

Grazer identity is crucial for facilitating growth of the perennial brown alga *Fucus vesiculosus*

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ABSTRACT: The positive top-down effects on macrophytes of the removal of fouling epiphytes by herbivores versus negative bottom-up effects of enhanced epiphyte growth through nutrient enrichment are known from previous works. However, few studies have differentiated effects within the suite of herbivore species, nor have they investigated the potential negative effects of these grazers on macrophytes. We conducted a mesocosm experiment to investigate the impact of different grazer compositions (no grazers, the isopod *Idotea baltica*, the gastropod *Theodoxus fluviatilis*, and a mixture of both species) and nutrient levels (ambient and enriched) on growth of the brown alga *Fucus vesiculosus*. Herbivore facilitation depended on grazer identity, as only the treatments that included *T. fluviatilis* increased the growth rate of *F. vesiculosus*. Since *I. baltica* reduced the epiphyte population by the same amount as *T. fluviatilis*, we suggest that the grazing activities of this isopod on *F. vesiculosus* itself may have counteracted any positive effect of epiphytic removal. The same explanation may account for the similar growth rates in the treatments with *T. fluviatilis* alone and with both herbivorous species together, despite the lower epiphytic load in the latter treatment. In contrast, earlier published data suggested that *T. fluviatilis* facilitation is greater than that of *I. baltica* because of different epiphytic algal preferences between the grazers. Nutrient addition treatments, despite significantly increasing epiphyte load, had no effect on the growth rate of *F. vesiculosus*.

KEY WORDS: *Fucus vesiculosus* · *Theodoxus fluviatilis* · *Idotea baltica* · Growth rate · Grazing · Facilitation · Nutrient uptake inhibition

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INTRODUCTION

In temperate rocky shore regions, slow-growing macroalgae play an important role in structuring coastal habitats. The main eutrophication effect found in these systems is an increasing amount of annual filamentous opportunistic algae (Schramm & Nienhuis 1996, Valiela et al. 1997). These algal species are often more nutritious than the slow-growing macroalgae (Chopin et al. 1996, Pedersen & Borum 1996), and are often favoured as food by mesoherbivores (Ravanko 1969, Goecker & Káll 2003, Orav-Kotta & Kotta 2004); there are, however, trade-offs between food quality and shelter from predation (e.g. Duffy & Hay 1991, Jormalainen et al. 2001). Slow-growing macroalgae are thus often more negatively affected by nutrient enrich-

ment and at the same time more positively affected by grazing than competing opportunistic epiphytic algal species. There are also reports that reduction of epiphyte load by grazers can have positive, indirect top-down effects on brown algal growth rate and cover (Worm et al. 1999, 2000a, Jormalainen et al. 2003, Honkanen & Jormalainen 2005), as well as reports showing indirect negative bottom-up effects through unsuccessful competition with opportunistic algal species (e.g. Kangas et al. 1982, Worm et al. 1999, Benedetti-Cecchi et al. 2001, Berger et al. 2003).

Concern about the loss of biodiversity in aquatic systems (e.g. Worm et al. 2006) has prompted increased investigation of the redundancy and/or specific effects of various herbivorous species, i.e. effects due to herbivore diversity (Duffy 2002). However, despite numer-

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ous studies of the effects of grazers on the production of structurally important macroalgae (Worm et al. 1999, 2000a, Jormalainen et al. 2003, Honkanen & Jormalainen 2005), there is a lack of research into the effects of different herbivorous species on facilitation of macroalgal communities. Except for Duffy & Hay (2000), the few studies that have explored the different individual versus the pooled effects of specific herbivores on macrophytes have all examined seagrass ecosystems (Duffy & Harvilicz 2001, Duffy et al. 2001, 2003, Hays 2005). Studies of the interactive effects of different combinations of herbivores and nutrient levels are even rarer (however, see Hays 2005).

Although grazing on epiphytic algae demonstrably facilitates slow-growing brown algal production, it may also have a reverse effect due to the direct consumption of these algae (e.g. Chapman 1989, Duffy 1990, Hemmi et al. 2005). Likewise, there are field observations of negative correlations between the cover of the large, perennial brown alga *Fucus vesiculosus* and the abundance of the herbivorous isopod *Idotea baltica* (e.g. Engkvist et al. 2004, Nilsson et al. 2004). Furthermore, the small gastropod species *Theodoxus fluviatilis* may have a negative effect on *F. vesiculosus* growth through its removal of hyaline hairs growing on the epidermis of this fucoid (Jormalainen et al. 2003). These hairs facilitate nutrient uptake (Hurd et al. 1993), and the lower growth rate of *F. vesiculosus* when exposed to *T. fluviatilis* may result from the reduction in nutrient uptake (Jormalainen et al. 2003).

