Shell-boring polychaetes affect gastropod shell strength and crab predation

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ABSTRACT: Crab predation may profoundly affect the structure of marine benthic mollusc populations and prey choice of crabs may be altered by organisms associated with their prey. We investigated effects of the shell-boring polychaete *Polydora ciliata* on shell strength of the periwinkle *Littorina littorea*, and the concomitant prey selectivity of one of its major predators, the crab *Carcinus maenas*. Shell strength of periwinkles measured as force required to cause cracking was significantly lower in snails infected with *P. ciliata* than those without infection. In laboratory predation experiments, *C. maenas* consumed more snails infected with *P. ciliata* than uninfected periwinkles in a given size class. This was true when infected and uninfected snails were offered independently and simultaneously. Although *C. maenas* preferred small-sized (13 to 17 mm shell height) over medium (18 to 21 mm) and large (22 to 24 mm) periwinkles, consumption of large snails with *P. ciliata* was twice as high as for medium-sized *L. littorea* without polychaetes. Thus, this shell-boring polychaete causes crabs to shift their prey choice, and may even eliminate a size refuge for large infected periwinkles. We conclude that *P. ciliata* modifies predator–prey interactions, and we propose more generally that a high prevalence of shell-colonising organisms may exert a strong indirect effect on the dynamics and size distributions of mollusc populations.

KEY WORDS: Predation · Prey choice · Direct effects · Indirect effects · Epibiosis · Population dynamics

INTRODUCTION

Predation is an important factor affecting the composition and structure of benthic communities in both rocky and sedimentary environments (e.g. Paine 1974, Reise 1985, Kerfoot & Sih 1987, Seed 1993). In communities structured by predation, prey selection by predators is a major forcing process (e.g. Paine 1976, Sih et al. 1985, Mascaró & Seed 2001). Of particular importance is the selection of prey by size categories (Elner & Hughes 1978, Lawton & Hughes 1985).

Many decapod crustaceans prefer small and medium-sized mollusc prey (Elner & Hughes 1978, Juanes 1992). According to the optimal foraging theory, crabs are able to choose their diet in a way that maximises the energy intake per unit effort (Elner & Hughes 1978, Hughes 1980). A consequence of this selective feeding behaviour is that large gastropods (e.g. Hughes & Elner 1979, Lawton & Hughes 1985, Ash 1989) and bivalves (e.g. Paine 1976, Seed 1993) may attain a size refuge from crab predation.

In addition to prey size, other factors, such as inducible predator defences of prey, the degree of predator satiation, total prey-handling time, as well as density and habitat of the prey, affect prey selection (Elner & Hughes 1978, Lawton & Hughes 1985, Sponaugle & Lawton 1990, Seitz et al. 2001). Prey preferences of crabs may also be affected by species growing on or in mollusc shells (e.g. Kent 1981, Feifarek 1987, Barkai & McQuaid 1988, Ambariyanto & Seed 1991, Laudien & Wahl 1999). For instance, the shore crab *Carcinus maenas* (L.), prefers mussels *Mytilus edulis* L. overgrown with barnacles over similarly sized clean mussels, while hydrozoans growing on mussels

may lower attractiveness of *M. edulis* (Enderlein et al. 2003). Barnacle epigrowth probably improves handling of mussel by crabs and provides an additional food source, whereas hydrozoans can lower crab predation by providing a chemical/tactile camouflage (Enderlein et al. 2003). Hence, organisms associated with mollusc shells have the potential to influence predator feeding behaviour and may indirectly increase or decrease host mortality.

