

Functional diversity of mesograzers in an eelgrass–epiphyte system

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Abstract Historically, small invertebrate grazers in marine plant communities have been considered to be a relatively homogeneous group in their impact on ecosystem processes. However, recent studies propose that species composition is an important agent in determining grazer effects. We used four mesocosm experiments to test the biomass-specific and density-dependent effects of common mesograzers in temperate regions (*Littorina littorea*, *Rissoa membranacea*, *Idotea baltica* and *Gammarus oceanicus*) on epiphyte and eelgrass biomass and productivity. Mesograzers species identity strongly influenced epiphyte accumulation and eelgrass growth, where *Rissoa* was the most efficient mesograzer (per biomass) and *Gammarus* had the weakest impact. Density-dependent effects varied considerably among species. Both gastropod species reduced epiphyte accumulation in direct proportion to their density, and *Littorina* had the strongest negative effect on epiphyte biomass. The impact of *Idotea* seemed to level off to a threshold value and *Gammarus* had no density-dependent effect on epiphyte accumulation at all. *Rissoa* and *Idotea* increased eelgrass productivity in accordance with their effect on epiphyte accumulation, whereas *Littorina* showed a less positive effect than could be expected by its strong impact on epiphyte biomass. *Gammarus* had no significant impact on eelgrass growth. Our results show that the different functional traits of superficially similar mesograzers can have important consequences for ecosystem processes in macrophyte systems.

Introduction

Marine benthic macrophyte communities are regulated by abiotic conditions, resource availability and food web structure. Small invertebrate consumers, primarily crustacean and gastropod species, are supposed to play a crucial role in controlling ecosystem processes. Most of these “mesograzers” preferentially feed on epiphytic algae and thus, promote seagrass growth and survival by releasing the plants from competition for light and nutrients (Brush and Nixon 2002; Hauxwell et al. 2003; Hughes et al. 2004). Thus, the detrimental effect of eutrophication on macrophyte communities may partially be mitigated by high mesograzer abundance (Williams and Ruckelshaus 1993; Hillebrand et al. 2000; Worm et al. 2000).

Furthermore, mesograzers are important in the transfer of primary production to higher trophic levels including commercially important fish species (Edgar and Shaw 1995; Taylor 1998).

Historically, mesograzers have been considered as a homogeneous functional group in many studies (Steneck and Watling 1982; Edgar 1990a). They are thought to feed rather unselectively on epiphytic algae and detritus. This view is indirectly corroborated by field experiments demonstrating a rapid compensatory response of mesograzers to manipulation of single mesograzer species abundances (Edgar 1990b; Edgar and Aoki 1993). However, some experimental studies showed a significant species-specific impact of mesograzers on biomass and taxonomic composition of primary producers in macrophyte assemblages (Jernakoff and Nielsen 1997; Duffy and Harvilicz 2001; Duffy et al. 2001; Duffy et al. 2003). A meta-analysis approach (Hughes et al. 2004) found that the effects of grazers were generally strong in seagrass systems, but were highly dependent on grazer species and experimental conditions. In particular, invertebrate

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mesograzers (e.g. *Idotea baltica*, *Idotea resicata* and *Rissoa membranacea*) potentially feed on both epiphytes and macrophytes, and can have positive, neutral or negative effects on macrophytes depending on circumstances like food availability and grazer abundance (Williams and Ruckelshaus 1993; Orav-Kotta and Kotta 2003; Fredriksen et al. 2004). Therefore, it is necessary to study the effect of varying grazer abundances to fully understand the functional characteristics of different mesograzers.

We manipulated mesograzer abundance in four mesocosm experiments to test for biomass-specific and density-dependent effects on primary productivity in an epiphyte–eelgrass system. The isopod *Idotea baltica*, the amphipod *Gammarus oceanicus* and the gastropods *Littorina littorea* and *Rissoa membranacea* were stocked in mesocosms that contained eelgrass (*Zostera marina*), and their impact on epiphyte and eelgrass productivity was measured. All studied species are potentially dominant grazers in temperate regions.