A mesocosm experiment was thus conducted to investigate the top-down impacts of two herbivorous species, viz. the isopod *Idotea baltica* (hereafter *Idotea*) and the gastropod *Theodoxus fluviatilis* (hereafter *Theodoxus*), singly and in combination, as well as the bottom-up effects of nutrient addition, on the growth rate of *Fucus vesiculosus* (hereafter *Fucus*). As illustrated in Fig. 1, we hypothesized that *Idotea* would decrease the growth rate of *Fucus* by directly grazing on *Fucus* thalli (H1a) and/or increase the growth rate indirectly by reducing the population of shading epiphytes (H1b). In contrast, the gastropod *Theodoxus* was hypothesized to have a negative effect on the growth rate of *Fucus* through inhibiting nitrogen uptake (H2a) and/or increase *Fucus* growth rate indirectly through reducing the population of fouling epiphytes (H2b). We further hypothesized that a mixture of the herbivores would facilitate *Fucus* growth rate even more than individual herbivore species (H3), due to a complementarity effect (Loreau & Hector 2001), resulting in the lowest epiphytic load on *Fucus*. In addition, nutrient enrichment was hypothesized to decrease the growth rate of *Fucus* (H4), due to indirect effects on the growth of fouling epiphytes.

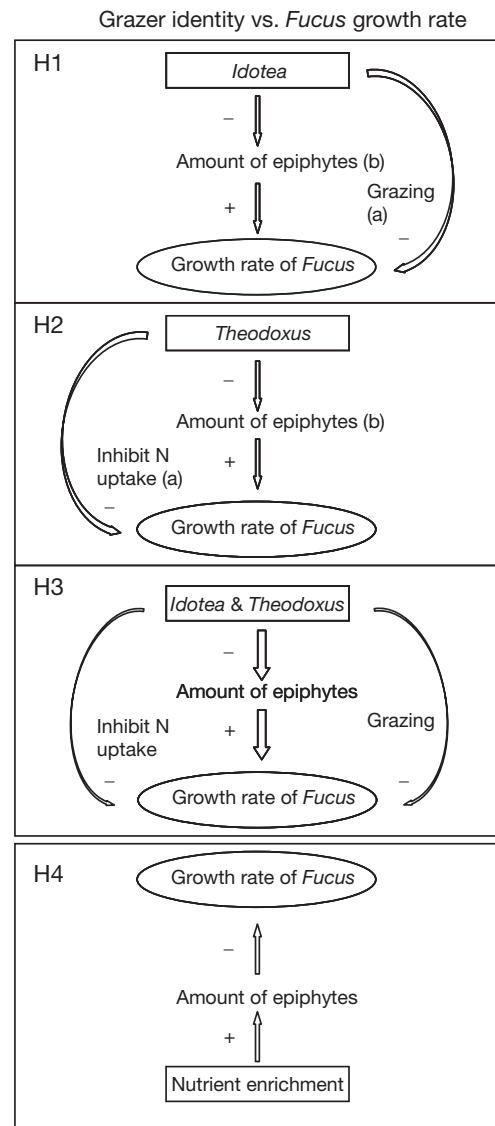


Fig. 1. Schematic of hypotheses tested experimentally. In the treatment with *Idotea baltica* (i.e. *Idotea*) as the only grazer, *Fucus* growth rate may be negatively affected by direct herbivore grazing (H1a) and/or indirectly and positively affected by the reduced population of fouling epiphytes (H1b). In the treatments with *Theodoxus fluviatilis* (i.e. *Theodoxus*) as the only grazer, *Fucus* growth rate may instead be negatively affected by inhibition of nitrogen uptake (H2a) and/or indirectly and positively affected by the gastropod's ability to reduce the epiphyte population (H2b). When *I. baltica* and *T. fluviatilis* are combined (i.e. the Mixed treatment), the negative effects of *I. baltica* and *T. fluviatilis* are still evident, though not as strongly as in treatments with single herbivore species, due to the reduced amounts of each herbivore species (the arrows are narrower) (H3). The reduction of the epiphyte population, due to complementarity in the utilization of epiphytic algae between the 2 herbivore species, however, is enhanced in this treatment, which in turn results in a higher growth rate of *Fucus* (thicker arrow) (H3). Nutrient enrichment, on the other hand, indirectly decreases the growth rate of *Fucus* by stimulating enhanced epiphytic growth (H4)