On northern Atlantic shores, periwinkles *Littorina littorea* (L.) are common crab prey (Bertness 1999). Shore crabs *Carcinus maenas* preferentially consume small to medium-sized snails. Larger snails are protected from predation by reaching a size refuge through achieving dimensions that crabs cannot handle (Hadlock 1980, Ash 1989). However, organisms associated with *L. littorea* may alter prey choice behaviour of crabs. Large-sized periwinkle shells are often perforated by holes drilled by the spionid polychaete worm *Polydora ciliata* (Johnston) (Warner 1997, present Fig. 1). *P. ciliata* has a planktonic larva, and after settlement it burrows into a variety of substrata, including soft clays, mud and rock. The adult worm lives inside U-shaped or flask-shaped burrows, and feeds mainly on detritus and suspended particles (Kent 1979, Ambariyanto & Seed 1991). *P. ciliata* also infects bivalves and has been shown to reduce their shell strength and to increase crab predation pres-

sure (Kent 1981, Ambariyanto & Seed 1991). For gastropods, no studies on the effects of *P. ciliata* on shell strength and concomitant crab prey choice behaviour exist. We hypothesise that the polychaetes weaken gastropod shell strength and affect crab prey selectivity. In this study, we test whether shell infections by *P. ciliata* have an effect on the shell strength of periwinkles and concomitantly on the feeding behaviour of the crab *C. maenas*. We postulate that *P. ciliata* weakens shells of the periwinkle *L. littorea* by boring into the shell and creating extensive galleries (Blake & Evans 1973, Warner 1997) making snails potentially more vulnerable and attractive for crabs.

To test the effect of *Polydora ciliata* on shell strength of *Littorina littorea*, we first measured the force required to crack periwinkle shells with and without shell-boring polychaetes. Second, we performed feeding experiments in which *Carcinus maenas* was offered *L. littorea* in different size classes with and without *P. ciliata* infections. We hypothesised that the presence of *P. ciliata* enlarges the size spectrum of littorinid prey selected and, thus, enables predation on larger-sized snails which are normally beyond the maximum size that *C. maenas* can master.

MATERIALS AND METHODS

Study area and prevalence of *Polydora ciliata*. Periwinkles *Littorina littorea* and crabs *Carcinus maenas* were collected on tidal flats east of the island of Sylt (54° 55' N, 008° 20' E) in the northern Wadden Sea (southeastern North Sea, German Bight) in July and August 2004. In this area, *C. maenas* is one of the most important predators of periwinkles (Scherer & Reise 1981, Reise 1985). The study area belongs to the cold temperate region with a mean annual water temperature of about 9°C, a summer average of 15°C, and a winter average of 4°C. Tides are semi-diurnal with a mean tidal range of 2 m. Salinity remains close to 30 psu. The area is protected from strong westerly winds and wave action by sand dunes. A detailed description of the area is given by Gätje & Reise (1998). In this exclusively sedimentary environment, epibenthic mussel beds (*Mytilus edulis* L.) represent the only major hard substratum and are the most favourable habitat for *L. littorea*, which reaches densities of >2000 m^{-2} (Buschbaum 2000).

To determine the prevalence of *Polydora ciliata* on *Littorina littorea* in our study area, we randomly collected periwinkles from 3 mussel beds (about 120 to 140 snails per mussel bed) along the low-water tide line within an area of 500 m × 500 m. In the laboratory, snail sizes were measured (from base to apex) with calipers and grouped into small (13 to 17 mm shell

Fig. 1. *Littorina littorea*. Damage to periwinkle shells caused by boring *Polydora ciliata*

height), medium (18 to 21 mm) and large (22 to 24 mm) categories. Previous studies have shown that periwinkles <13 mm shell height are not infected with *P. ciliata* in the area (Buschbaum 1997). The occurrence of *P. ciliata* was determined for each snail using a binocular microscope.

Additionally, we counted the number of *Polydora ciliata* individuals in infected periwinkles with a shell height of 18 to 21 mm. This was done to estimate the natural abundance of *P. ciliata* per infected snail in the size class that we used in our shell strength and predation experiments. The number of *P. ciliata* individuals snail^{-1} was determined using a binocular microscope while the snails were submersed in water.

Shell strength measurements. To investigate the effects of *Polydora ciliata* infestation on *Littorina littorea* shell strength we measured the force required to crack the shells of *L. littorea* with and without polychaetes to the nearest 0.1 N. To determine the force expended at shell fracture for each snail, we used a measuring device (Fig. 2), similar to that of Kent (1981).

