

Research Article

Alien epibiont (*Crassostrea gigas*) impacts on native periwinkles (*Littorina littorea*)

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Abstract

In marine sedimentary coastal environments such as the Wadden Sea (coastal south-eastern North Sea) shells of epibenthic molluscs are the only major available settlement substrate for an increasing number of alien sessile organisms. We investigated the effects of Pacific oyster *Crassostrea gigas* epibionts on body weight, mobility and fecundity of the native common periwinkle *Littorina littorea*. Body dry weight of snails without oyster overgrowth was twice as high compared to periwinkles covered with oysters. Also crawling speed of snails with oyster epigrowth was significantly slowed down and about ten times lower than in unfouled periwinkles. Additionally, oyster epibionts caused a strong decrease in reproductive output. In laboratory experiments, egg production of fouled *L. littorea* was about 100-fold lower than in periwinkles free of oysters. Field surveys in different years and habitats demonstrated that up to 10% of periwinkles occurring on epibenthic bivalve beds and up to 25% of snails living on sand flats may be fouled by *C. gigas*. However, oysters are not the only epibionts on *L. littorea* in the area. In previous studies it was shown that periwinkles can also be strongly overgrown by other alien epibionts such as Australian barnacles *Austrominius modestus* and American slipper limpets *Crepidula fornicata*. These epibiotic structures may cause similar effects as revealed for *C. gigas*. Thus, we conclude that an alien epibiont accumulation on *L. littorea* may have a significant impact on periwinkle population dynamics and its ecological functions in the Wadden Sea.

Key words: *Littorina littorea*, epibiosis, alien species, *Crassostrea gigas*, Wadden Sea

Introduction

In recent decades, an increasing number of biological invasions have been observed in Atlantic European waters due to the growing magnitude of global trade and associated transport vectors (Galil et al. 2009). The predominant vectors for transportation of alien species are aquaculture, ballast water and hull fouling (Carlton 1985; Minchin and Gollasch 2003). In the North Sea about the half of the non-native species were introduced via hull fouling and aquaculture activities explaining the high share of sessile alien macroalgae and invertebrates occurring in the area (Gollasch et al. 2008). For example, Haydar (2010) identified 35 species that have been introduced together with non-native oysters to the Netherlands and found a high number of epibiont species attached to the oyster shells. In particular, the imports of Pacific oysters *Crassostrea gigas* (Thunberg, 1793) since the beginning of the 1960s are

responsible for the largest number of associated established introductions (Wolff 2005; Haydar 2010). Apart from its own epibionts, *C. gigas* itself represents a sessile organism and its larvae require hard substrates for settlement (Reise 1998).

In the northern Wadden Sea (south-eastern North Sea), *C. gigas* were first detected in the field in the beginning of the 1990s (Reise 1998; Diederich et al. 2005), attached to shells of blue mussels *Mytilus edulis* Linnaeus, 1758, because mussel beds provided the only major hard substrate available in an otherwise sedimentary dominated environment. In recent years, a dramatic increase in oyster abundance has been observed (Wehrmann et al. 2000; Diederich et al. 2005; Nehls and Büttger 2007; Kochmann et al. 2008; Markert et al. 2010). Consequently most former mussel beds have turned into oyster reefs with high numbers of oysters on every hard substrate available including shells of the gastropod *Littorina littorea* (Linnaeus, 1758).

Periwinkles *L. littorea* may achieve high abundances of several hundred individuals per m² in the area (Buschbaum 2000). They are important structuring elements because their grazing activity has a strong influence on benthic community composition and recruitment success of macroalgae and sessile invertebrates (Wilhelmsen and Reise 1994; Albrecht 1998; Buschbaum 2000). As *L. littorea* lacks anti-fouling substances (Wahl and Sönnichsen 1992) it is a suitable hard bottom surface for many marine organisms. Previous investigations revealed that overgrowth with native organisms such as barnacles causes detrimental effects such as reducing snail mobility, fecundity, growth and survival (Dittmann and Robles 1991; Wahl 1996, 1997; Buschbaum and Reise 1999; Thieltges and Buschbaum 2007). Therefore, barnacle epibionts may affect population dynamics in *L. littorea* and indirectly influence its ecological function in the Wadden Sea. An increasing number of non-native epibionts attached to periwinkles may intensify this effect and may cause similar harmful impacts on *L. littorea*. Therefore, in this study we investigated the occurrence and the effects of Pacific oyster *C. gigas* epibionts on the periwinkle *L. littorea* and hypothesized that snail mobility, body weight and reproductive output is reduced in overgrown snails.

