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ORIGINAL ARTICLE

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Effects of barnacle epibionts on the periwinkle *Littorina littorea* (L.)

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Abstract In a sandy bay with mussel beds in the Wadden Sea (Island of Sylt, eastern North Sea), periwinkles *Littorina littorea* (L.) were often strongly overgrown with the barnacle *Balanus crenatus* Bruguière in the lower intertidal zone. Consequences of this epibiosis on mobility, reproduction and mortality of the snail were examined. *B. crenatus* growing on *L. littorea* increased snail volume up to 4-fold and weight up to 3.5-fold and crawling speed of fouled *L. littorea* was significantly slowed down. The epibiotic structure also caused a decrease in reproductive output. In laboratory experiments, egg production of fouled *L. littorea* was significantly lower than in snails free of barnacles. Presumably, copulation of the periwinkles is hampered by the voluminous and prickly cover of barnacles. Field studies demonstrated an increased mortality of overgrown *L. littorea*. A decrease in reproductive output and a lower survival of snails with a cover of barnacles suggest that *B. crenatus* epibionts may have a significant impact on the population of *L. littorea*.

Key words Epibiosis · *Littorina littorea* · Barnacles · Effects on mobility, reproduction and mortality

Introduction

In the marine environment any solid surface will become fouled by a great number of hard bottom organisms. On rocky shores organisms may settle directly on the substrate. However, in the rather unstable sediments of the Wadden Sea, sessile algae and invertebrates depend on biogenic hard substrates, such as epibenthic molluscs. Periwinkles *Littorina littorea* (L.) are common epibenthic organisms in the Wadden Sea (Wilhelmsen and Reise 1994), providing suitable attachment sites for sessile organisms.

Attachment of hard bottom organisms on living substrate constitutes an epibiosis, which is one of the closest interspecific associations, including both direct and indirect interactions between the basibiont (substrate organism) and epibiont (fouling organism) (Wahl 1996). Several beneficial and disadvantageous consequences for epibionts are reported (e.g. Keough 1984, 1986; Novak 1984; Oswald et al. 1984; Oswald and Seed 1986). In the Wadden Sea, the epibiont will always profit from the association, because the basibionts provide the only hard substrate available. For the basibionts, the association may also be beneficial. For example, camouflage effects protect the substrate organisms from predation (e.g. Vance 1978; Feifarek 1987; Wahl and Hay 1995). More often, however, epibiosis may have disadvantageous properties for the basibiont (Dixon et al. 1981; Bulthuis and Woelkerling 1983). In the case of molluscs, shell-covering epibionts may reduce growth of bivalves and snails (Dittmann and Robles 1991; Wahl 1996, 1997) and reproduction rate of mussels (Dittmann and Robles 1991). Furthermore, increased drag by epibionts may increase the risk of dislodgement in bivalves (Witman and Suchanek 1984; Ansell et al. 1988). Due to such negative effects, basibionts have developed defence mechanisms against epibiosis. This defence can be mechanical, physical or chemical. An overview of basibiont defense strategies is given by Davis et al. (1989) and Wahl (1989).

L. littorea lacks typical antifouling defense mechanisms (Wahl and Sönnichsen 1992). Accordingly, many sessile species may be attached to the shell of this snail. In our research area, the barnacle *Balanus crenatus* Bruguière is the most abundant epibiont on *L. littorea*. We therefore examined the effects of barnacle epigrowth on periwinkle mobility, reproduction and mortality.

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Fig. 1 *Littorina littorea* with barnacle (*Balanus crenatus*) overgrowth

Materials and methods

Study area

Field experiments were carried out in 'Königshafen', a shallow intertidal bay at the northern end of the island of Sylt (German Bight, North Sea). Hydrography, geology, sediments and biota have been described by G. Austen (1994), I. Austen (1994), Bayerl and Higelke (1994), Reise (1985), Reise et al. (1994) and Wohlenberg (1937). Tides are semi-diurnal and average tidal range is 1.8 m. Salinity remains close to 30‰. The average water temperature is about 15°C in summer and 4°C in winter. For experiments, fouled and unfouled *L. littorea* were collected from a mussel bed (*Mytilus edulis* L.). In this paper we consider only the epigrowth by *Balanus crenatus*, and the term 'fouled snails' is used when shells are almost entirely covered by these barnacles (Fig. 1).