For measurements, we used periwinkles with a shell height of 18 to 21 mm, because smaller snails have very low levels of *Polydora ciliata* infection (Buschbaum 1997, Warner 1997). Snail collection and shell strength determination occurred on the same day. We
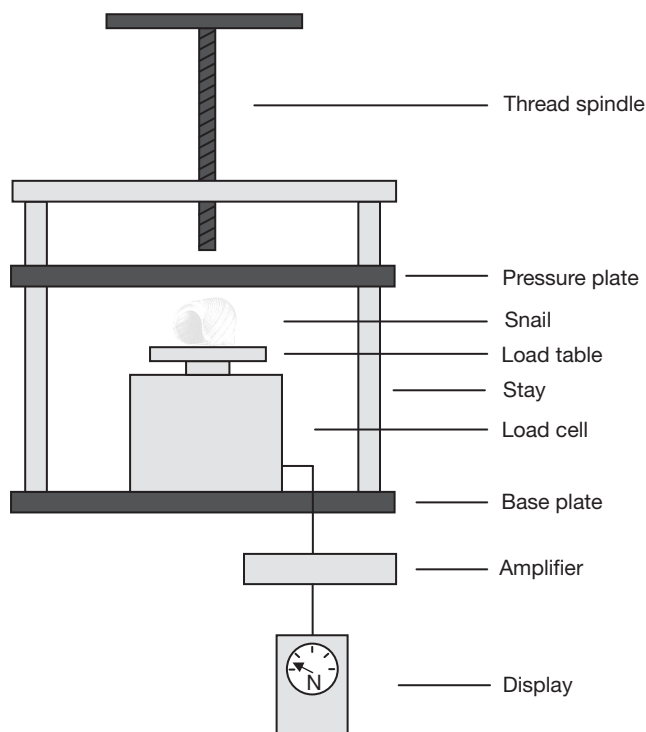

Fig. 2. Shell strength measuring instrument. Upper plate applied pressure on shell of the snail *Littorina littorea*, which was placed on load table of the load cell. The instrument measured the maximum force required to crack the shells

tested 2 groups of snails (55 individuals each): (1) *Littorina littorea* without *P. ciliata* infection and (2) *L. littorea* with infections of 10 to 25 *P. ciliata* per shell.

The measurements were carried out on live snails in air. Periwinkles were always placed in the same direction on the load table of the measuring instrument (with the outer lip on the table, see Fig. 2). This method measures the force required to crack shells in one particular plane. Although forces applied to different parts of the shell, such as the outer lip or columella, may also be important in nature, our method provides an estimate of general shell robustness. The speed of the moving pressure plate, which was lowered by the thread spindle, was kept constant at 0.5 cm s^{-1}.

Predation experiments. To avoid the problems associated with multiple-choice feeding experiments (e.g. lack of independence of the data; Peterson & Renaud 1989, Roa 1992), we decided to run 2 types of laboratory experiments.

First, in a no-choice experiment we offered only one type of prey (1 size class with *Polydora ciliata* infection or without) to crabs, measured daily consumption rates and finally determined preferences by comparing consumption rates.

Second, in a choice experiment we simultaneously offered *Polydora cilata*-infected and uninfected snails within the same size class to crabs, allowing inferential statistical treatment of the data (Peterson & Renaud 1989, Roa 1992).

For both experiments, crabs of 58 to 68 mm carapace width were collected by hand from mussel beds near the low water tide mark, and starved for 5 d to standardise hunger levels. Only male crabs were used in the experiments to avoid potential bias caused by sexual differences in morphology and predatory behaviour. We used 5 l aquaria containing seawater, a 5 cm sediment layer and fucoid algae to provide shelter for crabs. Aquaria were covered with sheets of vinyl plastic to prevent snails from escaping. Water was exchanged once daily. Light and water temperature (15 to 18°C) were adjusted according to field conditions.

No-choice experiments: In our first (no-choice) experiment, a single *Carcinus maenas* individual was offered 3 *Littorina littorea* within 1 aquarium. All snails within an individual aquarium were either without or with *Polydora ciliata* infestation (20 to 50 *P. ciliata* snail^{-1}) and within 1 size class. We used 3 size classes of *L. littorea*: (1) 13 to 17 mm shell height (for this treatment we used only *L. littorea* without *P. ciliata* due to the low levels of *P. ciliata* infection in snails <18 mm), (2) 18 to 21 mm shell height, (3) 22 to 24 mm shell height. Snails larger than Category 3 are rare in the area. The experiment lasted for 5 d. Consumed snails were recorded and replaced daily with equivalent specimens. For Snail Size Class 1 there were 20 indi-

vidual replicate crabs; Size Classes 2 and 3 there were 10 individual replicate crabs. Individual crabs were not exchanged during the course of the experiments.

