Indirect Effects of Epibiosis on Host Mortality: Seastar Predation on Differently Fouled Mussels

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With 4 figures

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Abstract. *In situ* experiments were run with the seastar *Asterias rubens* to investigate the influence of epibiosis on predation preferences. Mussels (*Mytilus edulis*) monospecifically fouled by different epibiont species (the barnacle *Balanus improvisus*, the red filamentous alga *Ceramium strictum*, the sponge *Halichondria panicea* and the hydrozoan *Laomedea flexuosa*) and macroscopically clean mussels were exposed and seastar predation was monitored by SCUBA. *Asterias rubens* preferred macroscopical unfouled mussels as prey. Fouling generally reduced predation pressure on the mussel hosts (associational resistance). Barnacles protected mussels less efficiently than hydrozoans or algae.

We hypothesize that in top-down controlled communities this influence of epibiosis on predation pressure should affect mussel community patterns. A survey of natural mussel–epibiont distribution in the presence or absence of *A. rubens* showed that the prevalence of differently fouled mussels differed between predation-exposed and predation-protected habitats. Natural mussel–epibiont associations reflected the preferential predation of the major local predators. Additionally, higher epibiotic diversity and evenness could be observed at locations accessible to benthic predators as compared with habitats protected from predation.

As blue mussels and seastars are important structuring and controlling elements in the shallow water community of Kiel Fjord, major consequences of epibiosis on the entire system are discussed.

Problem

Blue mussels, *Mytilus edulis*, are one of the dominant inter- and subtidal species of the northern hemisphere with regard to biomass and ecological role (Seed &

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Suchanek, 1992). In the western Baltic Sea, *M. edulis* lives attached to rock surfaces and other hard substrata and forms vast beds in the soft-bottom subtidal (Schütz, 1964; Schwenke, 1969; Reusch, 1994; authors' personal observation). The ecological impact of blue mussels encompasses the filter-cleansing of eutrophic waters (Kellermann, 1981; Brey, 1984), the support of bentho-pelagic coupling and the enhancement of the distribution of eelgrass meadows (Reusch, 1994). Mussel associations are a structural basis for a rich and diverse community (Asmus, 1987; Enderlein, 1996; authors' personal observation).

Blue mussels are often predation-controlled. One of their main predators in the Baltic Sea, the seastar *Asterias rubens*, which is responsible for 85% of mussel mortality in Kiel Bight (Reusch, 1994), is present and active throughout the year (Nauen, 1978; Seed, 1993; Reusch, 1994). Menge (1995) attributed predation control of potentially dominant competitors to be a predominant structuring influence in many benthic communities.

Food quality and defence adaptations are important factors for the survival of a prey-organism which is also affected by the predators' ability to localize, recognize and handle the prey. This is closely linked to the surface qualities of the prey, such as form, size, texture, consistency, colour, smell and/or taste. The presence of epibionts may be expected to drastically alter or mask one or several of the host's surface properties and, consequently, control predation pressure.

As in most marine ecosystems, epibiosis, one of the closest possible associations between different species, is a common phenomenon in the *Mytilus*-community. The fouling of the basibiont creates a new interface between the organism and its environment and thus modifies essential surface features of the host. When epibiosis modulates host-predator interactions, increased survival of host and epibionts (associational resistance) or reduced survival of host and epibionts (shared doom) may ensue (Hay, 1986; Littler et al., 1986; Feifarek, 1987; Barkai & McQuaid, 1988; Pfister & Hay, 1988; Menge, 1995; Wahl & Hay, 1995). Vance (1978) observed removing epibionts from the jewel box clam *Chama pellucida* enhances detection and/or attack of *Chama* by the predatory seastar *Pisaster giganteus* and substantially increases *Chama* mortality through *Pisaster* predation in the field. Furthermore a recent study (Wahl et al., 1997) showed that epibiosis does substantially affect the susceptibility of blue mussels to predation by the generalist predator *Carcinus maenas*. The presence of low-preference epibionts led to avoidance of the basibiont (associational resistance). In contrast, high-preference epibionts increased predation pressure on the host (shared doom).

