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Associational resistance of fouled blue mussels (*Mytilus edulis*) against starfish (*Asterias rubens*) predation: relative importance of structural and chemical properties of the epibionts

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Abstract Several epibiotic species reduce starfish (*Asterias rubens*) preference for the blue mussel *Mytilus edulis* in the Baltic. The aim of this study was to reveal whether this associational resistance was caused by structural or chemical aspects of the different epibionts. To assess structural epibiont effects, an in situ experiment was conducted with unfouled mussels and mussels equipped with artificial epibionts ('dummies') exposed to natural predation by *A. rubens*. The chemically inert dummies closely matched the structural properties of the locally common epibionts *Balanus improvisus* (barnacle), *Ceramium strictum* (red alga), *Halichondria panicea* (sponge), and *Laomedea flexuosa* (hydrozoan). Starfish fed indiscriminately in all treatments. Chemical effects of epibionts on the attractiveness of mussels for *A. rubens* were investigated by incorporating freeze-dried epibionts or mussel tissue into Phytigel pellets at natural concentrations. Starfish were allowed to choose among these structurally similar but chemically different prey items in an in vitro experiment. The predators exhibited significant preferences among the food pellets, which closely matched their preferences for corresponding natural mussel–epibiont associations. Thus, chemical aspects of epibionts appear to play a larger role in this associational resistance than do structural aspects. Implications of these indirect interactions for benthic communities are discussed.

Keywords *Asterias rubens* · *Mytilus edulis* · Epibiosis · Structural vs. chemical defence · Associational resistance

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Introduction

Epibiosis, one of the closest possible interspecific associations, is a common phenomenon in shallow subtidal mussel communities. In the Baltic Sea, the blue mussel *Mytilus edulis* dominates subtidal communities (e.g. Brey 1984) and generates a three-dimensional hard substrate (e.g. Reusch and Chapman 1997; Laudien and Wahl 1999). In the western Baltic these bivalves are often colonised by the barnacle *Balanus improvisus*, the hydrozoan *Laomedea flexuosa*, the sponge *Halichondria panicea*, diverse filamentous algae such as *C. strictum*, the polychaete *Polydora* sp. and, to a lesser extent, the bryozoan *Membranipora pilosa*. Fouling of the basibiont creates a new interface between the basibiont and its environment. Most interactions between a living organism and its biotic and abiotic environment (e.g. predation, mating, defence, mutualism, parasitism, symbiosis, drag) are linked to essential surface features of the organism in question (e.g. form, size, texture, consistency, colour, smell, or taste). A modification of the interface between an organism and its environment can affect one or more of the above interactions. A more detailed description of these interactions is given by Wahl (1989, 1997). To date, epibiosis has been shown to influence drag (Wahl 1996; Gonzalez et al. 2001), fungal infection (Gil-Turnes et al. 1989), and consumption pressure (see references in Table 1).

Recent studies (e.g. Wahl et al. 1997; Laudien and Wahl 1999; Saier 2001) have demonstrated that epibiosis can substantially affect predation by the two locally common mussel predators, the shore crab *Carcinus maenas* and the starfish *Asterias rubens*. Low-preference epibionts such as hydrozoans simply led to avoidance of the basibiont by both consumer species (associational resistance; 'preference' in this article refers to feeding on one prey item instead of others when offered simultaneously). In contrast, barnacles increased predation by shore crabs (shared doom effect) while they decreased predation by starfish (associational resistance effect). There is circumstantial evidence that the interactions between mussels, epibionts, and their consumers may be of

Table 1 Examples of epibiont effects enhancing or reducing predation risk

Epibiont on basibiont	Predator	Shared doom (risk increased)	Associational resistance (risk reduced)	Reference
Bryozoan on kelp	Fish	Optical or chemical attraction (?)		Bernstein and Jung 1979
Bacteria on crustacean embryos	Fungus		Chemical defence	Gil-Turnes et al. 1989
Bryozoans on whelk	Lobster		Chemical defence	Barkai and McQuaid 1988
Bryozoans on whelk	Rock lobster		Chemical defence	Gray et al. 2000
Sea anemones on hermit crab	<i>Octopus joubini</i>		Defence (?)	Brooks and Mariscal 1985
Protists on <i>Daphnia</i>	Salamanders	Optical apparency		Threlkeld and Willey 1993
Algae on algae	Sea urchin		Chemical attraction	Wahl and Hay 1995
Algae on algae	Sea urchin	Chemical camouflage		Wahl and Hay 1995
Hydrozoans on blue mussel	Shore crab		Chemical repellency	Wahl et al. 1997
Barnacles on blue mussel	Shore crab	Chemical attraction		Wahl et al. 1997
Bryozoans on kelp	Snails		Mechanical or chemical defence	Durante and Chia 1991
Sponges on scallops	Starfish		Camouflage	Pitcher and Butler 1987
Algae on clam	Starfish		Chemical camouflage	Vance 1978
Sponge, barnacles, red alga, hydrozoa on blue mussel	Starfish		Chemical camouflage	This study
Sponge on oyster	Starfish		Optical and chemical camouflage	Feifarek 1987
Sponge on scallop	Starfish		Tactile-mechanical protection	Bloom 1975
Sponge on scallop	Starfish		Tactile-mechanical protection	Forester 1979
Trapeziid crabs on corals	Starfish		Defence (?)	Pratchett 2001

