

Grazer diversity effects in an eelgrass–epiphyte–microphytobenthos system

Sybill Jaschinski · Nicole Aberle ·
Sandra Gohse-Reimann · Heinz Brendelberger ·
Karen H. Wiltshire · Ulrich Sommer

Received: 7 December 2006 / Accepted: 13 November 2008 / Published online: 10 December 2008
© Springer-Verlag 2008

Abstract The dramatic loss of biodiversity and its consequences for ecosystem processes have been of considerable interest in recent ecological studies. However, the complex and interacting processes influencing diversity effects in multitrophic systems are still poorly understood. We used an experimental eelgrass system to study the effects of changing richness of three consumer species on the biomass, diversity and taxonomic composition of both epiphytic and benthic microalgal assemblages. After 1 week, consumer richness enhanced the grazing impact on epiphyte biomass relative to single consumer treatments and a positive effect of consumer richness on prey diversity was found. Moreover, strong effects of consumer species identity on taxonomic composition were found in both microalgal assemblages. However, the effects of consumer richness were not consistent over time. The consequences

of high nutrient availability seemed to have masked consumer richness effects.

Keywords Biodiversity · Seagrass · Mesograzer · *Zostera marina* · Species richness

Introduction

Numerous studies in terrestrial food webs have shown that the diversity of primary producers can strongly influence ecosystem functioning (see Hooper et al. 2005 for overview). However, the consequences of the loss of consumer diversity have been studied only recently (Jonsson and Malmquist 2000; Duffy et al. 2001, 2005; O'Connor and Crowe 2005; Gamfeldt et al. 2005). Since all natural ecosystems include more than one trophic level and consumer species can exert strong impacts on ecosystem processes and community structure (Duffy 2002), it is important to consider the effects of diversity in multitrophic systems. Furthermore, the fact that species at higher trophic levels seem to be more often subject to extinction than species at lower trophic levels (Jackson et al. 2001; Petchey et al. 2004) underpins the necessity of exploring the consequences of losses in consumer diversity.

Conceptual models predict that changes in consumer diversity and composition can generate a wider range of effects on ecosystem processes than changes in primary producer diversity alone (Thébault and Loreau 2003; Petchey et al. 2004; Fox 2004). Resource availability, food web structure, functional traits of lost species and bidirectional effects can create complex responses of ecosystem processes to changes in diversity in a multitrophic system (Duffy 2002; Worm and Duffy 2003; Hillebrand and Cardinale 2004).

Communicated by Dag Olav Hessen.

S. Jaschinski (✉) · U. Sommer
Experimental Ecology,
IFM-GEOMAR Leibniz Institute of Marine Sciences,
Düsternbrooker Weg 20, 24105 Kiel, Germany
e-mail: sjaschinski@ifm-geomar.de

N. Aberle · K. H. Wiltshire
Biologische Anstalt Helgoland, AWI, P.O. Box 180,
27483 Helgoland, Germany

N. Aberle
Max-Planck-Institute for Limnology,
August-Thienemann-Strasse 2, 24306 Plön, Germany

S. Gohse-Reimann · H. Brendelberger
Zoological Institute, University of Kiel,
Olshausenstrasse 40, 24098 Kiel, Germany

In this study we focus on these questions:

1. How does consumer richness affect total prey biomass?
2. Does consumer richness have a positive influence on prey diversity?
3. Does high nutrient supply affect the impact of grazer richness?

There are two classes of biodiversity effects: the selection and the complementarity effect (Loreau and Hector 2001; Hooper et al. 2005). The selection effect hypothesis postulates that species with a large impact on prey biomass are more likely to be present with increasing diversity, and thus dominate the mixtures. The complementarity effect enhances resource use via niche partitioning and facilitation. Experimental studies addressing the impact of consumer diversity on primary producer biomass are rare in marine systems and the results are ambiguous. Gamfeldt et al. (2005) reported a reduction of microalgae biomass with growing ciliate diversity. No evidence for mesograzer diversity effects were found on algae biomass in rock pools (Matthiessen et al. 2006), whereas Duffy et al. (2005) documented that mesograzer diversity enhanced epiphyte grazing only in the presence of predators.