Choice experiments: In the second (choice) experiment, a single crab was offered simultaneously within 1 aquarium 1 uninfected and 1 *Polydora ciliata*-infected *Littorina littorea*. For this experiment we used only medium-sized snails (18 to 21 mm shell height), i.e. Size Class 2. Experimental setup, size of *Carcinus maenas*, and *P. ciliata* infection rate per snail were the same as in the first feeding experiment. Prey items consumed were replaced daily; the number of crab replicates was 10; the experiment lasted for 8 d.

Statistical analysis. Data are presented as arithmetic means with standard error (SE). Differences in prevalence of *Polydora ciliata* in different size classes of *Littorina littorea* was analysed by a chi-square test. We used a *t*-test to check for significant differences in shell strength of *L. littorea* with and without *P. ciliata* infection. A *t*-test was also applied to check for size differences between infected and uninfected *L. littorea* with a shell height of 18 to 21 mm used in the shell strength measurements.

Because of the incomplete experimental design in our no-choice predation experiments (no availability of *Littorina littorea* <18 mm strongly infected by *Polydora ciliata*) data on crab predation on different snail size classes and data on predation on *L. littorea* with and without *P. ciliata* were analysed separately. Consumption rates on different size classes of *L. littorea* were analysed by analysis of variance (ANOVA), with shell size being the experimental (fixed) factor. In both size classes (medium and large periwinkles), differences in predation rate of infected vs. uninfected *L. littorea* were analysed with a *t*-test.

The prey choice experiments in which infected and uninfected *Littorina littorea* were offered simultaneously to *Carcinus maenas* were analysed with a *t*-test for paired samples. This test allows an analysis of dependent data arising from the design of the prey choice experiments (Peterson & Renaud 1989).

Cochran's test was used to test for homoscedasticity of variances, and dependent variables were log (x+1)-transformed when variances were heterogenous. In the analysis of predation of *Carcinus maenas* on different size classes of *Littorina littorea*, variances remained heterogeneous despite transformation, but were strongly reduced. However, we also applied ANOVA to analyse these data, because, with a relatively high number of replicates (n > 6), ANOVA is quite robust (Underwood 1997). Different levels within a significant experimental factor were analysed using Tukey's honestly-significant-difference (HSD) multiple comparison test. Effects were considered to be statistically significant if p < 0.05.

RESULTS

Prevalence of *Polydora ciliata*

Polydora ciliata prevalence on *Littorina littorea* differed significantly over the 3 size classes (chi-square test, χ^2 = 142.387, df = 2, p < 0.0001). Prevalence of *P. ciliata* strongly increased with increasing periwinkle shell size and was 22% (n = 146) in small snails (13 to 17 mm shell height), 69% (n = 137) in medium-sized (18 to 21 mm) and 97% (n = 93) in large *L. littorea* (22 to 24 mm).

Mean number of *Polydora ciliata* per infected snail with a shell height between 18 and 21 mm was 32.9 ± 2.1 (n = 95).

Shell strength of *Littorina littorea*

Shell strength of *Littorian littorea* without shell-boring *Polydora ciliata* was significantly higher than in snails with *P. ciliata* infection (*t*-test, *t* = 5.580, df = 108, p < 0.0001; Fig. 3). The mean force expended to crush uninfected periwinkle shells was 298.0 ± 11.9 N, and 212.4 ± 9.5 N for infected shells. Shell size of periwinkles with and without *P. ciliata* were not significantly different (*t*-test, *t* = 0.004, df = 108, p = 0.997).