strong structuring importance in western Baltic communities. In fact, a survey of mussel–epibiont associations showed that habitats exposed to predation by *C. maenas* had a large proportion of unfouled and hydroid-fouled mussels while habitats sheltered from these predators had mostly barnacle-fouled mussels (Wahl et al. 1997). A similar pattern was observed in habitats with and without benthic predators (Laudien and Wahl 1999).

After establishing the fact that epibionts do, in many instances, affect predation, we tried to gain insight on how these effects are brought about. The major steps in predator–prey interaction are identification, handling, and ingestion. In this study we focussed on the first two steps. Predation by starfish is responsible for about 85% of mussel mortality on Kiel Bight soft bottoms (Reusch and Chapman 1997). According to Nauen (1978), *A. rubens* mainly uses olfactory (smell) and tactile information (taste, touch) for the identification of prey. It is conceivable that epibionts may alter both types of signals. Additionally, epibionts may interfere with handling of the prey, for example, by inhibiting tube feet adhesion to the mussel shell. In this study we investigated both possibilities by offering starfish (1) mussels equipped with artificial epibionts simulating epibiotic barnacles, hydrozoans, and sponges, respectively (near-natural structural effects, no chemical effects), and (2) smooth artificial food pellets containing ground prey species (near-natural primary and secondary chemical effects, negligible structural effects).

Methods

In situ experiment to test structural influence of epibionts on starfish predation

A shallow near-shore habitat of Kiel Fjord (western Baltic, 54°22.3'N, 10°9.4'E) was chosen to carry out an in situ experiment. At this location, mussel communities with their common epibionts (the hydroid *Laomedea flexuosa*, the barnacle *Balanus improvisus*, the sponge *Halichondria panicea*, the red alga *Ceramium strictum*) and their major predators, the starfish *Asterias rubens* (all year) and the shore crab *Carcinus maenas* (April–November) are abundant (Wilhelmy 1996; J. Laudien, personal observation). All test mussels *Mytilus edulis* were collected by SCUBA at the experimental site. As the 30- to 50-mm mussel size class is preferred as prey by adult *A. rubens* (Reusch and Chapman 1997) only mussels within this length range were used. Bivalves were brushed clean to remove macroscopic epibionts and assigned randomly to one of the five treatment groups: 'hydrozoan/alga-fouled' (i.e. erect filamentous epibionts), 'barnacle-fouled', 'sponge-fouled', 'glue control', and 'clean'. The following materials were used as epibiont dummies: aquarium filter filaments imitating filamentous epibionts such as *Ceramium strictum* (red alga) and *L. flexuosa* (hydroid), and soft foam material imitating *H. panicea* (sponge). *B. improvisus* dummies were hand modelled using two-component glue (Z-Spar, A-788 Splash Zone Component, Koppers Co.). All materials were chosen to match closely the mechanical properties (size structure, flexibility, consistency, etc.) of the epibiont species they were intended to imitate. To fix these materials onto the air-dried mussel shells, the periostracum was roughened with a sanding disc connected to a hand drill. The dummies were attached using Z-Spar. To be able to assess effects of the glue itself, mussels of a control group were covered by a thin glue layer only. Clean mussels represented the fifth treatment.

Fourteen experimental platforms (35×35×7 cm, described in Laudien and Wahl 1999), which allowed access by *A. rubens* to the prey but prohibited access by *C. maenas*, were installed by SCUBA at 100-cm intervals in a straight line at a depth of 6.5 m. A randomised block design was chosen: five mussels of each treatment (a total of 25 statistically dependent mussels) were positioned on each platform. A total of 14 statistically independent (Hurlbert 1984)

platforms were used. Prey items were placed randomly on the experimental platforms. For 1 week they were sheltered from predation by a plastic grid to allow mussels to attach and adapt. Further, any diffusive substances from glue and dummy material could dissipate during this phase. The removal of the grid on day 8 started the experiment. Twice a week, we noted which mussel(s) of each platform had been consumed by starfish (last control on day 36) as described in Laudien and Wahl (1999).