Methods

Study area

Investigations were conducted in the intertidal zone of the List tidal basin (54°50'–55°10'N and 08°20'–08°40'E) near the island of Sylt, located in the northern Wadden Sea (Figure 1). The List basin captures an area of about 404 km² and is partly enclosed in the south and north by dams. The only connection to the open North Sea is the Lister Deep, a slender tidal inflow of 2.8 km width (Reise and Riethmüller 1998). Mean water temperature is about 9°C, with a winter average of 5°C and a summer average of 15°C. Tides are semi-diurnal and the mean tidal range is 2 m. Average salinity is 30 PSU. More detailed descriptions of geology, sediments and hydrography of the study area are given by Reise (1985), Austen (1992, 1994a, b) Bayerl and Higelke (1994), Reise et al. (1994) and Gätje and Reise (1998). A number of mixed beds of native blue mussels *M. edulis* and introduced Pacific oyster *C. gigas* are situated in the intertidal zone

of the List basin along the east coast of the island of Sylt, including the sampled Diedrichsenbank (55°2'N and 8°26'E), the bivalve bed in the Oddewatt (55°01'N and 8°25'E) and Leghörn (54°57'N and 8°23'E).

Pacific oyster overgrowth on *Littorina littorea*

Live periwinkles were collected on three intertidal mixed beds of mussels and oysters during low tide in September/October 2007, 2008 and 2010. To determine abundance of overgrown snails a frame (30 cm × 30 cm) was randomly placed on the bottom. All periwinkles with and without oyster epigrowth (Figure 2) inside the frame were counted and size of snails and oysters was measured to the nearest 1 mm using a calliper. At each mussel bed six replicate samples were taken. Next to bivalve beds, samples were also taken from an adjacent sand flat area in September 2010. Due to lower snail densities, an area of 5 × 5 m was searched for periwinkles and all *L. littorea* with and without oyster epibionts were counted. For all investigations on oyster overgrowth only snails > 10 mm were used.

Body weight of *Littorina littorea*

To examine soft tissue weight in periwinkles with and without oyster epibionts, we collected live snails (n = 32) of the same size class (17–18 mm shell height measured from base to apex) with and without oyster epigrowth in September 2007. After detaching oysters (mean size 3.6 ± 0.4 cm) from the shells, snails were boiled in water for 2 minutes and then soft bodies were carefully removed from shells and dried for three days at 70°C up to weight constancy. Weight was determined to the nearest of 0.01 g.

Mobility of *Littorina littorea*

To investigate the effects of oyster epigrowth on periwinkle mobility we measured crawling speed of periwinkles i) with oyster epigrowth, ii) without oysters and iii) with removed oysters in September 2007. Mean size of attached and previously removed oysters was 3.6 ± 0.5 cm. For each treatment 40 periwinkles of the same size (17–18 mm shell height) were used. Snails were placed in line on a sand flat at low tide, each with its own numbered starting point, marked with a flag with the snail code number.