We wanted to answer two questions with this approach:

- (1) Are the four studied mesograzers functionally redundant in their impact on the epiphyte–eelgrass assemblage?
- (2) How does realistic variation in mesograzer abundance influence ecosystem processes?

Methods

Experimental design

We conducted four mesocosm experiments to test the impact of the common mesograzer species *Idotea baltica*, *Gammarus oceanicus*, *Littorina littorea* and *Rissoa membranacea* (referred to hereafter by genus names) on primary productivity in an eelgrass–epiphyte system. The experiments took place in a constant temperature chamber. Six 125 l aquaria (50 × 50 × 50 cm) were divided into four compartments with 1 mm metal mesh resulting in 24 mesocosm units (25 × 25 × 50 cm). This corresponds to the minimum size recommended for experiments with sea grass (Short et al. 2001). Summer conditions were established concerning light and temperature. The aquaria were illuminated by HQI-lamps with a 16 h day and 8 h night cycle. The light intensity was 100 μmol m⁻² s⁻¹ at the water surface. The temperature in the constant temperature chamber was set to 17°C. However, due to a warming-effect of the lamps the water temperature in the aquaria was slightly higher (18.6 ± 0.3°C). Sand-filtered brackish deep water from the Kiel Fjord (salinity 14.1 ± 2.2 PSU) was used and additionally filtered with a 0.8 μm membrane filter to avoid contamination with plankton species.

Continuous water circulation was created using pumps and the water was exchanged (up to 90% of the total volume) every day. Periphyton growing on the walls was removed every day before the water exchange.

The mesocosms were filled with 1 mm-sieved homogenized sediment (5 cm), which consisted mainly of fine sand with low organic content. After 24 h, 20 freshly harvested and washed eelgrass shoots were planted in each mesocosm (320 shoots m⁻², average abundance in the Kiel Fjord in summer). Only shoots with at least four leaves were selected and the average length of shoots was 40 cm. On the following day, the mesocosms were stocked with mesograzers. All experimental material was collected at Falkenstein beach in the inner Kiel Fjord, Germany (54°21′/10°9′). The experiment was terminated after ten days. At this time, the eelgrass was harvested, placed in plastic bags and stored frozen until further processing.

Each experiment included four treatments: a grazer-free control and low, medium and high abundances of one mesograzer species (Table 1). Each treatment was replicated in six independent mesocosms in a randomized block-design. All treatments in one aquarium were regarded as one block. Mesograzer densities were chosen based on summer density data collected within a monitoring program for eelgrass-associated macrofauna in the Kiel Bight (1997–2001). One treatment in each experiment contained a mesograzer biomass of 0.06 mg AFDM to compare the different impact of the four mesograzer species at the same biomass level. The number of mesograzers corresponding to 0.06 mg AFDM was 16 for *Idotea*, 20 for *Gammarus*, 4 for *Littorina*, and 80 for *Rissoa*.

Our experiment focused on the different feeding selectivity and behaviour of the studied mesograzer species. A preliminary experiment showed that the optimal experimental duration for such an approach was 10 days. Thereafter, overgrazing, cannibalism and reproduction occurred in the crustacean treatments.

Epiphyte and eelgrass biomass

Epiphyte biomass was measured using chlorophyll *a* as proxy. Six eelgrass shoots were randomly selected from each

Table 1 Grazer abundances in all experiments

Grazer abundance	Density (m ⁻²)			Biomass (g AFDM m ⁻²)		
	Low	Medium	High	Low	Medium	High
<i>Gammarus oceanicus</i>	80	160	320	0.24	0.48	0.96
<i>Idotea baltica</i>	128	256	512	0.48	0.96	1.92
<i>Littorina littorea</i>	64	128	256	0.96	1.92	3.84
<i>Rissoa membranacea</i>	320	640	1280	0.24	0.48	0.96