No-choice experiments

Shell size

Shore crab predation on *Littorina littorea* without *Polydora ciliata* infestation differed significantly between size classes (1-way ANOVA, df = 2, MS = 9.881, *F* = 10.987, p < 0.001; Fig. 4). Consumption of small snails with a shell height of 13 to 17 mm (1.71 ± 0.29 snails crab^{-1} d^{-1}) was significantly higher than
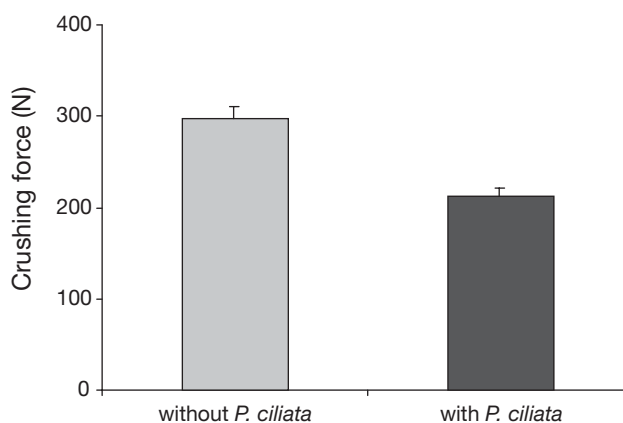

Fig. 3. *Littorina littorea.* Mean (+SE) force expended to crush shells without and with *Polydora ciliata* infection. n = 55 snails

for medium periwinkles of 18 to 21 mm shell height (0.40 ± 0.14 snails crab^{-1} d^{-1}, Tukey's test, p < 0.01) and large *L. littorea* >21 mm (0.22 ± 0.08 snails crab^{-1} d^{-1}, Tukey's test, p < 0.001). Thus, predation on small periwinkles was about 8 times higher than on large snails.

Polydora ciliata infection

Of the medium-sized *Littorina littorea*, *Carcinus maenas* consumed significantly more infected than uninfected periwinkles (*t*-test, $t = 2.545$, df = 18, p = 0.020) (Fig. 4). This was also the case in large-sized *L. littorea* with differences being marginally significant (*t*-test, $t = 1.954$, df = 18, p = 0.066). In both size classes together (pooled data of consumption of medium and large snails), differences in predation on infected vs. uninfected periwinkles were clearly significant (*t*-test, $t = 3.164$, df = 38, p < 0.01). The consumption rate of medium- and large-sized snails infested with *Polydora ciliata* was 3 to 4 times higher than that of uninfected individuals. Of the medium-sized periwinkles, a total of 61 infected and 20 uninfected snails were consumed. Of the large snails, 38 with *P. ciliata* and 20 without polychaetes were eaten by *C. maenas*.

Furthermore, the crab's feeding rate on large infected *Littorina littorea* (0.76 ± 0.24 snails crab^{-1} d^{-1}) was about twice as high as that on uninfected medium-sized *L. littorea* (0.40 ± 0.14 snails crab^{-1} d^{-1}) (Fig. 4). These differences were not significant, but the trends indicate that *C. maenas* prefers large *L. littorea* with *Polydora ciliata* infection over smaller uninfected snails.

Choice experiments

When *Littorina littorea* individuals of 18 to 21 mm shell height with and without *Polydora ciliata* infestation were offered simultaneously, crabs preferred snails infected by shell-boring polychaetes (Fig. 5). The consumption rate of snails with *P. ciliata* was 0.19 ± 0.08 snails crab^{-1} d^{-1}, and significantly higher than that on uninfected periwinkles (0.04 ± 0.02 snails crab^{-1} d^{-1}) (paired *t*-test, $t = 2.343$, df = 9, p = 0.043). In total, 15 *L. littorea* with *P. ciliata* were eaten by *Carcinus maenas*, but only 3 uninfected snails were consumed during the 8 d experimental period.

DISCUSSION

The shell-boring spionid polychaete *Polydora ciliata* significantly reduced shell strength of *Littorina littorea*, and affected prey choice behaviour of *Carcinus maenas*, which preferentially consumed periwinkles infected with *P. ciliata*. The observed reduction of shell strength in infected snails is certainly caused by the extensive galleries in the shells excavated by the worms. For our shell strength measurements we selected snails with an infection rate (10 to 25 *P. ciliata* snail^{-1}) lower than naturally found in *L. littorea* living on mussel beds near the low water tide line (about 30 worms periwinkle^{-1}). This indicates that even low infection by *P. ciliata* may cause a strong reduction in periwinkle shell strength.