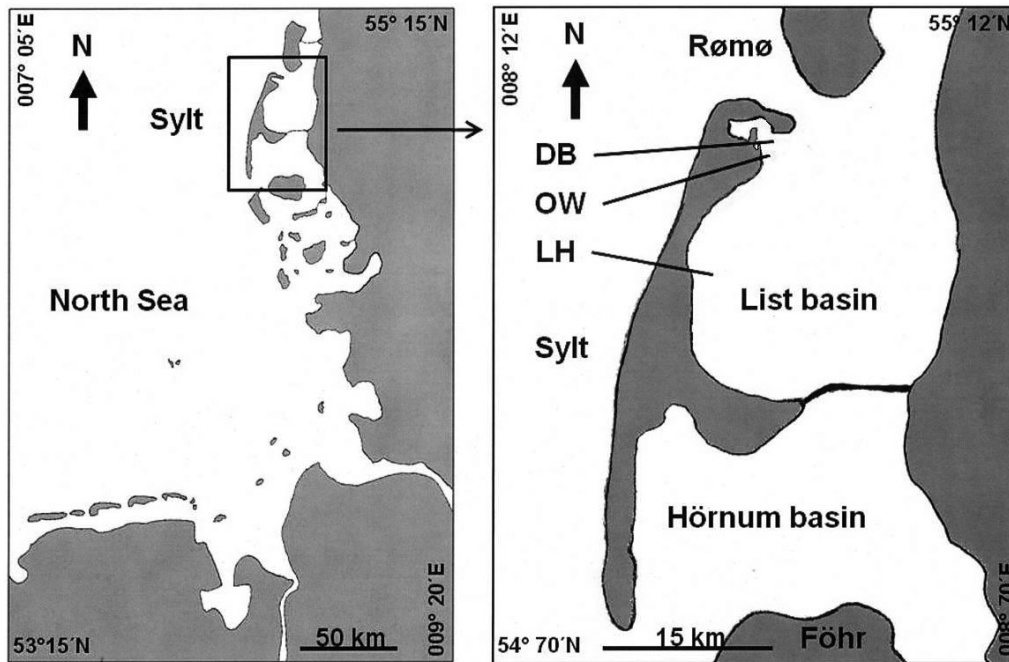


Figure 1. Study area in the south-eastern North Sea. Investigations and field experiments were performed on mixed beds of invasive oysters *Crassostrea gigas* and native blue mussels *Mytilus edulis* [Diedrichsenbank (DB), Oddewatt (OW), Leghörn (LH)] and sand flat regions in the Oddewatt (OW) in the List basin of the island of Sylt, 2007–2010.

After one hour crawled distance was recorded by measuring the length of the crawling track.

In a second experiment, we analyzed the capability of snails to return to crawling position once turned upside down in three treatments: (i) snails with oyster epigrowth ($n = 40$), (ii) periwinkles without oysters ($n = 40$) and (iii) *L. littorea* of which oysters had been removed from the shells ($n = 15$). Snails were placed in supine position into basins, filled with a 1 cm wet sediment layer, representing low tide conditions. After one hour all snails which had turned around were counted. Experiment was repeated with a new number of *L. littorea* of the same size class (17–18 mm shell height) and with the same replicate number to imitate high tide conditions with a 5 cm water layer.

Egg production of Littorina littorea

Periwinkle reproductive output with and without oyster epibionts was investigated with a method similar to that described in Buschbaum and Reise (1999) (Figure 3) in May 2009. We determined

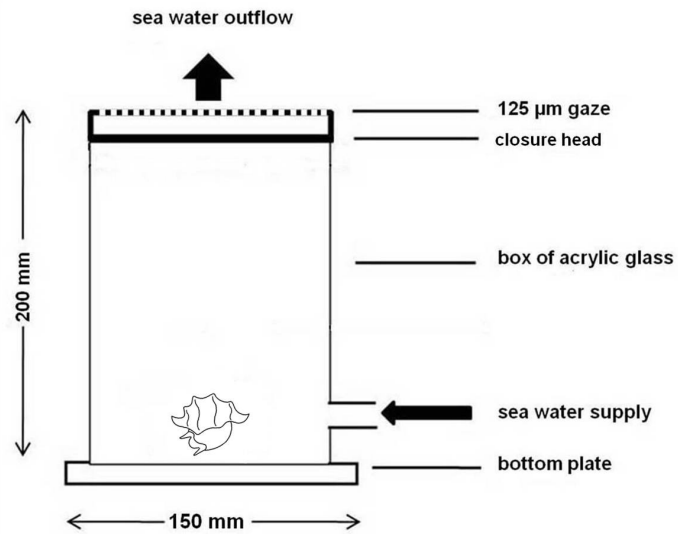
the egg release of *L. littorea* i) without oyster epibionts ii) with *C. gigas* overgrowth iii) with oysters removed. Mean size of attached and previously removed oysters was 3.7 ± 0.6 cm.

For each treatment we used six cylindrical boxes ($n=6$) which were covered with a 125 μ m gauze to prevent losses of egg capsules. At the bottom the boxes were supplied with running seawater of ambient temperature and salinity. Each box contained five females and five males. Because of low densities of male periwinkles covered with oysters, we used only males without epibionts. Depending on the specific treatment females were overgrown or free of oysters. Snail sex was determined just before the beginning of the experiment. Thalli of the green algae *Ulva lactuca* Linnaeus served as food for *L. littorea*. The experiment lasted 12 days. Daily, the content of each box was filtered through a 125 μ m sieve. Snails and algae were carefully washed and transferred back into the boxes. Retained egg capsules per box were counted. For further details see Buschbaum and Reise (1999).