Treatments with the same biomass are shown in bold

mesocosm. Epiphytes were carefully scraped from the eelgrass blades using a special plastic scraper and a scalpel and transferred to small amounts of filtered seawater. This suspension was filtered on precombusted (450°C, 24 h) Whatmann GF/F filters. Pigment analyses with HPLC, carried out on scraped eelgrass blades and epiphytes, indicated that removal efficiency by scraping was up to 99%. Chlorophyll *a* concentration was calculated according to Lorenzen (1967). The cleaned eelgrass blades were dried to a constant weight for 48 h at 60°C and subsequently combusted for 8 h at 540°C to determine the ash-free dry mass (AFDM). The eelgrass surface area was calculated using the formula, surface (mm²) = AFDM (g) × 588.88 ($R^2 = 0.97$), determined by measuring and weighing 100 eelgrass shoots. All epiphytic chlorophyll concentrations were normalized to unit eelgrass surface area.

Eelgrass growth

Eelgrass leaf production was measured by a variation of the leaf-marking technique (Sand-Jensen 1975). All eelgrass shoots were marked with a needle hole 1 cm above the first node with roots before being planted in the experiment. At the end of the experiment, six shoots from each mesocosm were cut 1 cm above the first node and the length and width of new leaves (without hole) and the growth of old leaves (with a hole) were measured. The growth of old leaves can be determined on basis of the displacement of the needle hole, because the meristematic region of eelgrass lies at the base of the leaves. The production of biomass was calculated as AFDM per day using the formula mentioned above.

Epiphyte productivity

Primary productivity estimations, based on ¹⁴C-measurements were carried out on the last day of the experiment. Four eelgrass shoots were randomly selected from each mesocosm and the mid-section of each shoot (10 cm) was transferred into a transparent Nalgene plastic bottle containing 250 ml seawater (0.2 μm filtrated). After inoculation with 26.4 μCi ¹⁴C-Na₂CO₃, three-hour incubations (between 1000 and 1400 hours) were carried out under experimental conditions. One bottle out of each mesocosm was wrapped up in aluminium foil and used as dark incubation. After incubation all eelgrass shoots were placed in plastic bags and stored frozen until further processing. Epiphytes were separated from the eelgrass blades by carefully scraping the blades using a special plastic scraper and a scalpel and then transferred into small amounts of filtered seawater. This suspension was filtered on pre-weighed membrane filters. The filters and the eelgrass blades were dried for 48 h at 60°C and weighed to

calculate dry weight. Then the filters were transferred into scintivials containing 10 ml Lumagel. Radioactivity was measured in a liquid scintillation counter. All counts were corrected for background and counting efficiency.

Productivity was calculated as follows:

$$\text{mg C (g dry wt)}^{-1}\text{h}^{-1} = \frac{\text{dpm}_1 \times {}^{12}\text{CO}_2 \times 1.06}{\text{dpm}_2 \times \text{wt} \times t},$$

where dpm₁ is the activity (decay per minute) of the samples minus the activity in the dark incubation as correction for non-photosynthetic uptake of ¹⁴C, dpm₂ the activity of the isotope added to the bottles and ¹²CO₂ the mg available inorganic carbon. The factor 1.06 is a correction for isotope discrimination. Wt is the dry weight of the epiphyte or eelgrass sample and *t* the length of the incubation period in hours (Penhale 1977).

Comparative effects

To compare the per biomass impact of the four studied mesograzers species on processes in the epiphyte–eelgrass system, mesograzers effects on epiphytes and eelgrass were calculated as the raw difference between controls and grazer treatments with the same biomass level (0.96 mg AFDM m⁻², Table 1).

Statistics

The influence of mesograzers abundance on epiphytes and eelgrass was initially analysed using randomized block ANOVAs, in which the different abundances were considered as fixed factors. The block effect was non-significant in all analyses, therefore, the block factor was ignored and the data were re-analysed with a one-factor ANOVA. Differences between treatments were tested with Tukey's test. To test for differences between experiments, one-factorial ANOVAs were conducted on grazer-free controls (epiphyte and eelgrass productivity).

Results

Per biomass effects of the four mesograzers on epiphytes and eelgrass

We found no significant differences between epiphyte and eelgrass productivity among the control treatments of our four experiments.