Consumer pressure shows a unimodal relationship with prey diversity (Worm et al. 2002), but the relationship of diversity effects on different trophic levels remains unclear (Hunter and Price 1992; Terborgh 1992). Dyer and Letourneau (2003) reported a positive effect of consumer diversity on prey diversity in an endophytic system as postulated by conceptual models (Dunne et al. 2002; Thébault and Loreau 2003; Petchey et al. 2004), but increasing mesograzer species richness decreased total benthic community diversity in a seagrass system (Duffy et al. 2003).

The diversity/productivity relationship at the primary producer level has been the topic of much debate in terrestrial ecology for more than 50 years (see Tilman 1999 for review). More recent studies focus on the influence of nutrient availability and productivity on the relationship between consumers and prey diversity (Proulx and Mazumder 1998; Hillebrand 2003). Multivariate models and empirical studies show that these factors have interactive effects on prey diversity (Kondoh 2001; Worm et al. 2002). High nutrient supply, and thus high productivity at the primary producer level, may change the effect of consumer richness in two ways. First, diversity effects may have a small impact in comparison with the availability of resources, as found for plant diversity and production (Huston 1994) and the effect of consumer richness on the decomposition of leaves (Bärlocher and Corkum 2003). Second, niche complementarity and facilitation may decrease in importance when the food supply is high. We found that high nutrient supply, and thus high epiphyte

biomass, reduced the selectivity of grazers (S. Jaschinski, unpublished data).

Here, we present the results of a mesocosm experiment testing the effect of grazer diversity on epiphyte and microphytobenthos assemblages within a multi-trophic eelgrass system.

Materials and methods

The study system

The eelgrass *Zostera marina* is one of the most abundant marine macrophytes in northern temperate regions and it is a structuring species of ecologically and economically important ecosystems. Some of the organisms associated with eelgrass, the so-called mesograzers (mainly small crustaceans and gastropods), play an important role in this system as they remove the epiphytes, and thus enhance eelgrass growth and survival (see Hughes et al. 2004 for overview). Furthermore, they are a crucial link between primary producers and higher trophic levels (Edgar and Shaw 1995).

Experimental design

We manipulated grazer species richness in 54 indoor mesocosm units (diameter 30 cm; height 60 cm), equally distributed in nine tanks (117 × 93 × 60 cm). Each mesocosm was filled with sieved (2 mm) sediment from the field (height 10 cm). Each experimental unit was planted with 20 freshly harvested eelgrass shoots (average abundance in the Kiel Fjord in summer, ~350 shoots m⁻²) and left undisturbed for 4 days. Three common mesograzers, the isopod *Idotea baltica* (*Idotea* hereafter), the amphipod *Gammarus salinus* (*Gammarus* hereafter) and the periwinkle *Littorina littorea* (*Littorina* hereafter), were used as consumers. In addition to the start and the control (no grazer) treatments, three richness levels were used (1, 2, 3, all combinations). Each treatment was replicated in six independent mesocosms in a randomised design. Grazer abundances introduced into the grazer treatments were related to average natural abundances in summer (Gohse-Reimann 2007). The initial grazer biomass was 60 mg ash-free dry mass (AFDM) corresponding to 18 *Idotea*, 24 *Gammarus* or 6 *Littorina* in the single grazer treatments. Mixed-grazer treatments were stocked using a substitutive design whereby the biomass of all grazers was kept constant.