MATERIALS AND METHODS

Experimental setup. The effects of nutrient enrichment and different grazer combinations on *Fucus* growth were tested in a factorial mesocosm experiment conducted outdoors with exposure to ambient light, temperature, and weather conditions. The experiment was carried out at the Askö Laboratory (58° 49' N, 19° 39' E) in summer from 27 May to 1 July 2003 (5 wk). *Fucus* thalli weighing approximately 220 g wet wt (i.e. approximately 40 g dry wt) and without any visible epiphytes were collected at a depth of 0.5 m in the vicinity of the laboratory. Each thallus was anchored to a brick with a plastic tie and placed in a circular 30 l plastic container. The containers were supplied with a constant flow (one l min⁻¹) of sand-filtered seawater (sand particle size 0.6–0.8 mm) pumped from an area 120 m from the shore at a depth of 15 m. Salinity and temperature in the containers approximately matched those in the sampling area (6.1 psu and 16 ± 1°C). Half of the containers received added nutrients from a commercial, slow-release NPK fertilizer (Plantacote Depot 6-M) consisting of pellets with a semipermeable polyurethane coating. This fertilizer continually released the following nutrients into the water column for at least 6 wk: N, as NH₄⁺ (8.3%) and NH₃ (5.7%); P as water-soluble P₂O₅ (9%); and K as K₂O (15%) (for evaluations of the method, see Worm et al. 2000b). In each container, 240 g of fertilizer pellets were enclosed in a polyethylene mesh roll 3 cm in diameter and 40 cm in length. To evaluate the effects of different grazer compositions, 4 grazer treatments were tested: (1) no grazers, (2) grazing by *Idotea* only, (3) grazing by *Theodoxus* only, and (4) grazing by *Idotea* + *Theodoxus* (hereafter Mixed). Each replicate of the different grazer treatments received approximately 1 g dry wt of grazers (the dry wt of one individual of *Idotea* is approximately 20 mg and that of *Theodoxus*, shell-free, is approximately 2 mg), and the ratio between the number of *Idotea* and *Theodoxus* individuals in the Mixed treatment was 1:15, a ratio common in the sampling area. The Mixed treatment thus contained 40% of the total mass of *Idotea* introduced into the *Idotea*-only treatment and 60% of the total mass of *Theodoxus* introduced into the *Theodoxus*-only treatment. The most common gastropod species found on *Fucus* collected during the study period was *Theodoxus*, while *Idotea* was the second most common crustacean species (the most common crustacean group comprises *Gammarus* spp.). The abundances of *Idotea* and *Theodoxus* in the experimental setup were in the upper range of the field abundances found on *Fucus* thalli in the area (Råberg & Kautsky 2007a). The grazers were transferred to the containers 1 wk after setting up the

Fucus specimens and the nutrient diffusers, and the experiment was run for 4 wk. Due to the natural mortality of *Idotea* in the summer, 20% of the initial numbers of individuals in each treatment were added to the containers every week during the experiment. Faecal pellets from the grazers were removed from the containers once a week to minimize nutrient contamination. Five replicates were run for each treatment for a total of 40 containers, arranged in a randomized design in two outdoor tanks.

Analysis of nutrients in the water column. Water samples for nutrient analysis were taken from both No grazer treatments (i.e. with ambient and enriched nutrients) at the beginning, halfway and end points of the experiment. A PVC tube with an attached 50 ml polyethylene syringe was used to sample water from the middle of the container. The water sample was immediately filtered through a 0.45 µm single-use filter and frozen at -80°C. The concentrations of NH₄⁺, PO₄³⁻, and NO₂⁻ + NO₃⁻ were measured by means of segmented flow analysis (SFA) using an Analytic Flow solution IV (ALPKEM/OI).

Over the whole experimental period (3 sampling occasions), the average amount of NH₄⁺ was calculated to be 0.26 µmol l⁻¹ in the ambient water and 3.85 µmol l⁻¹ in the nutrient-enriched water (a 15-fold increase). The NO₂⁻ + NO₃⁻ level was 0.30 µmol l⁻¹ in the ambient water and 4.13 µmol l⁻¹ in the nutrient-enriched water (a 14-fold increase). The PO₄³⁻ level was 0.28 µmol l⁻¹ in the ambient water and 0.81 µmol l⁻¹ in the nutrient-enriched water (a 3-fold increase).

***Fucus* growth measurements.** To study the grazing activity of *Idotea*, changes in the surface area of *Fucus* were measured by scanning five growing tips from each replicate (equivalent to approximately 120 cm² of *Fucus* thallus) of the No grazers, *Idotea*, and Mixed treatments (i.e. all treatments except *Theodoxus*-only) at the start of the experiment, marking the growing tips with plastic ties, and scanning them in the same manner at the end of the experimental period. The changes in thallus area from the beginning to the end of the experiment were calculated using the program Image Tool Version 2.01 Alpha 4 and transformed to cm² wk⁻¹.

In addition, the growth rate of *Fucus* was also measured as increase in length in order to investigate the impact of factors other than direct grazing (e.g. light and nutrient availability) in all treatments. However, this measurement also includes direct grazing to some extent when *Idotea* chose to graze *Fucus* tips. A small hole was punched 4 cm from the ends of 15 to 20 growing tips on each *Fucus* specimen at the start of the experiment. After the experiment, the tips were measured again and the mean value of the length increase of these 15 to 20 tips was recalculated.

lated as the growth rate in mm wk^{-1} of each *Fucus* thallus.

