community are potentially greater than those of feeding specialists, because the former may reduce the abundance of preferred prey species to very low levels while gradually shifting to alternative prey (e.g. Bence and Murdoch, 1986; Pacala and Crawley, 1992; Reusch and Chapman, 1997). In the western Baltic, two abundant generalist consumers (*Asterias rubens* and *Carcinus maenas*) prey preferentially on blue mussel. Despite the high feeding pressure we suggest five possible reasons for mussel persistence on hard substrata: (1) recruitment is temporally restricted and intense enough to swamp predator capacity, (2) in the eutrophic waters of Kiel Bight, mussels grow extremely fast and reach refuge sizes of 33 mm for *Asterias* (Reusch and Chapman, 1997) and 40 mm for *Carcinus* (own unpubl. obs.) within 7 to 20 months (Schuster, 1984), (3) during winter (November through April, own obs.) crabs move to deeper waters giving mussels a temporary respite from predation, (4) as pelagic predation on mussels does not seem to be of any importance in this habitat, any substratum not easily accessible to benthic predators (floating object, upper portions of pilings etc.) represents a refuge for source populations of blue mussels, and (5) at increasing consumer densities per capita feeding efficiency decreases as a consequence of behavioural interference (Enderlein, 2000).

Concluding, when benthic consumers are absent, the blue mussel *Mytilus edulis* tends to dominate hard substrata in the western Baltic, reducing and sometimes excluding other sessile species. The clear competitive dominance of the blue mussel is brought about by three properties of this species: extremely dense spat fall, fast individual growth (both bottom-up factors) and the ability to hinder further colonisation by cumulative filtration, a fouling-reducing microtopography and chemistry of the shell periostracum (Petraitis, 1995; Wahl et al., 1998). Natural grazing activities of the benthic consumers *Carcinus maenas*, *Asterias rubens* and *Littorina littorea* strongly control recruitment and succession of shallow subtidal communities on hard substrata in the Western Baltic (top-down control). Blue mussels partially compensate predation-induced mortality by intense recruitment and fast growth (bottom-up compensation). A combination of direct and indirect interactions permits the establishment and

persistence of mixed assemblages consisting of barnacles, algae, mussels, cnidarians and other sessile species despite strongly asymmetrical competition for space between mussels and other sessile species. This balance between bottom-up and top-down forces corresponds to the situation described by Menge (1992) for a *Pisaster*/mussel interaction with the notable difference that western Baltic mussels experience a seasonal release from predation during winter and that diversity is decreased more by mussel dominance than by species exclusions.

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### References

- Adelung, D., Ponat, A., 1977. Studies to establish an optimal diet for the decapod *Carcinus maenas* under culture conditions. Mar. Biol. 44, 287–292.
- Andersson, M., Berntsson, K., Jonsson, P., Gatenholm, P., 1999. Microtextured surfaces: towards macrofouling resistant coatings. Biofouling 14, 167–176.
- Asmus, H., 1987. Secondary production of an intertidal mussel bed community related to its storage and turnover compartments. Mar. Ecol. Prog. Ser. 39, 251–266.
- Bence, J.R., Murdoch, W.W., 1986. Prey size selection by the mosquitofish relation to optimal diet theory. Ecology 67, 324–333.
- Bourget, E., Harvey, M., 1998. Spatial analysis of recruitment of marine invertebrates on arborescent substrata. Biofouling 12, 45–55.
- Brey, T., 1984. Gemeinschaftsstrukturen, Abundanz, Biomasse und Produktion des Markzoobenthos sandiger Boeden der Kieler Bucht in 5–15 m Wassertiefe. Ber. Inst. Meeresk. Kiel 106, 165–191.
- Connell, J.H., 1978. Diversity in tropical rain forests and coral reefs. Science 199, 1302–1310.
- Day, R.W., 1977. Two contrasting effects of predation on species richness in coral reef habitat. Mar. Biol. 44, 1–5.
- Dürr, S., Wahl, M., in press. Competition, species exclusion and diversity on benthic communities. J. Exp. Mar. Biol. Ecol. (in press).
- Elnor, R.W., 1981. Diet of the green crab *Carcinus maenas* (L.) from Port Herbert, Southwestern Nova Scotia. J. Shellfish Res. 1, 89–94.
- Elnor, R.W., Hughes, R.N., 1978. Energy maximization in the diet of the shore crab *Carcinus maenas*. J. Anim. Ecol. 47, 103–116.
- Enderlein, P., 2000. Direkte und indirekte Wechselwirkungen zwi-