Figure 2. Periwinkle *Littorina littorea* with *Crassostrea gigas* (left) and without oyster epigrowth (right).
Photo by N. Eschweiler.



Figure 3 Schematic drawing of the experimental set-up to investigate egg production of *Littorina littorea* with and without oyster overgrowth and periwinkles from which oysters were removed.



Statistical analyses

Results are presented as arithmetic means \pm standard deviation. Differences in body dry weight were analyzed by Mann-Whitney *U*-test. Chi-Square-test was used to analyse differences in snail ability to return to normal crawling position. Crawling speed and egg production in periwinkles with and without oyster epibionts were verified using Kruskal-Wallis H-test,

following Wilcoxon's matched pairs signed rank test. Comparisons between abundances of periwinkles were tested by using a Mann-Whitney *U*-test, comparisons between abundances of fouled and uncovered periwinkles were tested using Kruskal-Wallis ANOVA followed by the Dunn's method for unequal treatment group sizes. If $P < 0.05$ effects were considered to be statistically significant. All computer analyses were carried out with the software package SigmaStat 3.5 by Statcon.

Figure 4. Mean abundance of *Littorina littorea* (\pm sd) with (black bars) and without Pacific oyster epigrowth (grey bars) on mixed beds of mussels and oysters and on a sand flat area in different years. Mean percentage of snails overgrown with oysters are diagrammed via black dots (\pm sd).

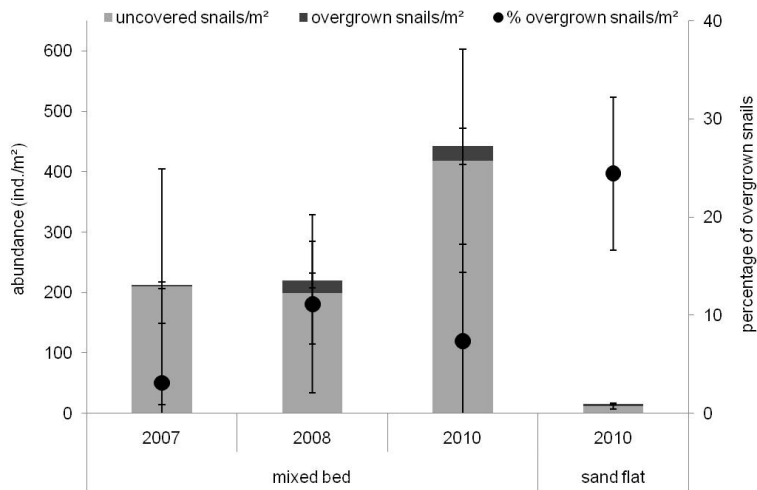


Table 1. Mean abundance (\pm sd) of *Littorina littorea* on mixed mussel/oyster beds in August 2007, September 2008 and September 2010 (average over three different beds) and mean abundance (\pm sd) of periwinkles on a sandflat area in September 2010.

Snails > 10mm/m ²	2007 mixed bed	2008 mixed bed	2010 mixed bed	2010 sandflat
total	212.17 (176.21)	219.35 (81.11)	440.12 (168.76)	15.35 (5.91)
overgrown	2.83 (5.72)	20.00 (12.30)	23.46 (29.98)	3.61 (1.51)
% overgrown	3.08 (6.03)	11.14 (9.07)	7.33 (9.85)	24.42 (7.81)

Results

Abundance of Littorina littorea and oyster epigrowth

Abundance of snails on mixed mussel/oyster beds was 212.17 ± 176.21 ind./m² in 2007 and 219.35 ± 81.11 ind./m² in 2008 with no significant difference (Mann-Whitney *U*-test, $p = 0.1$). In 2010 density (440.12 ± 168.76 ind./m²) was twice as high as in previous years and significantly different (Mann-Whitney *U*-test, (2007) $p < 0.001$, (2008), $p < 0.001$) (Table 1, Figure 4). Abundance of snails overgrown with oysters, by contrast, increased significantly from 2007 ($3.08 \pm 6.03\%$) to 2008 ($11.14 \pm 9.07\%$) (Tukey's test, $p < 0.05$) but decreased in 2010 ($7.33 \pm 9.85\%$). In comparison to mixed mussel/oyster beds, sand flat areas revealed a significantly higher mean percentage of fouled snails (mixed beds: $6.29 \pm 8.62\%$, sand flat: $24.42 \pm 7.81\%$) (Kruskal-Wallis ANOVA, Dunn's-method, $p < 0.001$).