Analyses of nitrogen content in *Fucus*. To investigate any inhibition of nitrogen uptake due to grazing by *Theodoxus*, the nitrogen contents of *Fucus* in the No grazers, Mixed, and *Theodoxus*-only grazer treatments (i.e. all treatments except *Idotea*-only) were analysed. Before and after the experiment, 1 tip (approximately 8 cm long) from each replicate was cut off the *Fucus* thallus and dried at 60°C for 2 wk. After drying, the tips were ground to a fine powder and their nitrogen contents were analysed with a CHNS-932 element analyser (LECO).

Biomass of epiphytes on *Fucus*. At the end of the experiment, a net bag with a mesh size of $100\ \mu\text{m}$ was carefully pulled over the *Fucus* thallus in each container, which was then cut off its mounting brick. The bags were quickly transported to the laboratory and transferred to a plastic tray containing seawater, and the grazers were sorted from the *Fucus*. A razor blade was used to scrape the algae growing on the *Fucus* into the seawater in the tray, which was then filtered through a net with a mesh size of $20\ \mu\text{m}$. The algal epiphytes and the *Fucus* thalli were dried at 60°C for at least 2 wk, and the epiphytic load was recalculated to g dry wt per 100 g dry wt *Fucus*.

Grazer survival and distribution. The grazers, both those occupying the *Fucus* material and those left in the containers, were counted after the experiment. The number of *Idotea* was reduced by 17% from the initial abundance, despite the additions made during the experiment, while the number of *Theodoxus* was reduced by only 2%. This reduction in the number of herbivores did not differ between the treatments. (A 2-way ANOVA testing effects of nutrient level and grazer composition gave p values of 0.23 to 0.44 and 0.12 to 0.93 for the reduction of *Idotea* and *Theodoxus* numbers, respectively). When counting the *Theodoxus* specimens, we noted that approximately half of the snails were distributed on the walls of the container and half on the *Fucus* itself; in contrast, the *Idotea* specimens occupied the *Fucus* thallus most of the time, only occasionally swimming in the water.

Statistical analyses. Two-way ANOVAs were used to analyse (1) the growth of *Fucus* and of epiphytic biomass, and (2) changes in nitrogen content over the duration of the experiment; nutrient level (ambient nutrient concentration versus nutrient enrichment) and grazer composition ($n = 4$) were used as fixed factors. When grazer composition had a significant effect or there was a significant interaction, pairwise differences between means were further explored using Tukey's HSD test. Epiphytic biomass was third-root transformed to meet the assumption of homogeneity of variances (Cochran's test). All tests were performed using Statistica 6.1 (StatSoft).

RESULTS

Effects of direct grazing on *Fucus* thallus area

Growth rate measured as increase in area of *Fucus* thalli was not affected by either nutrient level or grazer compositions that included *Idotea* (i.e. the *Idotea*-only and Mixed treatments) (Table 1). The grazer composition factor had a p value of 0.050 (Table 1), and a post-hoc test indicated p values of 0.07 between the No grazers and Mixed treatments, and of 0.09 between the *Idotea* and Mixed treatments, respectively. Contrary to what was expected, the area increase of *Fucus* thalli was almost the same in the treatment with no *Idotea* present (i.e. the No grazer control) and the treatment with the greatest abundance of *Idotea* (i.e. the *Idotea*-only treatment) (Fig. 2A).

Effects of grazing activities on *Fucus* nitrogen content

The change in nitrogen content over the course of the experiment was unaffected by grazer composition (Tables 1, 2). Thus, it appears that *Theodoxus* may not have inhibited *Fucus* nitrogen uptake. Instead, nitro-

Table 1. Two-way ANOVAs testing effects of nutrient level (ambient nutrients, nutrient enrichment) and grazer composition (No grazers, *Idotea baltica*, *Theodoxus fluviatilis*, and *I. baltica* + *T. fluviatilis*) on growth of *Fucus* thallus area, *Fucus* nitrogen content, growth of *Fucus* thallus length, and epiphytic algal mass

Source of variation	df	F	p
Growth of <i>Fucus</i> thallus area ($\text{cm}^2\ \text{wk}^{-1}$)			
Nutrient level	1	0.03	0.596
Grazer composition	2	3.39	0.050
Nutrient level \times Grazer composition	2	0.12	0.888
Residual	24		
Growth of <i>Fucus</i> nitrogen content (% dry wt)			
Nutrient level	1	42.4	<0.001
Grazer composition	2	0.93	0.406
Nutrient level \times Grazer composition	2	2.06	0.149
Residual	24		
<i>Fucus</i> thallus length ($\text{mm}\ \text{wk}^{-1}$)			
Nutrient level	1	0.53	0.474
Grazer composition	3	6.36	<0.01
Nutrient level \times Grazer composition	3	0.04	0.988
Residual	32		
Epiphytic algal mass ($\text{g dry wt } 100\ \text{g}^{-1}\ \text{dry wt } \textit{Fucus}$)			
Nutrient level	1	31.5	<0.001
Grazer composition	3	75.7	<0.001
Nutrient level \times Grazer composition	3	1.57	0.217
Residual	32		