Infection by *Polydora ciliata* has been observed in a variety of gastropod and bivalve species such as *Buccinum undatum* L., *Crepidula fornicata* (L.), *Nucella lapillus* (L.), *Ostrea edulis* L. and *Mytilus edulis* (Kor-
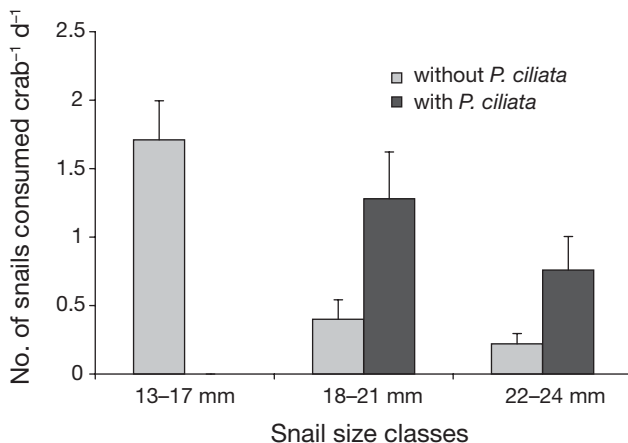

Fig. 4. *Littorina littorea*. Mean (+SE) number of snails without and with *Polydora ciliata* consumed per day and crab *Carcinus maenas* in different snail size classes (small, n = 20; medium, n = 10; large, n = 10 crabs). Small periwinkles with *P. ciliata* were not available. Duration of experiment = 5 d
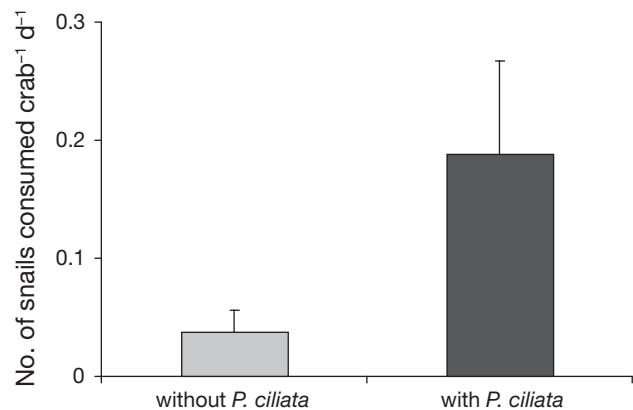

Fig. 5. *Littorina littorea*. Mean (+SE) number of snails without and with *Polydora ciliata* consumed by crabs *Carcinus maenas* when snails were offered simultaneously within 1 aquarium (n = 10 crabs). Duration of experiment = 8 d

ringa 1954, Hughes & Elner 1979, Kent 1979, 1981, Ambariyanto & Seed 1991). However, a reduction in shell strength was only quantitatively investigated for the bivalve *M. edulis* (Kent 1981). Our results from a gastropod indicate that a reduction of shell strength by *P. ciliata* infections may be a general phenomenon in both bivalves and gastropods. The burrowing activity of *P. ciliata* may also reduce the physiological condition and fecundity of its host by causing injuries as soon as excavations penetrate the interior surface of the shells. Infected mollusc hosts expend a large amount of energy on shell repairs which may lead to a trade-off effect (Kent 1979, Stefaniak et al. 2005). Such trade-off effects may also arise by inducible defences in periwinkles, because under high crab predation pressure, snails thicken their shells to reduce vulnerability (e.g. Palmer 1990, Trussel & Nicklin 2002, Trussel et al. 2003).

The direct negative effects of *Polydora ciliata* are accompanied by indirect detrimental effects caused by changes in predator prey choice induced by the worms. Since crushing snail shells weakened by infections of *P. ciliata* should require less energy for the crabs, infected snails are a more rewarding prey according to optimal foraging criteria (Elner & Hughes 1978). The results of both of our experiments with a natural infestation rate of *P. ciliata* are consistent with this hypothesis, since crabs consumed more or preferred infected over non-infected snails. Such a predation-enhancing effect of *P. ciliata* infections was also observed in bivalves such as *Mytilus edulis* (Kent 1981, Ambariyanto & Seed 1991). Hence, *P. ciliata* generally leads to a higher crab predation pressure on infected compared to uninfected bivalves and gastropods.