Consequently, the ecological impact of epibiosis is not limited to its influence on interactions between the basibiont and its abiotic environment (*e.g.*, drag increase, Wahl, 1996, 1997a,b) but includes strong influences on various interactions between the basibiont and other members of the community (Wahl & Hay, 1995; Enderlein, 1996). A detailed description of these interactions is given by Wahl (1997a,b).

The aim of this study was to investigate the effects of epibiosis on *Mytilus*-*Asterias* interactions, this seastar species being the other important mussel predator in the Western Baltic (Reusch & Chapman, 1997). In this context we asked the following questions: (1) do mussel epibionts affect predation preferences by seastar? (2) do different types of epibionts affect *Asterias*-*Mytilus* interactions differently? If certain epibiont species change *Mytilus* mortality through seastar predation, and if the seastar is a top-down controller of the community, the community patterns

should reflect these effects of epibiosis: under predation pressure, *Mytilus* bearing low-preference epibionts should come to dominate, while mussels bearing high-preference epibionts should be reduced through intense predation. We also asked: (3) are epibiotic patterns different in the absence versus presence of seastar, and (4) can different patterns be explained by the epibiont-controlled predation preferences of the seastars?

Material and Methods

1. Location and experimental design

In situ experiments were carried out in a shallow near-shore habitat of Kiel Fjord (54°22.3' N 10°9.4' E). All test organisms – the seastar *A. rubens*, fouled and clean mussels *M. edulis* – were collected by SCUBA near the experimental site. At this location, mussel communities and their major predators, *A. rubens* (all year) and the shore crab *C. maenas* (April–November) were abundant (Wilhelny, 1996; authors' personal observation).

An *in situ* experiment was run to investigate whether different mussel epibionts affect seastar predation on mussels. Fourteen 35 cm × 35 cm × 7 cm polyethylene baskets were individually fixed onto as many cement-filled buckets. These experimental platforms, separated by 100 cm, were installed in a row by the divers at a depth of 6.5 m. The smooth walls of the buckets could not be climbed by the shore crab but allowed *A. rubens* to reach the prey.

A randomized block design was employed. 14 statistically independent baskets were used and in each basket 25 statistically dependent mussels were planted. This batch consisted of five mussels of each of five association types. Seven days after installation of buckets and baskets the experiment was started by randomly placing the mussels in the baskets.

All blue mussels tested had a length between 3 and 5 cm, this being the preferred prey-size range of adult *A. rubens* (Reusch, 1994). The five mussel-epibiont association types were (i) unfouled, and monospecifically fouled by (ii) *Laomedea flexuosa* (hydroid), (iii) *Balanus improvisus* (barnacle), (iv) *Halichondria panicea* (sponge) or (v) *Ceramium strictum* (filamentous red alga). These were the most common mussel epibionts at the experimental site.

Those mussel(s) on each platform that had been consumed by seastars was/were noted during diving surveys (twice a week until day 37). A mussel was considered 'consumed' when it was open and empty or when a seastar had begun the extra-intestinal digestion. If seastars had begun to open the fifth mussel of a given association on a basket, the results of this block were not included in the analyses. During the surveys, consumed mussels were not replaced.

2. Statistics

As the five mussels on each experimental platform could not be regarded as independent, a one-way analysis of variance was not appropriate (Peterson & Renaud, 1989). Therefore we used the nonparametric Friedman test (rank-variance analysis, Friedman, 1937, 1940) as Stachowicz & Hay (1996) suggested. This test is conceived as a one-factorial analysis of variance with dependent treatments (mussels of one platform), as it compares the preference rank sums of differently fouled mussels. The replicates (platforms) were independent (Conover, 1980; Coon, 1988). In order to test for differences between treatments, multiple comparisons were carried out by an advanced U-statistic developed by Sokal & Rohlf (1995). Since these tests are not available in standard statistical software, a Visual-BASIC module programmed by Köhler (1997) for Microsoft Excel 5.0 was used.

To test whether predation preference was affected by mussel size, all shells of consumed mussels with still recognizable epibiotic species were collected and measured with a caliper rule to the nearest millimetre in the laboratory. Since the five mussel-epibiont associations (dependent) of a basket were used independent with respect to size, a Kruskal-Wallis test was carried out to test whether all mussels used belong to the same size population.