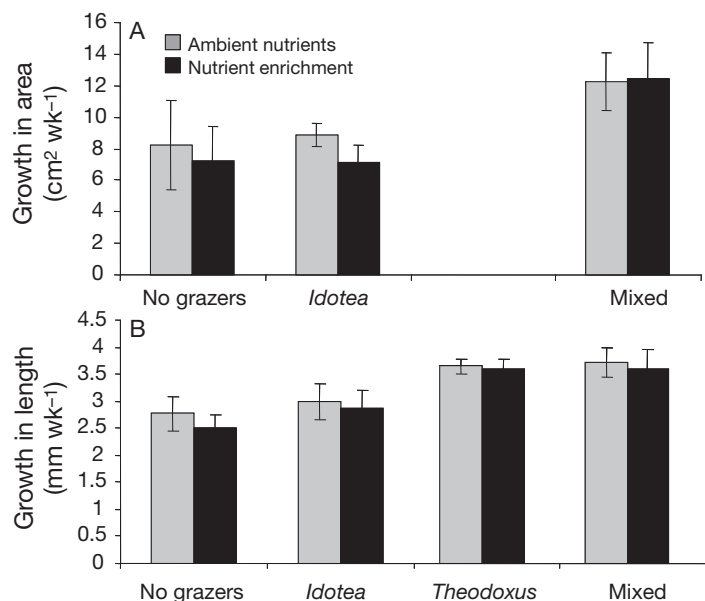


Fig. 2. *Fucus vesiculosus*. Growth of (A) thallus area and (B) length. The 4 grazer treatments are: No grazers, *Idotea baltica* (*Idotea*), *Theodoxus fluviatilis* (*Theodoxus*), and *I. baltica* + *T. fluviatilis* (Mixed). Means \pm SE (n = 5)

gen content changed significantly over the study period depending on whether or not nutrients were added (Table 1), and it was only under ambient nutrient conditions that change occurred over the time course of the experiment (nitrogen content decreased, Table 2).

Treatment effects on increase in *Fucus* thallus length

Grazer composition had a significant effect on the growth in length of *Fucus* thalli (Table 1, Fig. 2B), and post hoc testing revealed a higher growth rate in the Mixed (3.65 mm wk⁻¹) and *Theodoxus*-only (3.62 mm wk⁻¹) treatments than in the No grazer treatment (2.64 mm wk⁻¹) ($p < 0.01$ in all cases). On the other hand, nutrient level had no impact on increase in thallus length (Table 1, Fig. 2B).

Biomass of epiphytic algae

Although both *Fucus* area and linear growth rates were unaffected by nutrient addition, the biomass of epiphytic algae (Table 3), thought to have a negative effect on *Fucus* growth, was significantly higher in enriched nutrient treatments (Table 1). Biomass of epiphytes also varied significantly depending on grazer composition (Table 1). Post hoc testing for grazer composition revealed differences between all grazer treat-

Table 2. *Fucus vesiculosus*. Percentage changes in nitrogen content (% dry wt) under ambient and enriched nutrient conditions over the course of the experiment. The 3 grazer treatments are No grazers, *Theodoxus fluviatilis* (*Theodoxus*), and *Idotea baltica* + *T. fluviatilis* (Mixed). Means \pm SE (n = 5)

	Ambient nutrients	Nutrient enrichment
No grazers	-1.13 \pm 0.26	0.24 \pm 0.18
<i>Theodoxus</i>	-1.24 \pm 0.22	0.40 \pm 0.22
Mixed	-1.07 \pm 0.26	-0.35 \pm 0.25

Table 3. *Fucus vesiculosus*. Epiphytic biomass (g dry wt per 100 g dry wt *F. vesiculosus*, means \pm SE; n = 5). The 4 grazer compositions are No grazers, *Idotea baltica* (*Idotea*), *Theodoxus fluviatilis* (*Theodoxus*), and *I. baltica* + *T. fluviatilis* (Mixed)

	Ambient	Enriched
No grazers	4.88 \pm 0.40	7.15 \pm 1.51
<i>Idotea</i>	0.68 \pm 0.10	2.15 \pm 0.33
<i>Theodoxus</i>	0.55 \pm 0.07	1.94 \pm 0.43
Mixed	0.26 \pm 0.04	0.52 \pm 0.08

ments ($p < 0.001$ in all cases), except between the *Idotea*- and *Theodoxus*-only treatments ($p = 0.86$). The No grazer treatment had the highest epiphytic biomass, whereas the Mixed treatment with 2 herbivore species had the lowest epiphyte biomass (Table 3).