- schen Konsumenten, Beute und deren Aufwuchs in *Mytilus*-Gemeinschaften der westlichen Ostsee. Ph.D. Thesis, Kiel University, Germany.
- Enderlein, P., Moorthi, S., Roehrscheid, H., Wahl, M., 2003. Optimal foraging versus shared doom effects: interactive influence of mussel size and epibiosis on predator preference. *J. Exp. Mar. Biol. Ecol.* 292, 231–242.
- Gaines, S.D., Bertness, M.D., 1992. Dispersal of juveniles and variable recruitment in sessile marine species. *Nature* 360, 579–580.
- Glasser, J.W., 1979. The role of predation in shaping and maintaining the structure of communities. *Am. Nat.* 113, 631–641.
- Gosselin, L.A., Qian, P.-Y., 1997. Juvenile mortality in benthic marine invertebrates. *Mar. Ecol. Prog. Ser.* 146, 265–282.
- Hawkins, S., Hartnoll, R., 1983. Changes in a rocky shore community: an evolution of monitoring. *J. Mar. Env. Res.* 9, 131–181.
- Hills, J.M., Thomason, J.C., 1998. The effect of scales of surface roughness on the settlement of barnacle (*Semibalanus balanoides*) cyprids. *Biofouling* 12, 57–69.
- Huston, M.A., 1979. A general hypothesis of species diversity. *Am. Nat.* 113, 81–101.
- Huston, M.A., 1999. Local processes and regional patterns: appropriate scales for understanding variation in the diversity of plants and animals. *Oikos* 86, 393–401.
- Jenkins, S.R., Norton, T.A., Hawkins, S.J., 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.
- Kitching, J.A., Sloane, J.A., Ebling, J.F., 1959. The ecology of Lough Ine VIII. Mussels and their predators. *J. Anim. Ecol.* 28, 331–341.
- Laudien, J., Wahl, M., 1999. Indirect effects of epibiosis on host mortality: seastar predation on differently fouled mussels. *Mar. Ecol.* 20, 35–47.
- Magurran, A.E., 1988. *Ecological diversity and its measurement*. Princeton Univ. Press, Princeton.
- Menge, B.A., 1992. Community regulation: under what conditions are bottom-up factors important on rocky shores? *Ecology* 73, 755–765.
- Menge, B.A., Sutherland, J.P., 1987. Community regulation: variation in disturbance, competition, and predation in relation to environmental stress and recruitment. *Am. Nat.* 130, 730–757.
- Nakaoka, M., 2000. Non-lethal effects of predators on prey populations: predator-mediated change in bivalve growth. *Ecology* 81, 1031–1045.
- Pacala, S.W., Crawley, M.J., 1992. Herbivores and plant diversity. *Am. Nat.* 140, 243–260.
- Peacor, S.D., Werner, E.E., 2000. Predator effects on an assemblage of consumers through induced changes in consumer foraging behavior. *Ecology* 81, 1998–2010.
- 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.
- Petraitis, P.S., 1990. Direct and indirect effects of predation, herbivory and surface rugosity on mussel recruitment. *Oecologia* 83, 405–413.
- Petraitis, P.S., 1995. The role of growth in maintaining spatial dominance by mussels (*Mytilus edulis*). *Ecology* 76, 1337–1346.
- Raffaelli, D., Hawkins, S., 1996. *Intertidal Ecology*. Chapman and Hall, London.