3. Distribution of mussel–epibiont associations in the habitat

We assessed whether the epibiont-mediated feeding preferences of *A. rubens* affect the composition of epibiotic communities on mussels in the natural environment. In order to avoid differences due to variability in current regimes at two different study sites, a nearby protected study area was chosen (out-of-use harbour basin, distance to *in situ* experiments: 150 m). The mussel communities on the vertical surface of pilings (diameter: 60 cm, accessible to benthic predators) and on the vertical surface of a concrete swimming pontoon (length: width: height = 5 m : 3.5 m : 1.7 m, not accessible to benthic predators) were inventoried at a depth between 50 cm and 150 cm. Only the south-facing section of the pilings and pontoon were investigated in order to avoid any between-sites differences resulting from different orientation. Due to the short horizontal distance between these two substrata (<30 m) and the identical study depth it was assumed that the mussels on pilings and those on the pontoon experience similar colonization pressure by the same epibiont species.

Haphazardly chosen (closed eyes) 109 mm × 164 mm areas of the mussel communities were photographed using a Nikonos V-reflex camera (35 mm lens) and Nikonos 102 UW-flash (TTL mode). Projecting the slides in the lab at 1 : 4.5 enabled macroscopic epibionts to be identified and their presence/absence noted. This method had provided reliable results: subsequently sampling the communities of photographed frames and comparing specific abundance as seen on the slides with those in the sampled material yielded no significant differences.

A Friedman test was applied as neighbouring mussels (on the same photograph) could not be regarded as independent. It was employed to determine whether the epibiotic species on mussels were differently distributed between the two sites. As described above, multiple comparisons were carried out by the U-statistics developed by Sokal & Rohlf (1995).

Results

Although seastars started to climb the buckets immediately, shore crabs were unable to reach the test mussels at all. It was assumed that fish did not prey on the mussels since they would not have left intact shells in the baskets. Therefore, *A. rubens* alone was responsible for all mussel mortality observed in this experiment.

1. In situ-experiment on predation preferences of Asterias rubens

One hundred and twenty (34.3%) of 350 tested mussels were opened during the 37 days of the experiment. Epibionts affected seastar predation preference significantly (Friedman test: 22.786; d.f. = 4; P < 0.0001), and the following trends were apparent (Fig. 1).

(a) Macroscopically clean mussels were opened by *A. rubens* significantly more often than any of the mussels fouled by the test epibionts.

(b) Mussels with *B. improvisus* or *H. panicea* were consumed significantly more than those fouled by *L. flexuosa*, and significantly less than macroscopically clean mussels. No significant differences were found between the two mentioned mussel–epibiont associations and *C. strictum*-fouled mussels (see Fig. 1, letter B).

(c) Mussels carrying *L. flexuosa* were least preferred. However, they did not differ significantly from *C. strictum*-fouled mussels in this regard (see Fig. 1, letter C).

Mussel size (within the range used) had no effect on seastar predation preference (Kruskal-Wallis test: $\chi^2 = 6.835$; d.f. = 4; P < 0.1449).
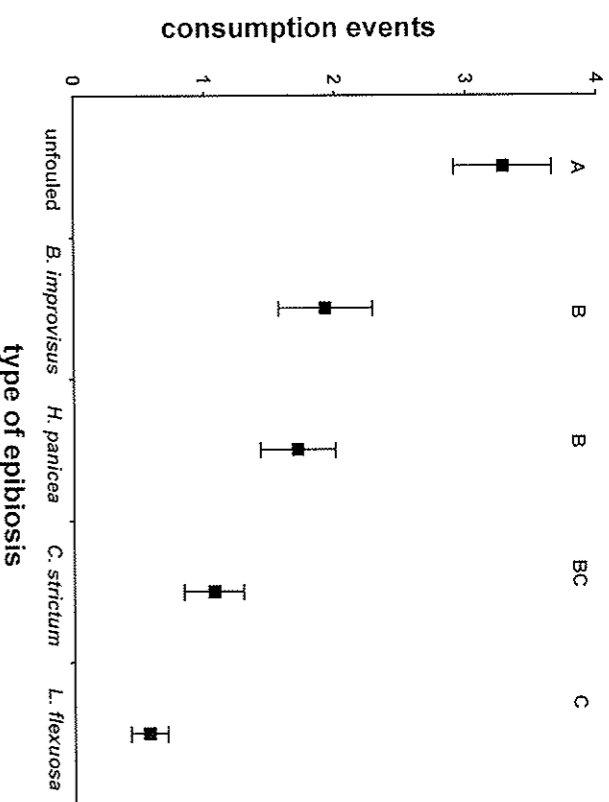

Fig. 1. *In situ* experiment: mean (±SE) frequency of *Asterias rubens* preference for a given mussel–epibiont pair given a choice of five alternatives. Treatments sharing a letter (top line) do not differ significantly.