Balanus epigrowth on *Littorina littorea*

The occurrence of *Balanus crenatus* on *L. littorea* was mapped in May–June 1996. Snails were collected from mussel beds and sandy flats in the lower intertidal zone of Königshafen. Previous studies had shown that roughly 74% of sexually mature *L. littorea* occur in these two habitats (Buschbaum, unpublished; Nicolaysen, unpublished). Snails were collected from these sites from areas of 0.09 m^2 on mussel beds and 0.25 m^2 on sandy flats, with 12 replicates each. In the laboratory, the coverage by barnacles of each shell surface was estimated to the nearest 20%. Only *L. littorea* of a shell height of ≥14 mm (measured from base to apex) were examined as these achieve sexual maturity at this size in our study area (Dethlefs, unpublished).

Volume and weight of epibionts

In the experiments, periwinkles with a shell height of 14 to 18 mm were used, corresponding to an age of 2 years (Smith and Newell 1955; Fretter and Graham 1980). The volume of barnacles, covering 100% of shells, was determined by water displacement in a 250-ml graduated cylinder to the nearest 0.1 ml. After removing the epibionts, measurements were repeated, and the difference in water displacement was taken as barnacle volume. Weight measurements were carried out correspondingly after drying snails on blotting paper, using a precision balance to the nearest 0.01 g.

Mobility experiment

To test the snails' ability to return to a normal crawling position once turned upside down, fouled and unfouled snails were placed in six aquaria (26×17.5×16 cm), under both emersed and submersed conditions. The aquaria were filled with a 5-cm layer of sandy sediment and moistened with seawater, representing a low tide situation. For simulation of a high tide, the sediment was covered by 5 cm of water. For each of the two experiments, 60 unfouled and 60 fouled *L. littorea* were used (10 snails per aquarium). The periwinkles were oriented with the aperture upwards and spaced 5 cm apart from each other to avoid contact between neighbours. During the experimental period of 1 h, each snail that had returned to normal crawling position was recorded and removed.

On a sandy tidal flat, the crawling speed of 40 unfouled and 40 fouled snails was measured during low tide emergence. Periwinkles were numbered and the starting position of each was marked with a flag bearing the snail's code number. *L. littorea* leaves a trail on wet sediment. This trail was marked by a lead ribbon after a period of 1 h, and the length of the ribbon was recorded.

Reproduction experiment

To determine reproductive output, the number of eggs released by *L. littorea* was measured in the laboratory. The egg release of three test groups of snails was determined: (1) periwinkles covered with barnacles; (2) as previous group, but balanids removed; (3) *L. littorea* without any fouling. All snails with a shell height of 14 to 18 mm were collected from a mussel bed.

In May 1996 20 snails of each test group were placed in a cylindrical polyvinyl chloride (PVC) box (200 mm in height, 120 mm in diameter) (Fig. 2). We used six boxes for each test group (20 snails in each box). A 125-µm gauze at the top of the boxes prevented losses of egg-capsules. A silicon tube at the bottom supplied the boxes with running seawater of ambient temperature and salinity.