The comparison of species-specific effects on epiphytes and eelgrass showed considerable differences among the four-mesograzers species. *Rissoa* had the strongest impact on epiphyte biomass and *Gammarus* had the weakest effect (Fig. 1a). The impact on epiphyte productivity showed the

same trends as for epiphyte accumulation (Fig. 1b). In accordance with its impact on epiphyte accumulation, *Rissoa* had the strongest positive effect on eelgrass productivity (Fig. 1c), whereas *Gammarus* had no effect at all. *Littorina*, in contrast, had far less positive effects on this parameter than could be expected from its negative impact on epiphyte accumulation.

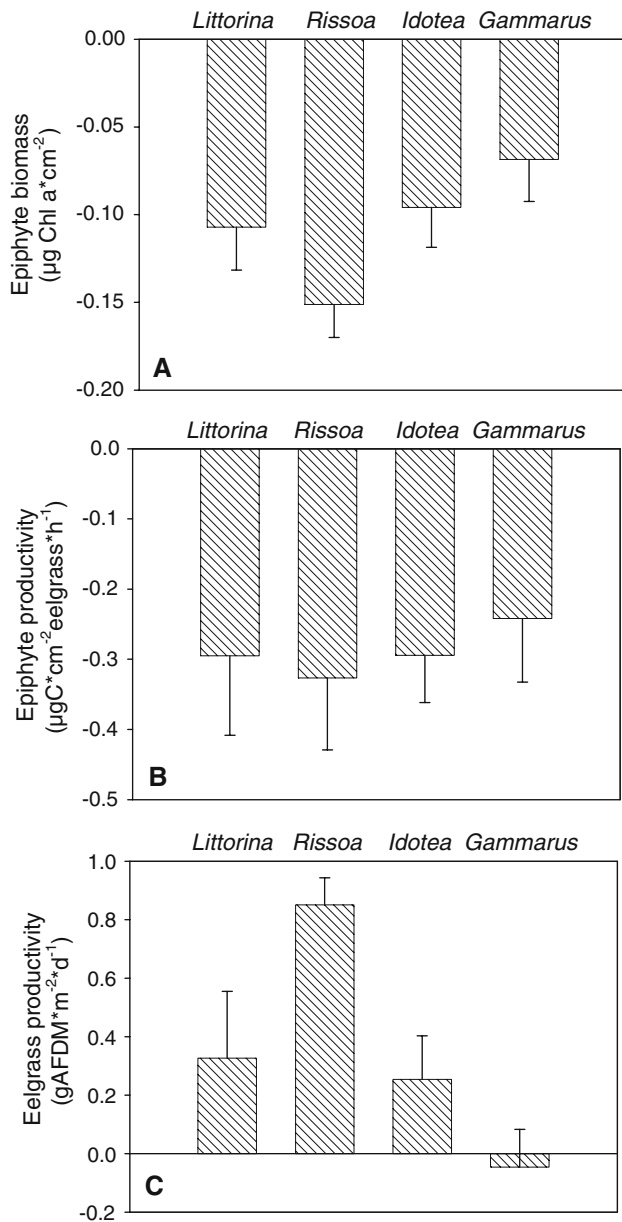


Fig. 1 Per biomass effects of mesograzers species on **a** epiphyte biomass, **b** epiphyte productivity, and **c** eelgrass productivity. Shown are the raw, arithmetic differences between grazer-free controls and the grazer treatments with the same biomass

Density-dependent effects

All studied mesograzers had a significant impact on epiphyte biomass compared to the grazer-free controls (Fig. 2), but the strength of this effect varied among the different species. *Littorina* affected epiphyte accumulation most strongly; this species reduced the epiphyte biomass to 12% of the control values in the high-density treatment. Epiphytes were virtually eliminated in this treatment. High densities of *Rissoa* and *Idotea* diminished epiphyte biomass to 42% and 49% of control values, respectively. *Gammarus* exerted the weakest effect. We found a decrease to 69% of the control values in the high-density treatment. An interesting difference was found between gastropods and crustaceans: the mean abundance of *Idotea* seemed to be a kind of threshold density, regarding its impact on epiphyte biomass. Further increase in animal abundance did not affect epiphyte biomass significantly. *Idotea* reduced epiphyte biomass to a minimum of 0.1 µg chlorophyll cm⁻². The presence of *Gammarus* always had the same effect regardless of density. The gastropods *Littorina* and *Rissoa* reduced epiphyte biomass significantly stronger in the treatments with high abundances. Epiphyte productivity showed essentially the same pattern as could be expected from epiphyte biomass (Fig. 3).