- Raimondi, P.T., 1991. Settlement behaviour of *Chthamalus anisopoina* larvae largely determines the adult distribution. *Oecologia* 85, 349–360.
- Reusch, T., 1994. Factors structuring the *Zostera*- and *Mytilus*-community in the western Baltic: an experimental approach. Ph.D. Thesis, Univ. Kiel, Germany.
- Reusch, T., Chapman, A.R.O., 1997. Persistence and space occupancy by subtidal blue mussel patches. *Ecol. Monogr.* 67, 65–87.
- Rittschof, D., Forward Jr., R.B., Cannon, G., Welch, J.M., McClary Jr., M., Holm, E.R., Clare, A.S., Conova, S., McKelvey, L.M., Bryan, P., Van Dover, C.L. 1998. Cues and context: larval responses to physical and chemical cues. *Biofouling* 12, 31–44.
- Ropes, J.W., 1968. The feeding habits of the green crab, *Carcinus maenas* (L.). *US Fish. Wildl. Serv. Fish. Bull.* 67, 183–203.
- Scherer, B., Reise, K., 1981. Significant predation on micro- and macrobenthos by the crab *Carcinus maenas* L. in the Wadden Sea. Lower organisms and their role in the food web. *Kieler Meeresforsch.* 5, 490–500.
- Schuster, S., 1984. *Tauchuntersuchungen an Mytilusgemeinschaften in der Flensburger Förde: zur Auswirkung von Eutrophierungsprozessen in einem Gradienten organischer Verschmutzung*. Master's Thesis, Univ. Kiel, Germany.
- Seed, R., 1969a. The ecology of *Mytilus edulis* L. (Lamellibranchiata) on exposed rocky shores. I. Breeding and settlement. *Oecologia* 3, 277–316.
- Seed, R., 1969b. The ecology of *Mytilus edulis* L. (Lamellibranchiata) on exposed rocky shores. II. Growth and mortality. *Oecologia* 3, 317–350.
- Sokal, R.R., Rohlf, F.J., 1995. *Biometry*. W.H. Freeman and Co, New York.
- Suchanek, T.H., 1985. Mussels and their role in structuring rocky shore communities. In: Moore, P.G., Seed, R. (Eds.), *The Ecology of Rocky Shores*. Hodder and Stoughton, London, pp. 70–96.
- Turner, S.J., Todd, C.D., 1991. The effects of *Gibbula cineraria* (L.), *Nucella lapillus* (L.) and *Asterias rubens* (L.) on developing epifaunal assemblages. *J. Exp. Mar. Biol. Ecol.* 152, 192–293.
- Wahl, M., Hoppe, K., 2002. Interactions between substratum rugosity, colonization density and periwinkle grazing efficiency. *Mar. Ecol. Prog. Ser.* 225, 239–249.
- Wahl, M., Sönnichsen, H., 1992. Marine epibiosis IV: The periwinkle *Littorina littorea* lacks typical antifouling defences - why are some populations so little fouled? *Mar. Ecol. Prog. Ser.* 88, 225–235.
- Wahl, M., Hay, M., Enderlein, P., 1997. Effects of epibiosis on consumer-prey interactions. *Hydrobiologia* 355, 49–59.
- Wahl, M., Kröger, K., Lenz, M., 1998. Non-toxic protection against epibiosis. *Biofouling* 12, 205–226.
- Watson, D.C., Norton, T.A., 1985. Dietary preferences of the common periwinkle, *Littorina littorea* (L.). *J. Exp. Mar. Biol. Ecol.* 88, 193–211.
- Wilhelmy, J., 1996. In: Hubner, F. (Ed.), *Tauchplätze in der Ostsee*. Jahr-Verlag, Hamburg.
- Worm, B., Lotze, H.K., Hillebrand, H., Sommer, U., 2002. Consumer versus resource control of species diversity and ecosystem functioning. *Nature* 417, 848–851.