2. Distribution of mussel–epibiont associations in the field

In 38 colour slides taken on the pilings (predation-exposed areas), a total of 757 mussels were examined for epibionts. The abundance of mussel epibionts here differed significantly (Friedman test: $\chi^2 = 96.402$; d.f. = 5; P < 0.01; Fig. 2).

Due to a higher stock density, 1235 mussels could be examined for epibionts in the 35 slides taken of the pontoon community (predation-protected areas) on the same day. As before, highly significant differences regarding epibiont prevalence were found (Friedman test: $\chi^2 = 122.637$; d.f. = 5; P < 0.01: Fig. 2).

The following significant differences were observed in the two habitats (Fig. 2):

(a) Under predation pressure, a higher proportion of mussels (> 80%) was fouled than when sheltered (50%).

(b) Under both conditions, *Balanus improvisus* was the most common epibiont, but its dominance is much more dramatic at the predator-free site.

(c) *Laomedea flexuosa* is common under predation, but rare in the absence of predators.

(d) *Polydora* sp. and chlorophytes were regularly found (5–10%) on predation-exposed mussels, while they were virtually absent under sheltered conditions.

(e) The epibiotic sponge *Halichondria panicea* was rare at this depth.

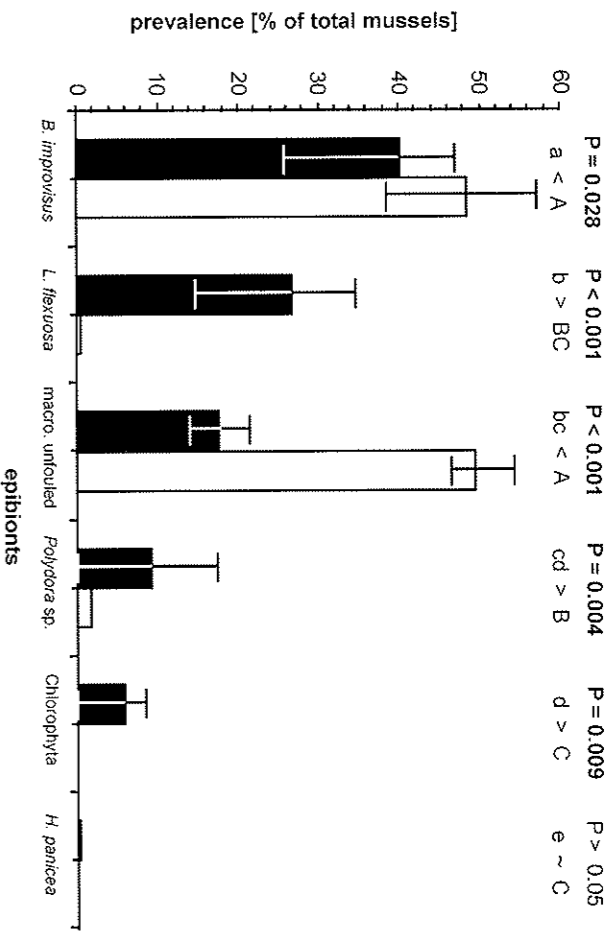The prevalence of most epibiont categories differed significantly between predator exposure conditions (Fig. 2).

prevalence [% of total mussels]

epibionts: B. improvisus, L. flexuosa, macro. unfouled, Polydora sp., Chlorophyta, H. panicea

P = 0.028   a < A
P < 0.001   b > BC
P < 0.001   bc < A
P = 0.004   cd > B
P = 0.009   d > C
P > 0.05   e ~ C

Fig. 2. Prevalence (median and interquartile) of different epibiont species in (black bars) predation-exposed (38 replicates) and (white bars) predation-protected (35 replicates) mussel communities. Significant differences between the two habitats are marked by letters. Treatments sharing a lower case letter (predation-exposed) or an upper case letter (predation-protected) do not differ significantly. P-values of species-specific differences between predation-exposed and predation-protected habitats are indicated at the top.