Eelgrass productivity measured as growth rate increased significantly with increasing abundances of *Idotea*, *Littorina*, and *Rissoa* (Fig. 4). *Gammarus* had no significant impact on eelgrass productivity, which was in accordance with the weak impact of this species on epiphyte accumulation. The highest eelgrass growth rate was found in the high abundance *Rissoa* treatment with 1.9 g AFDM m⁻² d⁻¹, an increase of 78% relative to control values. The impact of *Idotea* and *Littorina* enhanced eelgrass production by 63 and 72%, respectively.

Discussion

Mesograzers functional differences and its impact on ecosystem processes

All four mesograzers had significant impacts on the studied ecosystem processes, but the effects varied considerably among different species and different response variables. Epiphyte biomass and productivity were differently affected, as was eelgrass productivity. Our results confirmed previous conclusions that mesograzers can exert strong top-down control on the fouling community in sea grass systems (Orth and van Montfrans 1984; Jernakoff et al. 1996; Duffy et al. 2001; Hughes et al. 2004). However, we found marked differences in the species-specific impact. First of all, the gastropods *Rissoa*

Fig. 2 Impact of mesograzer abundance on epiphyte biomass (measured as chlorophyll *a*; mean and standard deviation). Capital letters indicate significant differences between treatments

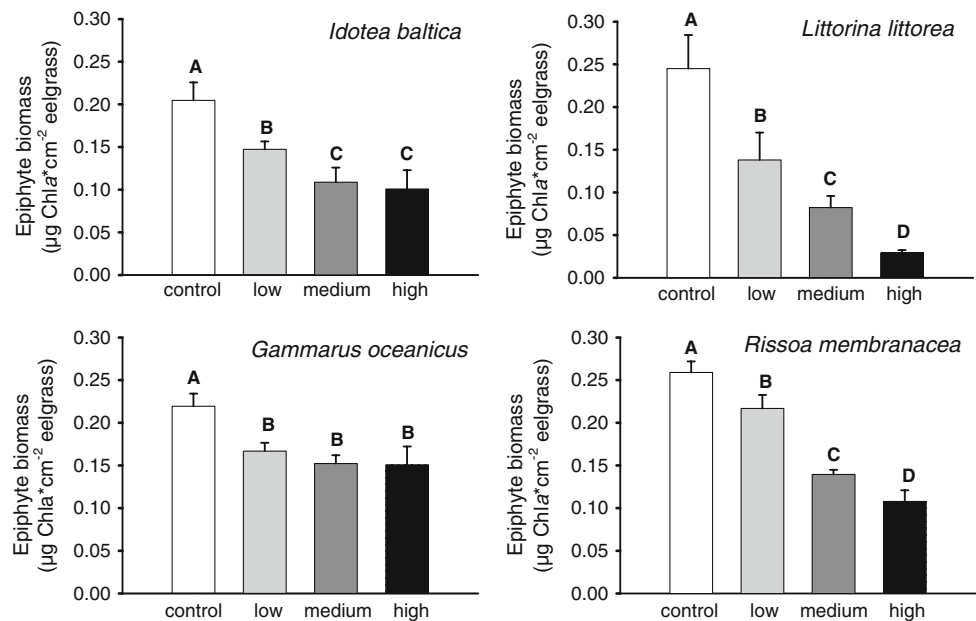
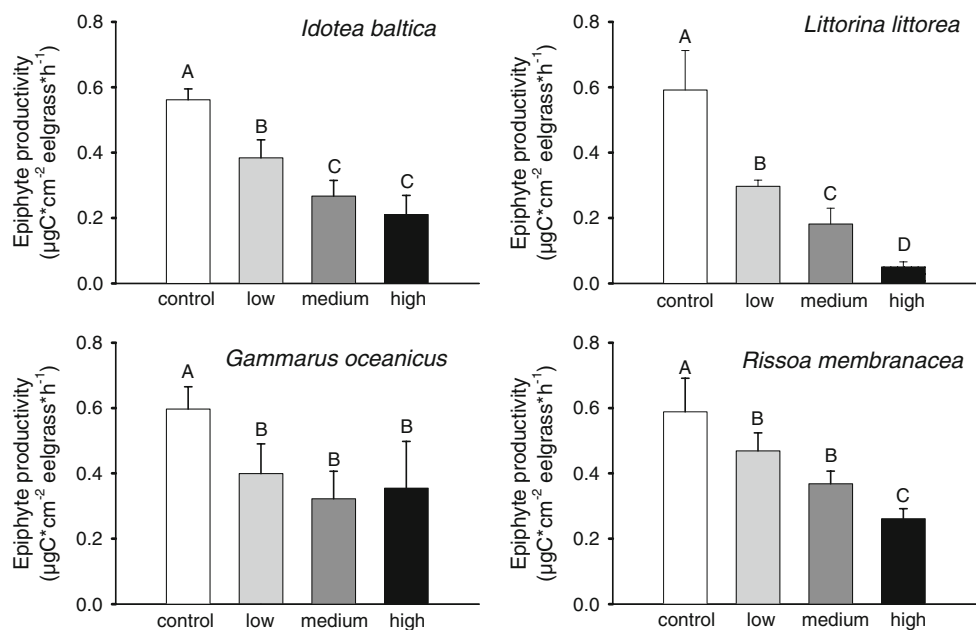