The light/dark rhythm was 17/7 h. Tides were not simulated. Experiments lasted 11 days. At daily intervals, the contents of the boxes were washed through a 125-µm sieve. Food algae (*Enteromorpha* spp.) and the snails were washed carefully and then transferred back into the PVC boxes. The retained egg capsules of each box were transferred to 100-ml Kautex bottles and fixed in 2% formaldehyde solution. As the egg number in the samples was very high, samples were diluted with seawater to 300 ml. Starting from this solution, 5-ml aliquots were removed with a plankton-stemp pipette and counted by using a stereo microscope. Egg numbers were calculated back to 300 ml and referred to the

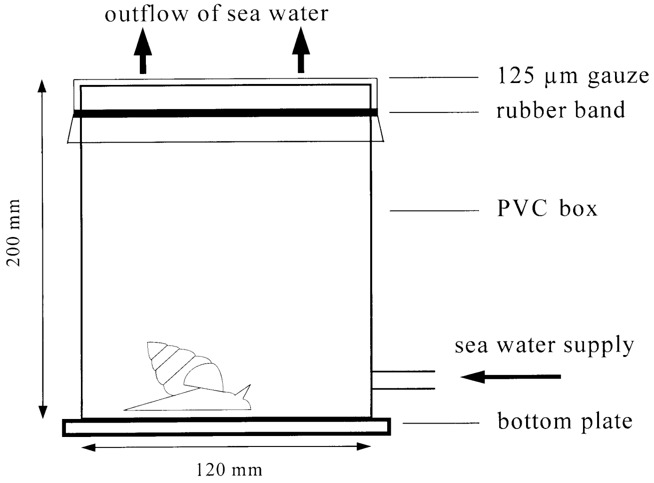

Fig. 2 Polyvinyl chloride (PVC) box for determination of the egg production of *Littorina littorea* with and without barnacle covering

number of females in each box. Snails were sexed at the end of experiments and also checked for parasites. *L. littorea* is a host for digenean trematodes which influence fecundity (Huxham et al. 1993). In a control experiment, we tested whether barnacles attached to snails fed on the egg capsules of *L. littorea*. Experiments were carried out in PVC boxes similarly constructed to those used in the reproduction experiments but smaller (92 mm in height, 72 mm in diameter). Boxes were filled with two males of either fouled or unfouled periwinkles (eight replicates each). About 200 eggs were added to each box. Again, boxes were connected to running seawater. After 24 h the number of egg capsules was counted.

Mortality experiment

In a field experiment, fouled and unfouled *L. littorea* with a shell height of 14 to 18 mm were placed in eight circular cages (0.3 m in diameter, 0.25 m in height) constructed of 5-mm wire netting. Cages prevented the escape of snails and excluded potential predators. In September 1996, the cages were placed on a sandy flat and anchored to the sediment using iron rods of 0.5-m length. Each cage was supplied with ten fouled and ten unfouled *L. littorea*. At weekly intervals, dead periwinkles (discernible by empty shells) were counted, removed and substituted by living snails. Thus, the density of periwinkles was kept constant in each cage over the experimental period of 13 weeks. In December 1996 drifting ice shoals terminated the experiment. Daily measurements of air and water temperature during the experimental period were obtained from the local weather station in List.

Results were calculated as mean values with standard deviation ($\bar{x}$±SD). Data of mobility and mortality experiments were analysed by Wilcoxon's matched pairs signed rank test (Sachs 1984). Data of the reproduction experiments were analysed by Kruskal-Wallis H-test, followed by Wilcoxon's matched pairs signed rank test (Sachs 1984). The number of egg-capsules in the control experiment was analysed by Mann-Whitney U-test (Sachs 1984).

Results

Occurrence and extent of barnacle overgrowth

A total of 78±23% of the sexually mature *Littorina littorea* showed barnacle cover in the lower intertidal zone. On mussel beds the rates were 70±26% and on sandy flats 86±16%. In both habitats about 20% of the investigated snails showed ≥40% shell surface covered by *B. crenatus*. Average volume of *L. littorea* entirely covered by barnacles increased 4-fold and average weight 3.5-fold as opposed to clean snails in the size range of 14 to 18 mm shell height (Fig. 3). *B. crenatus* considerably increased the size and the load of the snails' shells, thus probably affecting the overall performance of the carrier.