DISCUSSION

Contrary to hypothesis H1a, *Idotea* had no measurable negative effects on *Fucus* growth rate (measured as increases in area and length of thallus). This is somewhat surprising, given the documented laboratory (Jormalainen et al. 2001, Hemmi et al. 2005) and field studies (e.g. Engkvist et al. 2004, Nilsson et al. 2004) demonstrating the negative effects of the grazing activities of *Idotea* on *Fucus* growth rate and cover. On the other hand, the similarity of the increases in area and length between the No grazer and *Idotea* only treatments may mask the effect of the *Idotea* grazing activities; this is because this herbivore, as well as grazing on *Fucus* itself, simultaneously reduces the epiphytic load on the *Fucus*, which in turn may have positively affected its growth. This possibility is supported by feeding preference studies showing that *Idotea* preferred filamentous algae over *Fucus* (Ravanko 1969, Goecker & Káll 2003, Orav-Kotta & Kotta 2004). The positive effects of *Idotea* sp. on the growth of eelgrass likewise result from the isopod's ability to reduce the population of algal epiphytes (Williams & Ruckelshaus 1993). Since no filamentous

algae were left after treatment with *Idotea* only (Råberg & Kautsky 2007b), it is possible that *Idotea* ate all available filamentous algae and pieces of *Fucus* tissue. Hence, the hypothesis that *Idotea* would increase the growth rate of *Fucus* by reducing the population of fouling epiphytes (H1b) may not have been upheld in this study because *Idotea* simultaneously grazed on *Fucus* itself.

The hypothesis that the gastropod *Theodoxus* would reduce the growth rate of *Fucus*, measured as increase in length, due to reduced nitrogen uptake (H2a) was not supported, since the nitrogen content was similar in the grazer treatments with and without *Theodoxus*. However, the hyaline hairs are only important for nutrient uptake in low-nutrient environments (Hurd et al. 1993). Thus, contrary to Jormalainen et al. (2003), who suggested that grazing *Theodoxus* inhibited nutrient uptake in *Fucus*, high nutrient concentrations in both the ambient and nutrient enriched treatments in the present study may have overshadowed any effect arising from grazing on hyaline hairs. The hypothesis that *Theodoxus* would increase the linear growth of *Fucus* thalli by reducing the population of growing epiphytes (H2b) was, however, confirmed. Other studies have also demonstrated the significance of *Theodoxus* as a grazer of fouling epiphytes, but with contrasting effects on *Fucus* growth (Jormalainen et al. 2003, Honkanen & Jormalainen 2005). Our results (that *Idotea* had no effect while *Theodoxus* had a positive effect on *Fucus* growth rate) are partly supported by a field survey of *Fucus*, showing that gastropod but not crustacean grazing was positively correlated with *Fucus* cover (Worm et al. 1999).

It is possible that the quite different impacts of *Idotea* and *Theodoxus* on the linear growth of *Fucus* thalli (despite the fact that 2 grazers reduced epiphyte load by approximately the same amount) may occur because *Idotea* simultaneously grazed on *Fucus* itself, as mentioned previously. An alternative hypothesis is that herbivores utilized different algal species (Råberg & Kautsky 2007b). While most of the remaining epiphytes in the treatments with *Idotea* only were microalgae (filamentous macroalgae were grazed away), those in treatments with *Theodoxus*-only consisted mainly of filamentous macroalgae (Råberg & Kautsky 2007b). The higher growth rate of *Fucus* in treatments with *Theodoxus* thus suggests that epiphytic microalgae shade *Fucus* to a greater extent than filamentous macroalgal epiphytes. Hence, *Theodoxus* is an efficient grazer on harmful, shading epiphytes and is thus important for maintaining *Fucus* communities in the Baltic Sea.

Even though the presence of both *Theodoxus* and *Idotea* (i.e. the Mixed treatment) resulted in significantly lower epiphytic biomass, this reduction in epi-