Statistics

As mussels of one experimental platform could not be regarded as independent we used the nonparametric Friedman test (rank-variance analysis, Stachowicz and Hay 1996). To test for differences between treatments, multiple comparisons were carried out by an advanced *U*-statistic including Bonferroni correction where required (Sokal and Rohlf 1995).

To test whether predation preference was affected by mussel size all shells of consumed mussels were collected and measured with a calliper rule to the lower millimetre. Possible size selectivity of *A. rubens* for different mussel size classes within a treatment was tested by a Kruskal–Wallis test.

Laboratory experiments to investigate chemical attraction

To assess the role of chemical cues in choice of prey by starfish an *in vitro* experiment was carried out. Individual *A. rubens* were allowed to choose among six types of smooth artificial food pellets containing freeze-dried, ground mussel or epibiont tissue.

All test organisms (the starfish *A. rubens*, unfouled mussels *M. edulis*, and common epibionts) were collected by SCUBA at the experimental site. The starfish were kept in a 2-m³ tank that was part of a closed-circuit system (volume 5-m³, salinity 17–18 psu, temperature 15°C). Preference experiments were conducted in experimental tanks (50×70×20 cm) without flow, since *A. rubens* exhibits positive rheotaxis to currents (Castilla and Crisp 1973; Lippert and Iken 2003). Before each test run the water of the experimental tanks was replaced and the tanks were cleaned with fresh water. All laboratory tests were carried out under a light:dark rhythm of 13:11 h, representing the actual *in situ* photoperiod.

Epibionts used were *H. panicea*, *C. strictum*, *B. improvisus*, and *L. flexuosa*. In the laboratory, epibionts were cleaned from associated organisms under a dissecting microscope. Mussel tissue and epibionts were frozen at –10°C and freeze-dried to constant mass. The samples were ground to a fine powder with an electrical grinder. To determine the organic contents of the samples, additional sub-samples were dried at 60°C for 24 h, weighed, then combusted at 500°C for 6 h and ash-free dry mass calculated (e.g. Gaffney and Diehl 1986; Rumohr 1990). Artificial food pellets were prepared according to Henrikson and Pawlik (1995). Gels were prepared by stirring 2.17 g Phytigel (Sigma Chemical) into 50 ml distilled water using a magnetic stirrer. This mixture was heated to boiling in a microwave and thereafter allowed to cool slowly in a 35°C warm water bath. Under constant stirring an amount of powdered prey (epibiont or mussel) yielding the estimated natural concentrations of organic material was added (*C. strictum* 2.8%, *B. improvisus* 4.9%, *H. panicea* 4.2%, *L. flexuosa* 10.5%, *M. edulis* 5.0%). The mixture was poured into a 150×150-mm square dish. After solidification, 16-mm-diameter circular discs were punched out of the 2-mm-thick gel layer. These ‘food pellets’ were stored in a water-saturated atmosphere at 4°C and used for testing within the following 2 days. Starfish (approximately 100 mm in diameter) were allowed to adapt to the laboratory’s closed-circuit system for 2 weeks. For each test, a single starfish was placed in a vertical opaque PVC pipe (height: 300 mm, diameter: 125 mm) in the centre of an experimental tank. Six ‘food-pellets’ (five with content, one pure Phytigel control) were positioned in random order but in equally spaced positions on a circle of 170 mm diameter around the pipe. The pellets were placed with the former lower, smooth side to the top to prevent artefacts from

structural properties (e.g. spicules). During the following hour, a chemical gradient was allowed to establish around the food pellets outside the pipe walls. The prey-choice test was started by carefully lifting the pipe, putting the starfish into contact with the presumptive chemical gradients. Subsequently, the pellet over which the starfish first assumed its characteristic feeding position (Hancock 1955; Lavoie 1956; Nauen 1978) was noted as ‘chosen’. In this way, the preference behaviour of 48 animals was assessed. Each food pellet and starfish was used only once.

Statistics

Since the six choice alternatives (offered food pellets) in any given run were not independent, the statistical evaluation was carried out by Cochran’s *Q*-test (Cochran 1950). Subsequently, multiple pairwise comparisons after Marascuilo and McSweeney (1967) allowed us to check for significant differences between the relative attractiveness of differently loaded food pellets.