Body weight and mobility of Littorina littorea with and without oyster epigrowth

Tissue dry weight in uncovered snails ($0.14 \text{ g} \pm 0.17 \text{ g/snail}$) was significantly higher than in *L. littorea* with oyster fouling ($0.06 \text{ g} \pm 0.02 \text{ g/snail}$) (Mann-Whitney *U*-test, $P < 0.001$).

Crawling speed of periwinkles differed significantly between the three treatments (Kruskal-Wallis *H*-test, $p < 0.001$) (Figure 5A). It was lowest in snails with oysters ($6.2 \pm 2.5 \text{ cm h}^{-1}$) and significantly different from periwinkles free of oysters ($96.6 \pm 73.0 \text{ cm h}^{-1}$, Wilcoxon's matched pairs signed rank test, $p < 0.001$) and conspecifics from which oysters were removed ($62.5 \pm 58.6 \text{ cm h}^{-1}$, Wilcoxon's matched pairs signed rank test, $p < 0.01$). There was also an apparent difference in crawling speed between periwinkles without oysters and snails with removed epigrowth, however, it was not statistically significant (Wilcoxon's matched pairs signed rank test, $p = 0.0736$, $n = 15$).

Ability to return to crawling position also differed significantly between the treatments. At low tide situation 42.5 % of snails without oyster epigrowth returned while none of the *L. littorea* with oyster cover (Chi-Square-test, $p < 0.001$) and only 13.3% of periwinkles from which oysters were removed (Chi-Square-test, $p < 0.05$) were observed at crawling position after one hour experimental period (Figure 5B). There was a significant difference in the number of snails which turned over between fouled and cleaned individuals as well (Chi-Square-test, $p < 0.05$). At submersed conditions we observed the same pattern with most unfouled periwinkles being able to return to crawling position (45%) (Figure 5C). Ability was significantly lower in overgrown snails (2.5 %, Chi-Square-test, $p < 0.001$) and in periwinkles from which oysters were removed (13.3%, Chi-Square-test, $p < 0.05$). The difference between fouled periwinkles and snails with removed oysters was not significantly different (Chi-Square-test, $p > 0.05$).

Reproduction of *Littorina littorea*

There was a significant difference of mean egg production between the treatments (Kruskal-Wallis H-test, $p < 0.001$) (Figure 6). Snails without oyster epigrowth (109 ± 83 eggs day⁻¹ female⁻¹) released significantly more eggs than fouled snails (1 ± 2 eggs day⁻¹ female⁻¹) and periwinkles from which oysters were removed (2 ± 2 eggs day⁻¹ female⁻¹) (Wilcoxon's matched pairs signed rank test, $p < 0.01$). Fouled *L. littorea* and snails with removed epigrowth showed no significant difference in egg production (Wilcoxon's matched pairs signed rank test, $p > 0.05$).

Discussion

Effects of oyster epigrowth

There are a number of detrimental effects on *Littorina littorea*, caused by epibionts. In the present case, oysters considerably impaired snail mobility. Crawling was either extensively slowed down or considered impossible, as was the capability to return to normal position once turned upside down. Crawling is an essential requirement for food ingestion, as *L. littorea* grazes on diatoms, germlings, ephemeral macroalgae and small invertebrates such as juvenile barnacles by bulldozing and crawling (Lubchenco 1978; Denley and Underwood 1979;