Another indirect effect may be that *Polydora ciliata* infections prevent molluscan prey from reaching a size refuge from predators. Our experiments indicate that this may be the case in the *Carcinus maenas*–*Littorina littorea* predator–prey system. Since size refuge decreases with increasing predator size, we chose the largest size class of *C. maenas* occurring in the study area (about 60 to 70 mm carapace width). In our feeding experiments with uninfected snails, vulnerability to *C. maenas* decreased significantly at about Size Class 2 (18 to 21 mm shell height). Thus, our investigations indicate that large uninfected periwinkles are well protected from crab predation, as has been shown in previous studies (Hadlock 1980, Ash 1989).

However, the prey size refuge of *Littorina littorea* infected with *Polydora ciliata* was severely reduced, because in both medium (18 to 21 mm shell height) and large infected periwinkles (>21 mm) consumption was more than double that for snails without *P. ciliata*. Additionally, crabs even consumed more infected

large *L. littorea* than uninfected medium-sized snails. Thus, *P. ciliata* infection has a strong influence on crab prey selection and may affect snail size refuge. These findings were confirmed by the choice experiments, because when each *Carcinus maenas* was offered 1 infected and 1 uninfected *L. littorea*, the crabs statistically significantly preferred snails with shell-boring polychaetes. In terms of the optimal foraging theory, the selection of large and infected *L. littorea* may be caused by a comparatively high energy net gain due to a strongly reduced effort for crushing the prey shell. In uninfected *L. littorea* of 9 to 18 mm shell height, Hadlock (1980) found that large *C. maenas* need about 10 min to crack the shells, while in our experiments crabs were able to open periwinkle shells with *P. ciliata* of the same size class and larger specimens within seconds (authors′ pers. obs.). Interestingly, *C. maenas* used different strategies to open uninfected and infected *L. littorea*. Uninfected periwinkles were commonly opened by peeling and progressively breaking back the lip of the shell aperture while infected *L. littorea* were crushed outright.

The effect of *Polydora ciliata* infections on crab prey preferences may have important consequences at the population level. In our study area, about 70% of medium-sized and more than 90% of large-sized *Littorina littorea* living on mussel beds near the low water tide line can be infected with *P. ciliata*. Similar to other study areas, the prevalence of *P. ciliata* in *L. littorea* increases with increasing shell size, and with decreasing elevation on the shore (Orrhage 1969, Warner 1997). Highest infection rates occur in large periwinkles just below the low water tide line (Buschbaum 1997). In the Wadden Sea, periwinkles also show a specific zonation pattern. On intertidal mussel beds, *L. littorea* may attain a density of some thousands m^{-2} (Buschbaum 2000, Saier 2000). On subtidal mussel beds, in contrast, snail densities abruptly decrease and predominantly larger periwinkles occur. Saier (2000) attributed this pattern to preferential periwinkle recruitment to the interdidal zone, to an active habitat choice and to high crab predation pressure subtidally. On other coasts, *L. littorea* is very abundant in the subtidal zone, and may achieve larger sizes there (e.g. Gilkinson & Methven 1991, Wahl 1996). Therefore, we assume that the high prevalence of *P. ciliata* may be an additional important factor affecting size and distribution patterns of *L. littorea* in our study area. Based on our investigations, we suggest that *P. ciliata* increases crab predation on both large *L. littorea* and individuals occurring in the subtidal zone. This may explain the rareness of periwinkles larger than 24 mm shell height and low snail abundances subtidally.

In conclusion, both direct and indirect effects of *Polydora ciliata* should be included in considerations of

population dynamics and distribution of *Littorina littorea* in addition to predation (Scherer & Reise 1981, Rangeley & Thomas 1987), parasitic infection (Lauckner 1984) and epibionts (Wahl 1996, Buschbaum & Reise 1999).

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