The entire pontoon was searched for benthic predators. No shore crabs or seastars were found.

Consequently, the composition of the epibiotic communities on mussels differed between predation-exposed and predation-sheltered habitats (Fig. 3). Multiple comparisons with the U-statistic developed by Sokal & Rohlf (1995) reveal that barnacle-fouled and clean mussels were more common in the latter, while hydrozoans, polychaetes and algae were more common in the former.

Furthermore, in the presence of predators (pilings) the epibiotic community is more diverse (Shannon-Wiener index; exposed: H′ = 1.43, protected: H′ = 0.81; evenness: exposed: 0.8, protected: 0.5).

Epibiont prevalences assessed on live material and from photographs of the same material did not differ (F-test: $\chi^2 = 0.857$; d.f. = 6; P > 0.05).

Discussion

1. Influence of epibiosis on seastar-predation

This study shows that epibiosis strongly affects the predation of *A. rubens* on the mussel *M. edulis*. The effects of epibiosis depend on the epibiotic species covering

Fig. 3. Typical aspects of the *Mytilus*-epibiont community (a) accessible to benthic predators and (b) inaccessible to benthic predators.

the potential prey. The following preference gradient from most to least preferred epibiont–prey association was found: clean mussel > *B. improvisus*/mussel ≥ *H. panicea*/mussel ≥ *C. strictum*/mussel ≥ *L. flexuosa*/mussel.

2. Associational resistance and shared doom effects

The observed protective effects (associational resistance) of epibiosis for the basibiont function such as an 'epibiotic protective casing' by chemical or mechanical (structural) means (Duffy & Hay, 1994; Durante & Chia, 1991; Bloom, 1975; Forester, 1979; Pitcher & Butler, 1987) or as visual or chemical camouflage (Littler *et al.*, 1986; Hay, 1986). This indirect defence of a species by association with another species was first described by Tahvanainen & Root (1972) and Root (1973) and subsequently confirmed by various authors for marine systems (Hay, 1986; Feifarek, 1987; Barkai & McQuaid, 1988; Gil-Turnes *et al.*, 1989; Wahl & Hay, 1995; Enderlein, 1996). Some investigations showed that potential prey find protection from predators in eelgrass meadows: the success of epibenthic and endobenthic predators may be reduced by structures on (Heck & Thoman, 1981; Weinstein & Brooks, 1983; Bell & Westoby, 1986) or within the sediment (Brenchley, 1982). Juvenile mussels (*Argopecten irradians*, *M. edulis*) are exposed to a lower predation pressure by benthic predators when they settle on eelgrass (Pohle *et al.*, 1991; Ambrose & Irlandi, 1992; Reusch, 1994). A snail species is protected from lobster predation by an epibiotic bryozoan (Barkai & McQuaid, 1988), whereas another epibiotic bryozoan reduces snail predation on kelp (Durante & Chia 1991). Bloom (1975) and Feifarek (1987) report that epibiotic sponges protect mussels from predation by seastar. Palatable algae may escape grazing by sea urchins when covered by low-preference epibionts (Wahl & Hay, 1995). Enderlein (1996) showed the reduced attractiveness of mussels to *C. maenas* when fouled by hydrozoans.

The opposite effect (shared doom) – the increase of prey attractiveness by more conspicuous or more palatable epibionts – has been described for fish preying on the seaweed *Macrocystis pyrifera* covered by bryozoans (Bernstein & Jung, 1979), for sea urchins grazing on normally avoided algae when these were covered by more palatable epibionts (Wahl & Hay, 1995) and for crab predation on mussels fouled by barnacles (Enderlein, 1996).

No effects of this kind were observed for predation on *A. irradians* fouled by algae and invertebrates (Prescott, 1990), on *Mytilus californianus* fouled by algal epiphytes (Dittman & Robles, 1991) or for crab predation on *M. edulis* fouled by *C. strictum* (Enderlein, 1996). Consequently, many epibiont species have the potential to increase or decrease predation-caused mortality of their hosts. When predation is a locally strong structuring factor, different epibiont–mussel associations should dominate in predation-exposed versus predation-sheltered sites.