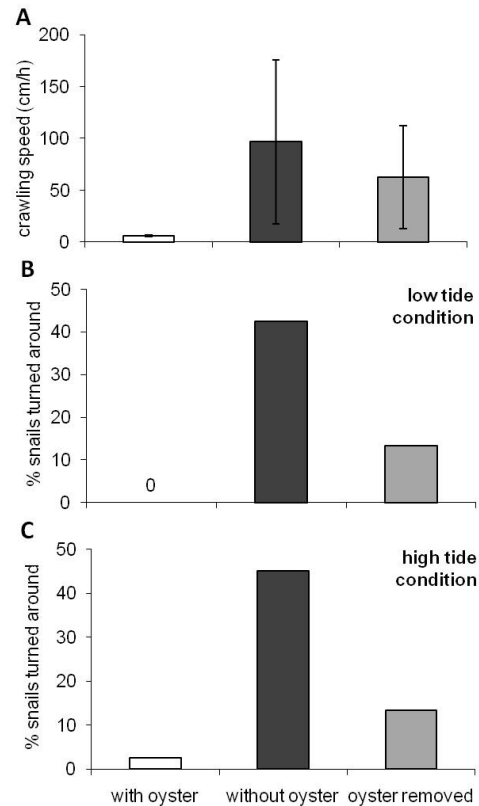


Figure 5. Mean crawling speed (\pm sd) of *Littorina littorea* at low tide (A) and percentage of *Littorina littorea*, which turned from upside down to normal crawling position within one hour at low tide (B) and high tide simulation (C), with and without oyster cover and with removed oysters in summer 2007.

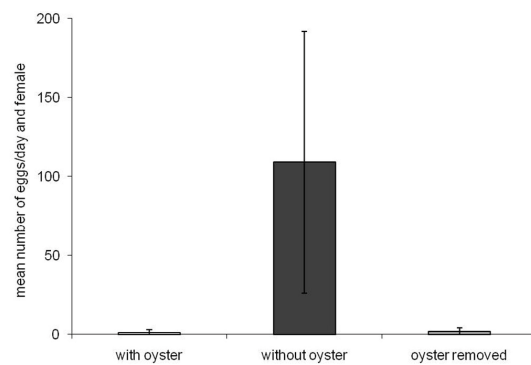


Figure 6. Mean egg production per day and female (\pm sd) of *Littorina littorea* with and without oyster cover and with removed oysters in a ten day experiment in summer 2008.

Hawkins 1983; Petraitis 1983; Farrell 1988; Wilhelmsen and Reise 1994; Fenske 1997; Albrecht 1998; Buschbaum 2000). Often periwinkles are naturally dislodged by wave and currents and may be positioned upside down in unfavorable habitats. This is especially true for overgrown snails that are subjected to increased drag (Witman and Suchanek 1984; Wahl 1996, 1997). In that case returning to crawling position is necessary for normal feeding and for returning to preferred habitats, activities which are strongly hampered by a heavy epibiotic load. The consequence of a reduced food intake in snails with attached epibionts is a decline in tissue weight (Wahl 1996, 1997) followed by a reduced overall fitness (Chan and Chan 2005), which may result in lower reproduction rates. In our experiment, egg production of periwinkles ceased almost entirely when overgrown with oysters, what was also true for the treatment in which oysters had been previously removed. Buschbaum and Reise (1999) suggest that a reduced general fitness of snails with epibionts and a disability in copulation by the voluminous epigrowth may be responsible for reduced egg production in overgrown *L. littorea*. This study revealed the same effects, but additionally showed, that even oyster cover solely on female snails suffices to constrain copulation, as male periwinkles were not fouled in our experiments. Therefore, gonadal analyses of fouled snails are recommended for further studies. It may be assumed that the oysters attached to the snails in our experimental treatment preyed on released egg capsules. However, egg production of periwinkles from which oysters were removed before the experiment had started hardly ever differed from the number of released eggs of overgrown snails, indicating a reduced overall fitness followed by a decline in gonad development and low egg production of *L. littorea* with oyster epigrowth. As Buschbaum and Reise (1999) previously showed, barnacle cover [*Balanus crenatus* (Bruguière, 1789)] on periwinkle shells, which was removed before the egg production measurements, did not negatively affect reproductive output of periwinkles. However, the weight of one oyster is apparently much higher than that of a multitude of barnacles, and may, therefore, cause a higher energy loss in *L. littorea*. Additionally, Pacific oysters are fast growing organisms reaching a size of about 50-80 mm shell length after two years (Reise 1998), with the capacity, to almost stop any movement and reproductive success of

snails due to their heavy load. Thus, every overgrown *L. littorea* is strongly impacted after a short period of time, which, in many cases, will end in the death of the snail.