phytic load did not translate into an increase in *Fucus* thallus length (i.e. there was no significant difference in thallus length between the Mixed and *Theodoxus*-only treatments). Thus, the hypothesis that a complementarity effect (Loreau & Hector 2001) should result in a higher growth rate (H3) could not be supported. There may be two reasons for this lack of enhanced growth, despite the significantly lower epiphytic load in this treatment. First, *Idotea* (as may have been the case in the *Idotea*-only treatment) counteracts the positive effect of the reduction of the epiphyte population by directly grazing on *Fucus* itself. Second, since *Fucus* is a slow-growing perennial algal species, the similar high growth rates in the *Theodoxus*-only and Mixed treatments may mean that inherent *Fucus* maximum growth rates had already been achieved in the treatment with only *Theodoxus* as a grazer. Thus, even though the Mixed treatment reduced the epiphytic load, and hence increased the light availability significantly more than the monocultural herbivore treatments, the inherently slow growth of *Fucus* hindered any additional growth in this treatment. The lack of increased plant biomass resulting from exposure to a higher diversity of grazers is also evident when combining 2 (Duffy & Harvilicz 2001) or 3 (Duffy et al. 2001) species of grazing crustaceans. However, some studies have demonstrated increased plant growth in response to different herbivorous species compositions (Duffy et al. 2003, Hays 2005). In a study including 6 different grazer species, the biomass of eelgrass increased depending on species composition, but not on grazer diversity per se (Duffy et al. 2003). When the diversity was maximized, the previous growth facilitation in response to reduced epiphytic load was replaced by the suppression of eelgrass biomass due to direct grazing on the host plant (Duffy et al. 2003). Given that *Idotea* also eats *Fucus*, similar results might have been obtained had the present study incorporated other grazer species that competed with *Idotea* for the macroepiphytes, e.g. *Gammarus* spp. and other species of the genus *Idotea*. Hays (2005), who studied a crab and a shrimp species with and without nutrient addition, demonstrated that the higher growth rate of turtle grass subjected to a combination of grazer species was dependent on both nutrient level and eelgrass source population. However, the treatment with the grazers in combination also contained a higher biomass of grazers (Hays 2005). Hence, it was impossible to distinguish the cause of the increased eelgrass biomass, i.e. whether it was due to overall higher grazing pressure or to complementarity between the two herbivorous species (Hays 2005).

An increased nutrient level did not decrease the growth rate of *Fucus* (measured as growth in either area or length) as was hypothesized (H4), even though

nutrient addition did increase the epiphytic load on *Fucus*. A meta-analysis of studies of seagrass beds demonstrated that the positive effect of grazers was comparable in magnitude to the negative effect of water column nutrient enrichment (Hughes et al. 2004). In the present study, however, grazing activity of the herbivores was the sole factor influencing *Fucus* growth rate.

In summary, different grazer species may have different capacities for facilitating the growth of large structuring macrophytes. *Theodoxus*, a common gastropod in the northern Baltic Sea, increased the growth rate of the ecologically important perennial brown alga *Fucus*. In contrast, even though the isopod *Idotea* reduced the epiphyte load by approximately the same amount as *Theodoxus*, *Idotea* grazing resulted in a *Fucus* growth rate as low as that in the treatment with no grazers present. When the two herbivorous species were mixed together, the epiphytic biomass was reduced even further, possibly due to a complementarity effect arising from resource partitioning between the species (Råberg & Kautsky 2007b). However, this lower biomass of epiphytes on *Fucus* did not increase the linear growth of *Fucus* thalli any further; instead, growth remained at the level measured in the *Theodoxus*-only treatment. Unlike the absence of grazers, the high nutrient load in the nutrient enrichment treatments did not have any negative effect on *Fucus* growth rate. This further demonstrates the important role of grazing communities for the health and maintenance of *Fucus* belts, since low-nutrient conditions without grazers produced lower linear growth of *Fucus* thalli compared to that of *Fucus* in the high-nutrient treatment with *Theodoxus* present.