Indeed, the two adjacent mussel communities examined here differed strongly, and the demonstrated predation preference behaviours of *A. rubens* and *C. maenas* (Enderlein, 1996) can explain the unequal distribution of epibionts: these two main predators have access to the pilings but not to the pontoon.

First, there were fewer mussels per unit area in the presence of predators (Enderlein, 1996). Of these, more were fouled by the low-preference hydrozoan

(as for *A. rubens* and *C. maenas*) and algae (as for *A. rubens*) compared with mussels from the pontoon, and fewer with high-preference (for *C. maenas*, see Enderlein, 1996) barnacles. Thus, under predation pressure, the prevalence of epibionts correlates directly with their predation-reducing effect, probably through differential survival of their hosts (shared doom and associational resistance, Fig. 4).
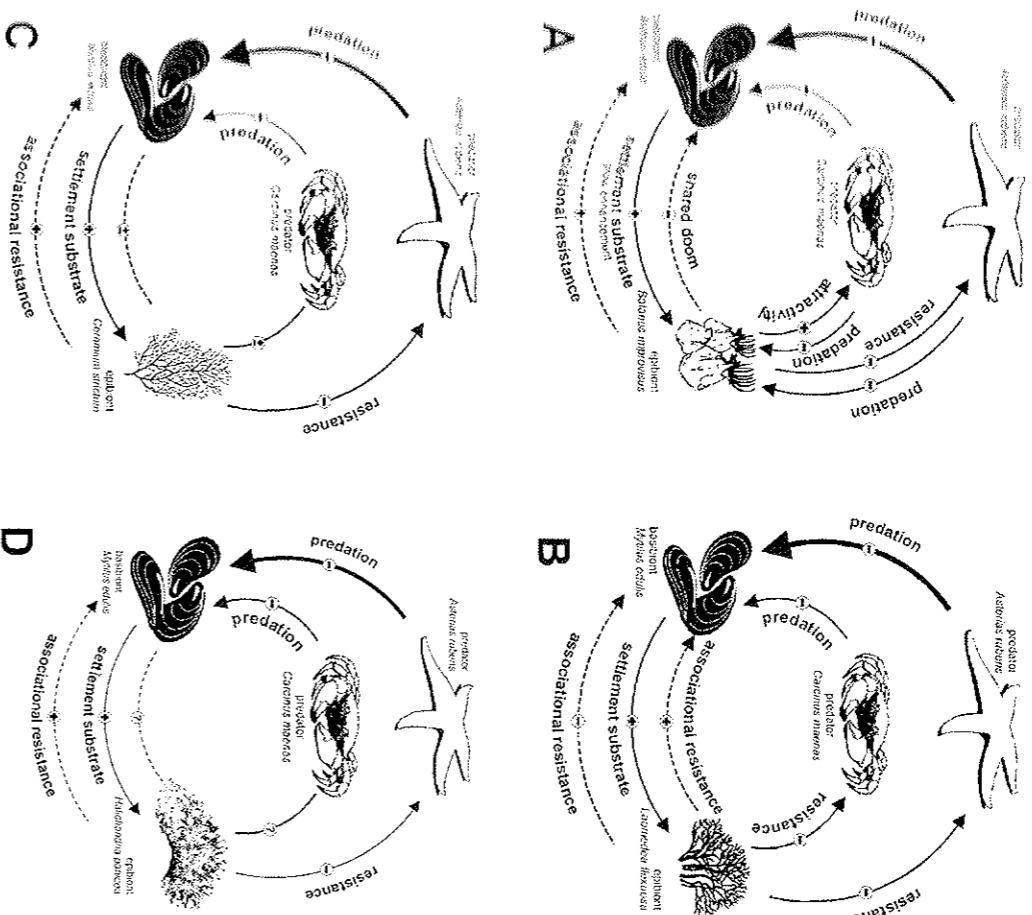

Fig. 4 Interactions between the basibiont *Mytilus edulis*, different epibiotic species and the predators (seastar *Asterias rubens* and *Carcinus maenas*). Interactions between predators, prey (mussel) and A: *Balanus improvisus*, B: *Laomedea flexuosa*, C: *Ceramium strictum* and D: between seastars, prey and *Halichondria panicea* (indirect interactions with *Carcinus maenas* not examined). The arrows give the direction of direct (solid line) and indirect (broken line) interactions caused by epibionts; + stands for positive, – for negative interactions. Increased survival of mussels is caused by 'associational resistance'; reduced survival by 'shared doom'. Interactions with *C. maenas* after Enderlein (1996).