Increasing alien epibionts

Oyster density continues to increase in the Wadden Sea (Nehls et al. 2009) and although percentage of fouled snails on mixed beds of blue mussels and Pacific oysters showed fluctuations over the last four years, a trend could be observed towards an increasing amount of oyster fouling on periwinkles. As indicated in this study, up to 10 % of snails on mixed bivalve beds and up to 25 % of snails on sandflats were covered with oysters. On sandflat areas, drift of snails with and without oyster cover by waves did not differ and was even significantly lower for infested periwinkles when placed in an area with comparatively high current velocities (Eschweiler, unpublished data). Nevertheless, dislodgment of fouled snails from mixed beds to sandflats may be an explanation for the higher amount of oyster covered snails on sandflat areas, as they would be unable to crawl back to the shellfish bed. If dislodged by waves above or below their preferred habitat, *L. littorea* could be observed to return to that habitat (Alexander 1960; Gendron 1977; Petraitis 1982). Two other factors may also be responsible for the differences in distribution. (i) On sand flat areas, where no other hard substrate is available, periwinkle shells are a proper settlement surface for oyster larvae. (ii) The high abundance of *L. littorea* on mixed beds of mussel and oysters results in a high mutual grazing pressure, as they are crawling over each other, simultaneously bulldozing and grazing and disengaging themselves from sessile organisms such as oyster larvae (Lubchenco 1978; Wahl and Sönnichsen 1992; Albrecht 1998). In general, oyster fouling on snails is not very high. Could oyster epibionts still be able to impair not only the activity of a single individual but also of entire benthic communities? Certainly, oyster cover alone is not sufficient to affect the entire periwinkle population dynamics and ecological functions.

However, oyster densities may still increase and many other sessile alien species have been introduced into the Wadden Sea (Reise et al. 1999). For example, the American slipper limpet *Crepidula fornicata* (Linnaeus, 1758) was first observed at the island of Sylt in 1934 and nowadays it occurs on almost all mixed bivalve

beds. The Australian barnacle *Astrominius modestus* (Darwin, 1854), formerly known as *Elminius modestus* (Buckeridge and Newman 2010), has been introduced in 1955 and shows a strong increase in the last decade, with numbers dominating over the native barnacles [*Semibalanus balanoides* (Linnaeus, 1767) and *Balanus crenatus*]. Presumably, both species profit from increasing water temperatures and milder winters in the southern North Sea, resulting in increasing abundances and higher occurrence of epibionts on *L. littorea* in the Wadden Sea in recent years (Harms 1999; Franke and Gutow 2004; Wiltshire and Manly 2004; Reichert and Buchholz 2006; Witte et al. 2010).

Second to oysters, *A. modestus* especially shows highest occurrence on bivalve and periwinkle shells (Witte et al. 2010) and may cause similar detrimental impacts as revealed for native barnacles *B. crenatus* (Buschbaum and Reise 1999) and alien oysters *C. gigas*.

Slipper limpet overgrowth causes increasing byssus thread production in blue mussels *M. edulis*. The required energy lacks for other processes such as growth and reproduction (Thieltges and Buschbaum 2007). A similar effect of overgrowth by the slipper limpet could be expected for periwinkles fitness, as *C. fornicata* was also detected in high abundances on shells of *L. littorea* (pers. obs.).

Each mentioned epibiont has an influence on the snail as an individual and may implicate appreciable diseases in its living conditions. Although one alien sessile species alone might not cause a profound effect on the entire periwinkle population, the sum of all alien epibionts together might tip the balance towards extensive changes in population dynamics and subsequently influence benthic community structures.

Conclusion

Epibionts in general strongly decrease reproductive output and hamper snail mobility, which results in reduced body weight of *Littorina littorea*.

Periwinkles predominantly occur in the intertidal zone of the Wadden Sea, whereas comparatively low snail densities were observed in the adjacent subtidal zone (Buhs and Reise 1997; Saier 2000). Buschbaum and Reise (1999) to some extent attributed this distribution pattern

to mortality, caused by high epibiotic load on *L. littorea* in the subtidal area. The recent increase of Pacific oysters is also responsible for intertidal snails now being exposed to high epibiotic loads. Additionally, other non-indigenous epibiotic species successfully established in the Wadden Sea, are facilitated by rising temperatures, and we assume that this process will continue. Although no profound detrimental effect could be observed on the periwinkle population so far, it seems to be only a question of time until the combination of a multitude of epibiotic alien species might strongly impair periwinkle population dynamics and consequently its ecological function in the Wadden Sea.

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