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LITERATURE CITED

- Benedetti-Cecchi LPF, Pannacciulli F, Bulleri F, Moschella PS, Airoldi L, Relini G, Cinelli F (2001) Predicting the consequences of anthropogenic disturbance: large-scale effects of loss of canopy algae on rocky shores. *Mar Ecol Prog Ser* 214:137–150
- Berger R, Henriksson E, Kautsky L, Malm T (2003) Effects of filamentous algae and deposited matter on the survival of *Fucus vesiculosus* L. germlings in the Baltic Sea. *Aquat Ecol* 37:1–11
- Chapman ARO (1989) Abundance of *Fucus spiralis* and ephemeral seaweeds in a high eu littoral zone: effects of grazers, canopy and substratum type. *Mar Biol* 102: 565–572
- Chopin T, Marquis PA, Belyea EP (1996) Seasonal dynamics of phosphorus and nitrogen contents in the brown alga *Ascophyllum nodosum* (L.) Le Jolis, and its associated species *Polysiphonia lanosa* (L.) Tandy and *Pilayella littoralis* (L.) Kjellman, from the Bay of Fundy, Canada. *Bot Mar* 39: 543–552
- Duffy JE (1990) Amphipods on seaweeds: partners or pests? *Oecologia* 83:267–276
- Duffy JE (2002) Biodiversity and ecosystem function: the consumer connection. *Oikos* 99:201–219
- Duffy JE, Harvilicz AM (2001) Species-specific impacts of grazing amphipods in an eelgrass-bed community. *Mar Ecol Prog Ser* 223:201–211
- Duffy JE, Hay ME (1991) Food and shelter as determinants of food choice by an herbivorous marine amphipod. *Ecology* 72:1286–1298
- Duffy JE, Hay ME (2000) Strong impacts of grazing amphipods on the organization of a benthic community. *Ecol Monogr* 70:237–263
- Duffy JE, MacDonald KS, Rhode JM, Parker JD (2001) Grazer diversity, functional redundancy, and productivity in seagrass beds: an experimental test. *Ecology* 82:2417–2434
- Duffy JE, Richardson JP, Canuel EA (2003) Grazer diversity effects on ecosystem functioning in seagrass beds. *Ecol Lett* 6:637–645
- Engkvist R, Malm T, Nilsson J (2004) Interaction between isopod grazing and wave action: a structuring force in macroalgal communities in the southern Baltic Sea. *Aquat Ecol* 38:403–413
- Goecker ME, Käll SE (2003) Grazing preferences of marine isopods and amphipods on three prominent algal species of the Baltic Sea. *J Sea Res* 50:309–314
- Hays CG (2005) Effect of nutrient availability, grazer assemblage and seagrass source population on the interaction between *Thalassia testudinum* (turtle grass) and its algal epiphytes. *J Exp Mar Biol Ecol* 314:53–68
- Hemmi A, Mäkinen A, Jormalainen V, Honkanen T (2005) Responses of growth and phlorotannins in *Fucus vesiculosus* to nutrient enrichment and herbivory. *Aquat Ecol* 39: 201–211
- Honkanen T, Jormalainen V (2005) Genotypic variation in tolerance and resistance to fouling in the brown alga *Fucus vesiculosus*. *Oecologia* 144:196–205
- Hughes AR, Bando KJ, Rodriguez LF, Williams SL (2004) Relative effects of grazers and nutrients on seagrasses: a meta-analysis approach. *Mar Ecol Prog Ser* 282:87–99
- Hurd CL, Galvin RS, Norton TA, Dring MJ (1993) Production of hyaline hairs by intertidal species of *Fucus* (Fucales) and their role in phosphate uptake. *J Phycol* 29:160–165
- Jormalainen V, Honkanen T, Heikkilä N (2001) Feeding preferences and performance of a marine isopod on seaweed hosts: cost of habitat specialization. *Mar Ecol Prog Ser* 220: 219–230
- Jormalainen V, Honkanen T, Koivikko R, Eränen J (2003) Induction of phlorotannin in a brown alga: defence or resource dynamics? *Oikos* 103:640–650
- Kangas P, Autio H, Hällfors G, Luther H, Niemi Å, Salemaa H (1982) A general model of the decline of *Fucus vesiculosus* at Tvärminne, south coast of Finland in 1977–81. *Acta Bot Fenn* 118:1–27
- Loreau M, Hector A (2001) Partitioning selection and complementarity in biodiversity experiments. *Nature* 412:72–76
- Nilsson J, Engkvist R, Persson LE (2004) Long-term decline and recent recovery of *Fucus* populations along the rock shores of southeast Sweden, Baltic Sea. *Aquat Ecol* 38:587–598

- Orav-Kotta H, Kotta J (2004) Food and habitat choice of the isopod *Idotea baltica* in the northeastern Baltic Sea. *Hydrobiologia* 514:79–85
- Pedersen MF, Borum J (1996) Nutrient control of algal growth in estuarine waters. Nutrient limitation and the importance of nitrogen requirements and nitrogen storage among phytoplankton and species of macroalgae. *Mar Ecol Prog Ser* 142:261–272
- Råberg S, Kautsky L (2007a) A comparative biodiversity study of the associated fauna of perennial furoids and filamentous algae. *Estuar Coast Shelf Sci* 73:249–258
- Råberg S, Kautsky L (2007b) Consumers affect prey biomass and diversity through resource partitioning. *Ecology* 88: 2468–2473
- Ravanko O (1969) Benthic algae as food for some invertebrates in the inner part of the Baltic. *Limnologica* 7:203–205
- Schramm W, Nienhuis PH (1996) Marine benthic vegetation: recent changes and the effects of eutrophication. *Ecological Studies* 123. Springer, Heidelberg
- Valiela I, McClelland J, Hauxwell J, Behr PJ, Hersh D, Foreman K (1997) Macroalgal blooms in shallow estuaries: controls and ecophysiological and ecosystem consequences. *Limnol Oceanogr* 42:1105–1118
- Williams SL, Ruckelshaus MH (1993) Effects of nitrogen availability and herbivory on eelgrass (*Zostera marina*) and epiphytes. *Ecology* 74:904–918
- Worm B, Lotze HK, Boström C, Engkvist R, Labanauskas V, Sommer U (1999) Marine diversity shift linked to interactions among grazers, nutrients and propagule banks. *Mar Ecol Prog Ser* 185:309–314
- Worm B, Lotze HK, Sommer U (2000a) Coastal food web structure, carbon storage, and nitrogen retention regulated by consumer pressure and nutrient loading. *Limnol Oceanogr* 45:339–349
- Worm B, Reusch BH, Lotze HK (2000b) *In situ* enrichment: methods for marine benthic ecology. *Int Rev Hydrobiol* 85: 359–375
- Worm B, Barbier EB, Beaumont N, Duffy JE and others (2006) Impacts of biodiversity loss on ocean ecosystem services. *Science* 314:787–790

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