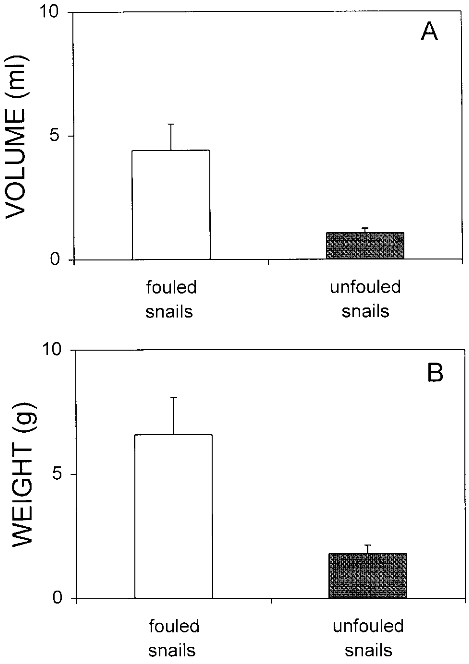

Fig. 3 Average volume (A) and weight (B) of fouled and unfouled *Littorina littorea* (+SD, *n*=50). Measurements were carried out before and after removing the barnacle *Balanus crenatus*

Mobility of fouled snails

The mobility of barnacle-covered *L. littorea* was strongly restricted. At simulated low tide, none of the balanid-covered periwinkles experimentally turned upside down was able to return to a normal crawling position, while 41 of 60 unfouled snails were able to do so. When submersed, none of the overgrown periwinkles succeeded in turning, while 29 of 60 unfouled periwinkles were able to turn over. We observed that snails need to contact the sediment surface with their foot to be able to return to the normal crawling position. However, the foot of barnacle-covered snails could not reach the sediment, because of the large volume of barnacle overgrowth.

In addition to this misfortune, the measurements of crawling speed in the field demonstrated restricted mobility of overgrown snails (Fig. 4). With an average speed of 2.4±5.4 cm h^{-1} (*n*=40), fouled *L. littorea* were significantly slower than unfouled snails which crawled at 35.4±43.2 cm h^{-1} (Wilcoxon's matched pairs signed rank test, $P < 0.01$).

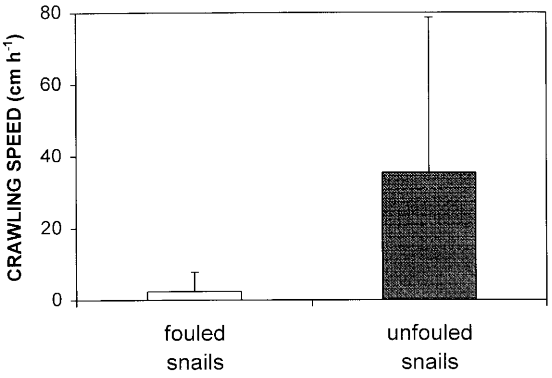

Fig. 4 Average crawling speed (+SD; *n*=40) of fouled and unfouled *Littorina littorea* on a sandy tidal flat. Barnacle-covered snails were significantly slower than unfouled periwinkles

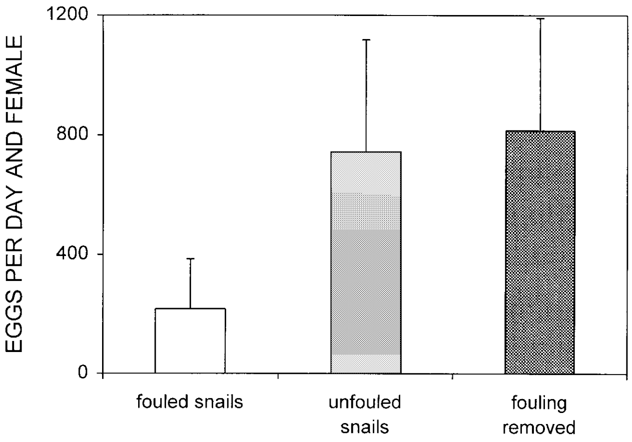

Fig. 5 Average egg number per day per female (+SD) in each test group of *Littorina littorea* (means over experimental period of 11 days). Egg number of fouled snails was significantly lower than that of clean snails and periwinkles with removed barnacles. There was no significant difference in egg number of unfouled snails and that of *L. littorea* with removed overgrowth

Reproduction experiment

Over the experimental period of 11 days, average egg production of balanid-covered periwinkles was 218±167 eggs per day per female (Fig. 5). Unfouled snails (744±74) and periwinkles with removed barnacles (815±376) produced significantly more eggs (Kruskal-Wallis H-test, $P < 0.05$; following Wilcoxon's matched pairs signed rank test, $P < 0.01$).