The decreased dominance of high-preference prey (clean mussels, mussels bearing barnacles) under predation pressure is probably caused by preferential predation by *C. maenas* and *A. rubens* on these. The conspicuous dominance of barnacles in the predation-sheltered site may be due to the competitive exclusion of other epibionts, mainly hydrozoans, when barnacles are freed from predation and when hydrozoans did not improve the survival of their hosts. The study area was well protected by a wall, because in nonprotected habitats problems with different current regimes could arise; the vertical surfaces of pilings probably deflect the current and thus deflect larvae away from the settling surface, reducing the number of settling larvae. The pontoon side, on the other hand, presents a vertically orientated surface that can be viewed as a plane. The current flow along this plane might encourage larval settlement, particularly since mussels create an irregular surface with a thick boundary layer. However, in the extremely calm harbour basin the effect of these factors on recruitment dynamics should be minimized.

3. Keystone species and epibiosis as controlling factors in a sessile community

Blue mussels play a central part in structuring the nearshore ecosystem of the Baltic Sea (Reusch, 1994; Reusch & Chapman, 1997). They provide habitat to many associated animals and plants, stabilize the sediment, promote the spreading of eelgrass, filter huge amounts of water, promote benthic-pelagic coupling, *i.e.* the transfer from pelagic primary production to the benthic community (faecal pellets, pseudo pellets and other organic debris) and are food for various species (Ebling *et al.*, 1964; Walne & Dean, 1972; Asmus, 1987; Brey, 1984). Changes in the abundance of *M. edulis* probably have widespread effects on the whole shallow-water community. According to the keystone predator concept (Paine, 1974), a community may be controlled by one or a few keystone species. While this concept remains controversial (*e.g.*, Elner & Vadas, 1990; Foster, 1990; Chapman & Underwood, 1990), it seems to apply in many locations (*e.g.*, Yamada & Boulding, 1991; Menge *et al.*, 1994), especially when bottom-up (eutrophication favouring mussel growth) and indirect effects like epibiont-modulation of predation pressure are taken into consideration.

Asterias rubens is an important predator in the soft-bottom community dominated by *M. edulis* beds of Kiel Bight. It is responsible for 85% of mussel mortality and thereby strongly influences mussel population dynamics (Kautsky, 1981; Himmelman & Dutil, 1991; Seed, 1993; Reusch, 1994; Reusch & Chapman, 1997). The second most important predator during the summer months is *C. maenas* (Kitching *et al.*, 1959; Ebling *et al.*, 1964; Walne & Dean, 1972). Both predators are keystone species in this community (Reusch, 1994). The results of this study on *A. rubens* and of an earlier investigation on *C. maenas* (Enderlein, 1996) show that epibiosis can control the interactions between these keystone predators and their main prey. Therefore, epibiosis itself, by modulating predation-caused mortality of mussels, can act as a structuring element of the community.

Thus, any factor changing the species composition of (*e.g.*, introduction of allochthonous epibionts or predators of epibionts) and relative abundance within

the epibiotic community on *M. edulis* (*e.g.*, eutrophication) may have a hitherto unexpected impact on this ecosystem.

Summary

When choosing *in situ*, the seastar *A. rubens* significantly preferred unfouled mussels (*M. edulis*) over mussels fouled by either barnacles (*B. improvisus*), hydrozoans (*L. flexuosa*) or filamentous red algae (*C. strictum*). This protection by epibionts (associational resistance) was more significant in the case of epibiotic hydrozoans and algae, than when mussels were colonized by barnacles.

A survey of two habitat types, accessible versus nonaccessible to *A. rubens* (and other benthic predators) revealed differences in epibiont prevalence which reflect (and presumably are caused by) the observed preferential predation of major local predators. Additionally, higher diversity and evenness of the epibiotic community was found in the presence of predation compared with habitats protected from this kind of biotic disturbance.

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