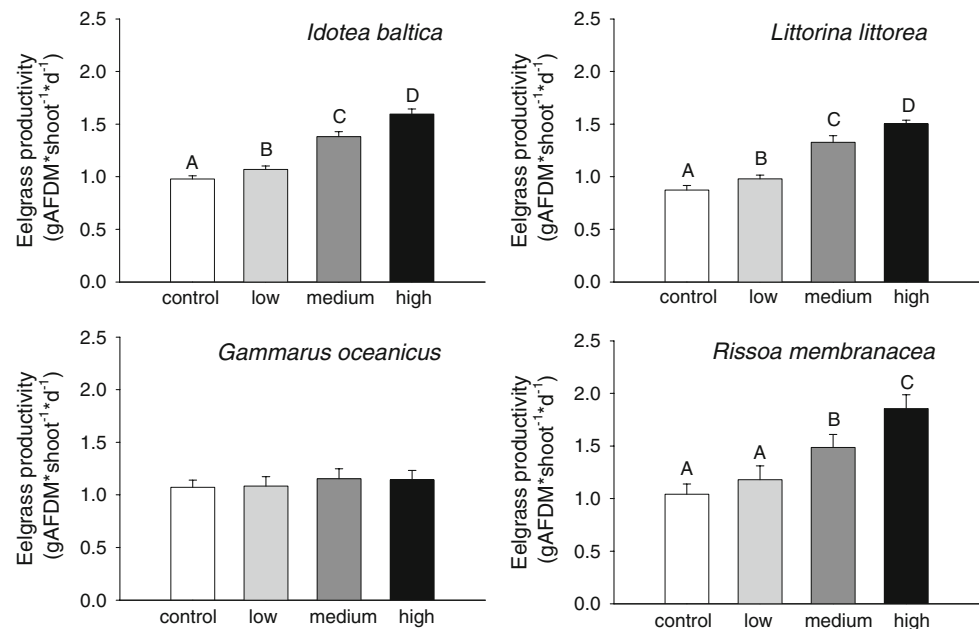
Fig. 3 Impact of mesograzer abundance on epiphyte productivity (mean and standard deviation). Capital letters indicate significant differences between treatments