Periwinkles with removed overgrowth and unfouled snails showed no significant difference in reproductive output (Wilcoxon's matched pairs signed rank test, $P > 0.05$). This indicates that there was no difference in gonad development. In addition, there was no significant correlation between the number of females infected by trematode parasites and egg number. The infestation rate of the females in the boxes was 2.9±4.1% of fouled *L. littorea*, 2.7±3.8% of periwinkles with removed barnacles and 8.5±10.3% of unfouled snails.

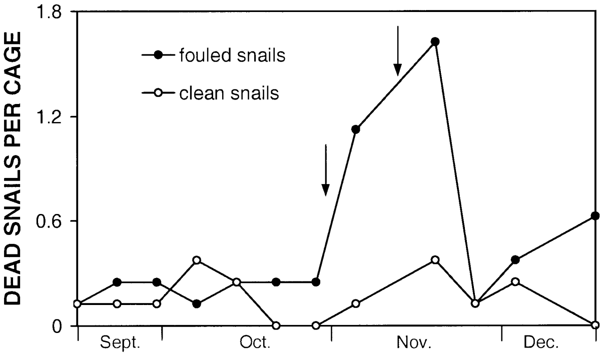

Fig. 6 Mean values of dead *Littorina littorea* per cage over experimental period 13 September to 12 December 1996. *Arrows* mark the first cold intervals of air temperature in autumn 1996 (air temperature <8°C)

The control experiment provided no significant evidence of *B. crenatus* feeding on eggs of the littorinids (Mann-Whitney U-test, $P > 0.05$). In direct observations we could not detect any feeding response of barnacles towards egg capsules of *L. littorea* when the capsules were offered to them.

Mortality of fouled periwinkles

Average mortality was 5.38±3.00 per cage (*n*=8) for barnacle-covered *L. littorea* and 1.88±1.96 for unfouled snails in 13 weeks of experimental time. In total, 43 of fouled and 15 of unfouled snails were found dead in the cages. Thus, mortality of fouled periwinkles was almost three times higher than that of unfouled snails (Wilcoxon's matched pairs signed rank test, $P < 0.05$). The first cold intervals of air temperature at the end of October and in November 1996 caused a considerable increase in mortality. At this time the highest number of overgrown snails died in the cages (Fig. 6).

Discussion

The heavy epigrowth of barnacles on the shells of the periwinkle *Littorina littorea* on the lower tidal flats near the island of Sylt caused impaired mobility, reduced reproduction and lower survival. How important is this for the population? Previous studies at the same locality showed that *L. littorea* aggregates on epibenthic structures (Wilhelmsen and Reise 1994), and maximum abundance (380 m^{-2}) and biomass (about 2 g of dry organic weight m^{-2}) were recorded at the mussel beds (Reise et al. 1994). Roughly 75% of the mature snails occurred in this lower intertidal zone, and in 1996 we estimated that 78% of them were covered by barnacles in an area of sandy flats with interspersed mussel beds. Although there is no long-term record of barnacle epigrowth on littorinid shells available in the locality, we noticed that this parameter may show high interannual variability.

Nevertheless, it is clear from the above that barnacle cover may be an important factor in the population dynamics of *L. littorea* on Sylt if these barnacles effectively impair the performance of the snails.