Results

Structural influence of epibionts on predation preferences of *Asterias rubens*

Twenty percent (69 of 350) of the test mussels were opened and consumed during the 36 days of the *in situ* experiment. The structurally different epibiont dummies did not affect starfish predation preference (Friedman test: 4.49, *df*=4, *P*>0.3; Fig. 1).

Chemical aspects of predation preference

Forty-two percent (20 of 48) of the tested starfish chose one of the artificial food pellets offered. Test animals discriminated significantly between the different food pellets (Cochran’s *Q*-test: 22.6, *P*<0.001, *n*=20). Food pellets containing dried mussel tissue were significantly preferred over pellets containing dried sponge, dried hydroid, or pure Phytigel, while pellets containing red alga powder or barnacle powder were of intermediate attractiveness (Fig. 2).

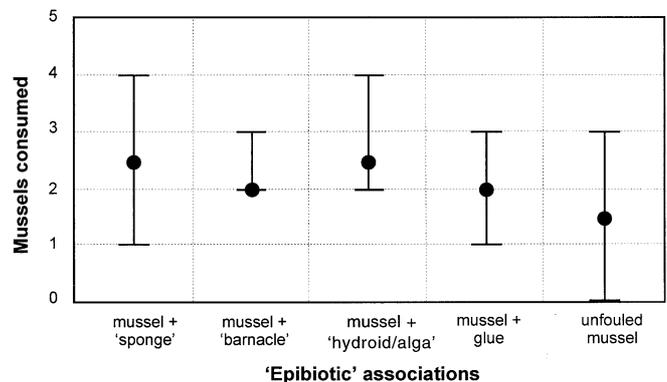


Fig. 1 *In situ* experiment: structural effects of epibionts. Numbers of mussels consumed bearing different epibiont dummies, glue only, or neither dummy nor glue (14 replicates with, initially, five mussels of each treatment); median and interquartile range

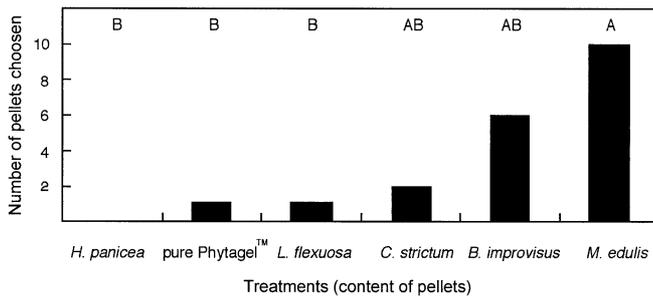


Fig. 2 Choice of differently loaded Phytigel ‘food pellets’ by *Asterias rubens*. Treatments sharing a letter (*top line*) do not differ significantly

Discussion

Epibiosis strongly affects predation by *Asterias rubens* on blue mussels *Mytilus edulis* (Saier 2001). Laudien and Wahl (1999) observed a preference gradient from most- to least-favoured prey (unfouled mussel > *Balanus improvisus*-fouled mussel > *Halichondria panicea*-fouled mussel > *Ceramium strictum*-fouled mussel > *Laomedea flexuosa*-fouled mussel). Given the locally strong predation pressure of *A. rubens*, selective consumption by this consumer influences the structure of epibiont–mussel communities in nature. The present study reveals that structural properties of the epibionts investigated do not affect identification and handling and thus are not important for the associational resistance of epibiotically protected bivalves. In contrast, Bloom (1975) suggested that the observed protection of scallop by epibiotic sponge was caused by a reduction of tube feet adhesion to the new interface. The lack of a comparable effect in our experiment could be due to the availability of non-fouled shell surface: matching typical local fouling prevalence, we had attached artificial epibionts to only 20–50% of the shell surface.

On the other hand, starfish preference behaviour closely matched the observed in situ epibiont–mussel–starfish interactions (Laudien and Wahl 1999) when offered ground mussel or epibiont tissues in artificial food. However, it should be kept in mind that grinding might have liberated chemical compounds that are not associated with natural odours. Unfouled mussels and, to a lesser extent, barnacles were preferred over the filamentous red alga, the hydroid, and the sponge species. We have no indication of any repulsive effects since even the least preferred foods (*L. flexuosa* and *H. panicea*) were not significantly less consumed than pure Phytigel. Since structural and physical aspects of the prey items were similar, we conclude that the observed differences in attractiveness were caused by chemical properties (secondary chemistry or nutritional value) of the incorporated organisms. In about 50% of the cases, the starfish moved directly to the prey they subsequently tried to ingest. In the remaining instances, other food pellets were contacted first and then rejected. Apparently, olfactory orientation due to the ability to discern chemical gradients across the