and *Littorina* exerted a stronger negative effect on epiphyte accumulation than the crustaceans *Idotea* and *Gammarus*. The per-biomass impact of *Rissosa* was the strongest and that of *Gammarus* the weakest. Our experiments support the results of Jernakoff and Nielsen (1997), who found that gastropods are more efficient grazers than amphipods. Earlier studies also found strong impacts of gastropods on epiphyte assemblages in sea grass systems (Klumpp et al. 1992; Philippart 1995; Fong et al. 2000). The evidence on grazing effects of amphipods is species-specific (Howard 1982; Duffy and Harvilicz 2001; Duffy et al. 2005).

Epiphyte consumption by mesograzers can generate a positive cascading effect on sea grasses, promoting the growth and survival of the foundation species of these systems, because epiphytes and sea grass compete for light and nutrients (Orth and van Montfrans 1984; Brush and Nixon 2002; Hauxwell et al. 2003; Hughes et al. 2004). In accordance with their impact on epiphyte biomass, per biomass effects of *Rissosa* on eelgrass productivity were strongly positive and those of *Idotea* were moderately positive. *Littorina* and *Gammarus* exerted weaker effects on eelgrass productivity than could be expected from their negative impact on the epiphyte assemblages. Our results

Fig. 4 Impact of mesograzer abundance on eelgrass productivity (mean and standard deviation). Capital letters indicate significant differences between treatments



are in accordance with previous studies that found a strong positive effect of gastropods and isopods on the growth and survival of sea grasses (Philippart 1995; Duffy et al. 2001; Schanz et al. 2002).

Gammarus species are not known to have strong impacts on eelgrass productivity (Duffy and Harvilicz 2001; Duffy et al. 2001). Although *Gammarus* had a significant albeit weak impact on epiphyte biomass in our study, the effect on eelgrass was essentially zero. The reduction in irradiance reaching the eelgrass leaves with higher epiphyte load is best described by a negative hyperbolic equation leveling off to a constant level (Brush and Nixon 2002). Thus, epiphytes must be reduced below a certain critical level to have a positive effect on eelgrass productivity due to increasing availability of light. Obviously, grazing of *Gammarus* was not efficient enough to generate this positive effect in our experiment. In contrast, *Littorina* exerted a strong grazing pressure on epiphytes, but only a weak positive effect on eelgrass productivity was found. *Littorina* is capable of feeding on macrophyte tissue (Steneck and Watling 1982; Norton et al. 1990). In our study, it was the only species that reduced the bottom layer of adnate diatoms (mostly *Cocconeis scutellum*) significantly, and completely freed the eelgrass leaves from epiphytes. This mesograzers species may have incidentally destroyed the outer layers of the eelgrass while feeding on the epiphytes, partially negating the effect of epiphyte reduction on eelgrass productivity.

The results from our four experiments indicated that species identity could potentially be important in sea grass systems. The co-occurring mesograzers varied substantially in their effect on epiphyte and eelgrass productivity.

The impact of mesograzers at natural abundances on ecosystem processes

Most studies on the interaction of grazing organisms and ecosystem processes in sea grass systems are restricted to test the presence and the absence of grazers (Williams and Ruckelshaus 1993; Philippart 1995; Jernakoff and Nielsen 1997; Fong et al. 2000). Experiments investigating density-dependent effects like our study are scarce (Nelson 1997).

The mesograzers tested in our study, decreased the epiphyte biomass and productivity even at low densities. However, we found species-specific differences with increasing mesograzers abundance. The gastropods *Rissoa* and especially *Littorina* were more effective in reducing epiphyte accumulations on eelgrass leaves than the crustaceans *Idotea* and *Gammarus*. Furthermore the impact of the gastropods increased continuously with increasing mesograzers abundance, whereas the impact of the isopod seemed to level off to a threshold value of epiphyte biomass. In contrast, the amphipod showed no density-dependent effects at all. Another gastropod, *Lacuna vineta*, has been found to exert a similar effect on epiphytes as the gastropods in this study (Nelson 1997).