Mobility

On the vast tidal flats, mobility is a crucial aspect of survival. Average crawling speed on these sandy flats varied between 0.6 and 1.5 m h^{-1}, and tended to be directed towards epibenthic structures, mussel beds in particular (Lieser, unpublished thesis). Snails dislocated by an occasional rough sea must be able to crawl back to their preferred habitat. Furthermore, we observed seasonal migrations, and this is also known from other habitats (Gowanloch and Hayes 1926; Gendron 1977). Crawling is also required during normal feeding when periwinkles browse on their diatom food on the sandy flats. Within mussel beds snails move very little but have to sneek through the interstices of epibenthic clumps of mussels. This cannot be done when snail size is increased fourfold by an epigrowth of barnacles. Therefore, unhampered mobility is essential for this epibenthic grazer on tidal flats in the Wadden Sea. Previous studies have pointed out the increased drag these snails are exposed to in a flowing regime when overgrown with epibionts. This enhances the danger of dislodgement (Witman and Suchanek 1984) and slows down growth (Wahl 1996, 1997). In addition to these two aspects, we demonstrate here that the impaired mobility of fouled snails has also to be considered.

Reproduction

Barnacle epigrowth reduced the reproductive output of fouled snails by about 75%. There may be three underlying mechanisms. (1) the barnacle *Balanus crenatus* may prey on released egg capsules. We tested for this, but found no evidence; (2) the epibionts may have decreased the general fitness of snails, resulting in a lower egg production. The experiment with snails which were overgrown with barnacles but had these removed before the start of the experiment suggests that this process was not responsible for the experimental outcome, although on a longer time scale this process ultimately increases in importance; (3) we suggest that copulation in these dioecious snails was hampered by the voluminous and prickly cover of barnacles. For copulation, the male crawls onto the shell of the female and then inserts his penis into the mantle cavity of the female underneath (Linke 1933). Thus, copulation depends on unimpaired mobility in the case of the male and a clean shell in the case of the female. In fact, we did not observe any copulation between snails with barnacle epigrowth, while this was frequently the case with unfouled snails. In the study area, the relatively large-sized snails living on the mussel beds provided 86% of the total egg production of the *L. littorea* population (Dethlefs, unpublished). Consequently, the observed impairment of reproduction by the barnacle epigrowth may affect the reproductive success of the entire population.

Mortality

In contrast to the fouled and then cleaned snails in the previous experiment performed in spring, fouled periwinkles showed a reduced fitness when caged on the tidal flats in autumn. At the end of May, shells had been covered by barnacles for about 6 weeks. Attachment of the barnacle larvae was observed in mid April. In autumn, snails had carried their growing load for approximately 6 to 7 months. In addition, the time course of mortality suggests that decreasing temperature caused a particular stress. Not only may the reduced fitness of fouled snails increase the mortality rate in the population, but also fouled snails which survive the winter are unlikely to be able to develop many eggs in the next season.

Conclusions

Many factors affect the reproduction and mortality of *Littorina littorea*. The size of littorinids (Erlandsson and Johannesson 1994) and the food supply (Fish 1972) influence the fecundity of periwinkles. Digenean trematodes use *L. littorea* as their first intermediate host. A parasitic infection can cause a decrease in reproduction and a parasitic castration (Huxham et al. 1993), and the parasitic infestation rate of littorinids influences mortality (Lauckner 1984). Predation is an important factor of mortality, too, because many young *L. littorea* are consumed by epibenthic predators such as shore crabs *Carcinus maenas* (L.) (Scherer and Reise 1981). Therefore, predation and parasitic infestation have been discussed as the key factors in population dynamics of *L. littorea*. However, a decreasing reproductive output of up to three-fold and a multiple increase in mortality in overgrown snails demonstrates that barnacle overgrowth on the shell of periwinkles must also be taken into consideration in the intertidal zone of a sedimentary environment. In adjacent subtidal habitats *L. littorea* is not regularly encountered (Buhs and Reise 1997), and below the low tide line abundance rapidly decreased (Saier, personal communication). We speculate that the predominant occurrence of *L. littorea* in the tidal zone of the Wadden Sea may be a consequence of a too heavy load of barnacle epibionts on their shells in the subtidal zone.

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