arms is a good (Castilla and Crisp 1970; Dale 1997; Swenson and McClintock 1998) but not always reliable way to locate favoured prey from a distance. Final identification seems to be made on contact especially by the sensory tube feet (for review see Sloan 1980; Sloan and Campbell 1982). The reason why the favoured food pellets were often not approached directly may also be a lack of strong odour plumes. Mackie (1975) noted the importance of different diffusion coefficients of macromolecules and low molecular mass amino acids, which stimulate feeding (for review see Sloan 1980); he stated that in the absence of water currents, any signal composed of amino acids would be short lived. Swenson and McClintock (1998) also suggested the lack of a highly concentrated odour plume as a reason for the observed non-linear movement of the asteroid *Concinasterias tenuispina* during an in vitro experiment. In the natural environment, *A. rubens* may respond to three-dimensional odour plumes favoured by currents to orient (chemically mediated rheotaxis). The low frequency of direct contact to the pellet the starfish finally tried to ingest contrasts with prey-choice behaviour of other echinoderms such as the urchin *Arbacia punctulata*, which in 90% of the observed events identified preferred prey from a distance of about 20 cm (Wahl and Hay 1995). The shore crab *Carcinus maenas* seems to need the simultaneous input of visual and olfactory cues to locate preferred prey (Wahl et al. 1997).

A few earlier investigations report on the influence of epibionts on the susceptibility of their hosts to consumption (Table 1). Carnivorous and herbivorous consumption as well as fungal infection (Table 1) have been shown to be affected by the presence of epibionts. The effects may be beneficial (associational resistance) or detrimental (shared doom) for the host (e.g. Wahl and Hay 1995). Toxic, repellent, structurally defensive and camouflaging effects of epibiosis have been evoked to account for the observed interaction modifications.

Some epibiont–basibiont associations, however, do not seem to modify predator–prey interactions. Prescott (1990) could not detect any influence of scallop epibionts (algae, gastropods, bivalves, polychaetes) on the predation pressure by gulls or whelks. Similarly, the red filamentous alga *C. strictum* did not affect its host’s (blue mussel) susceptibility to predation by the shore crab (Wahl et al. 1997). Apparently in these cases host properties essential for identification and handling by the consumer in question were not sufficiently modified by the presence of epibionts, or deterrent factors were counterbalanced by stimulatory effects.

Summing up, this study shows that the important mussel predator *A. rubens* discriminates between differently fouled blue mussels. Chemical cues are apparently important for this discrimination. *M. edulis* is one of the most dominant competitors for space in many locations (Kautsky 1981; Himmelman and Dutil 1991; Seed 1993). In the Kiel Fjord (western Baltic), for instance, blue mussels would—if not controlled by starfish and shore crab predation—monopolise space to 100% within 1 or

2 years (Reusch and Chapman 1997). *A. rubens* alone accounts for over 80% of mussel mortality on soft bottom (Reusch and Chapman 1997). Epibionts on *M. edulis* have the potential to modify the top-down control by starfish and crabs, by changing or masking prey properties the predators cue upon or by exhibiting their own repellent or toxic characteristics. Only some epibiont species were tested in this regard; it can be expected, however, that other common facultative epibiotic species such as the green algae *Enteromorpha intestinalis* and *Bryopsis plumosa*, the brown algae *Pilayella* sp. and *Fucus serratus*, the hydroid *Clava multicornis*, the bryozoans *Membranipora pilosa* and *Alcyonidium gelatinosum*, the polychaete *Polydora ciliata*, and others may cause similar associational resistance. In still other ways, epibiosis may influence the mortality of mussels. Large epibionts increase drag (e.g. Wahl 1996; Gonzalez et al. 2001) and thereby the risk of dislocation (J. Laudien, personal observation); boring species such as some algae and *P. ciliata* may weaken the shell and thereby increase the risk of breakage or predation; bushy or filtering epibionts such as some algae, hydrozoans, and sponges/barnacles could interfere with filtering of the mussel, reducing growth rate and consequently prolonging exposure to predation (mussels longer than 5 cm are rarely preyed upon in the western Baltic: Reusch and Chapman 1997; Sommer et al. 1999).

Thus, epibiosis may impact on the mortality of blue mussels in many ways, of which the modulation of predation pressure seems one of the most important. Given this key role of epibionts in the interaction between a competitive dominant species and its predators, we expect epibiosis to contribute significantly to the dynamics and structure of local benthic communities.

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