The four studied mesograzers are known to consume a diverse array of micro- and macroalgae (Warén 1996; Norton et al. 1990; Duffy and Harvilicz 2001; Orav-Kotta and Kotta 2003). The actively swimming, omnivorous *Idotea* and *Gammarus* are, in general, considered to reduce the microalgal community homogeneously (“lawn-mower” type of grazer), whereas the slow moving, predominantly herbivorous *Littorina* and *Rissoa* produce a feeding trail by scraping the surface with their radula (“bulldozer” type of

grazer, Sommer 1999). The taenioglossan radula of the studied gastropods enables these species to feed in a rasping mode that is especially useful for the grazing of microalgae and filamentous algae (Steneck and Watling 1982), and taenioglossan gastropods have the ability to completely remove the epiphytic layer on eelgrass leaves (van Montfrans et al. 1982).

The epiphyte assemblage on eelgrass in our system consisted of a basic monolayer of prostrate, strongly adhering diatoms, mostly *Cocconeis scutellum*, stalked forms like *Licmophora* sp. and diatom chains. Tube-living diatoms and filamentous algae were of minor importance. Analyses of taxonomic composition of epiphytes in our study showed that *Littorina* uniformly reduced all growth forms and *Rissoa* diminished mostly stalked and chain-forming diatoms (Jaschinski and Sommer, in prep.). This indicated that *Littorina* removed the epiphytic matrix completely and unselectively in its feeding trail, and therefore, this species had the strongest impact on the epiphyte assemblage, whereas the *Cocconeis* crust remained virtually unaffected by *Rissoa* resulting in a slightly weaker grazing effect. The feeding activity of *Idotea* was further restricted mainly to chain-forming diatoms with a weak impact on stalked forms, whereas *Gammarus* only had a negative impact on diatom chains. The difference in the functional morphology of their mouthparts (molluscan radula vs. crustacean mandibles) and different feeding behaviour presumably are responsible for the diminished impact of the crustacean grazers.

Our results supported the hypothesis that top-down forces can influence the fitness of eelgrass, the structuring species of this system. The positive effect on eelgrass productivity increased with growing mesograzer abundance. *Rissoa* increased eelgrass growth up to 78%. *Littorina* showed a less positive effect than could be expected by its strong impact on epiphyte biomass. This effect could have been caused by the earlier mentioned potentially disruptive effect of the periwinkle on eelgrass tissue. Direct grazing on living eelgrass is known for *Idotea* and *Rissoa* (Duffy et al. 2001; Fredriksen et al. 2004). Grazing scars on eelgrass were found in the *Idotea* treatments, but eelgrass growth still increased with higher *Idotea* densities. In our study the positive effect of epiphyte consumption compensated for the negative effect of direct grazing on eelgrass. Detrimental effects of *Idotea* on macrophytes have usually been observed in longer-term experiments when the population reached very high abundances and other food sources were scarce (Duffy et al. 2003). During a 2-year monitoring period we noticed very few scars of *Idotea* grazing on eelgrass in the Kiel Fjord, implying that this mechanism plays no important role in this region. Grazing scars of *Rissoa* were observed not at all in the field, but occurred during cultivation of this

species under extremely high densities in the laboratory. The deterioration of eelgrass found in southern Norway was also associated with very high *Rissoa* densities and found to be a single incident (4,200 m⁻², Fredriksen et al. 2004).

In conclusion, the survival of the structuring species in this ecosystem—the eelgrass—is strongly connected with mesograzer identity and the effect of mesograzers can vary from mutual, to neutral, to antagonistic with changing density.

We found that species-level characteristics of mesograzers had important effects on plant populations, and therefore, the functional group concept should only be used with cautiousness as proposed by Duffy et al. (2001). Grazer species identity and abundance are likely to be both essential factors in estimating the potential impact of mesograzers. We found that the functional differences among generalist mesograzers varied considerably at the same abundance and with increasing grazing activity. This emphasises the importance of integrating the effect of the local and temporal variability of mesograzer abundances in the assessment of grazing effects in macrophyte communities.

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