The mesocosms were supplied independently with a constant flow of sand-filtered brackish deep water from the Kiel Fjord (salinity 14.7 PSU ± 0.7). Water flowed out of each mesocosm continuously through a hole, 2 cm in diameter, that was covered with a 1-mm plastic mesh. Nutrients from

the inflow to the experimental units were determined on a daily basis by using an auto-sampler (Skalar SAN⁺ System). Nutrient concentrations of the inflowing water were as follows: nitrate $9.1 \mu\text{mol l}^{-1} \pm 2.7$, ammonium $3.7 \mu\text{mol l}^{-1} \pm 1.2$, phosphate $0.8 \mu\text{mol l}^{-1} \pm 0.3$ and silicate $18.4 \mu\text{mol l}^{-1} \pm 1.2$. The nutrient concentrations in the Kiel Fjord were as follows: nitrate $1.6 \mu\text{mol l}^{-1}$, ammonium $1.3 \mu\text{mol l}^{-1}$, phosphate $0.2 \mu\text{mol l}^{-1}$ and silicate $5.1 \mu\text{mol l}^{-1}$. Thus, the experimental nutrient concentrations were about 4 times enriched compared to the field data. The light and temperature regime was adapted to summer conditions with a 16-h day and 8-h night cycle ($100 \mu\text{mol s}^{-1} \text{m}^{-2}$, 18.5°C).

In our experiment, we focused on the microalgae assemblages in the experimental eelgrass system. Microalgae can be successfully used as model systems to explore the consequences of diversity loss at the consumer level (Gamfeldt et al. 2005; Matthiessen et al. 2006). Results can be obtained over a short period because of the short generation time of the microalgae. Mesocosms have the additional advantage of providing a more natural environment than small-scale experiments.

Sampling and sample processing

Samples were taken at the beginning (time 0, three control mesocosms), after 7 days (three mesocosms of each treatment) and after 21 days (three mesocosms of each treatment). Microphytobenthos on the sediment surface was sampled according to Aberle and Wiltshire (2006). Subsequently, the sediment samples were preserved with liquid nitrogen by using the cryolander technique (Wiltshire et al. 1997). The micro-slicing of the sediment surface was carried out according to Wiltshire (2000) and the sediment layers were fixed with Lugol's solution. For the determination of the number of algal cells, their biovolume, and taxonomic composition, the samples were transferred to a Sedgewick Rafter chamber. After settlement the sampled cells were counted under an inverted microscope and converted to biovolume following the methods of Hillebrand et al. (1999).

After the sediment samples were taken, all eelgrass shoots were uprooted and transferred to a container with filtered seawater to collect attached grazers. Subsequently, the eelgrass was placed in plastic bags and stored frozen until further processing. Two eelgrass shoots out of each mesocosm were carefully scraped to transfer attached epiphytes to a defined volume of filtered seawater. The samples were fixed with 1% Lugol's iodine and counted under an inverted microscope in 3 ml Utermöhl chambers. A minimum of 400 cells was counted for dominant species and the whole chamber was counted to account for rare species. Biovolume was used as proxy for biomass.

The eelgrass shoots were dried to constant weight for 48 h at 60°C and subsequently combusted for 8 h at 540°C

to determine AFDM. The eelgrass surface area was calculated using the formula: surface (mm^2) = AFDM (g) $\times 588.88$ ($R^2 = 0.97$, $P \leq 0.001$), determined by measuring and weighing 100 eelgrass shoots (Jaschinski and Sommer 2008). Eelgrass leaf production was measured by a variation of the leaf-marking technique: at the beginning of the experiment all the eelgrass shoots were marked with a needle hole 1 cm above the first node with roots. Six shoots from each mesocosm were cut at the marking place and the length and the width of new leaves (without hole) and the growth of old leaves were measured. The production of biomass was calculated as AFDM per day using the formula above.

Statistics

To test for significant differences between grazer treatments one-way ANOVAs were implemented using the factor grazer composition and the response variables microalgal biovolume and diversity, and eelgrass and secondary production, followed by Newman–Keuls post hoc tests (composition effect). To detect significant grazer species richness effects, planned contrasts comparing the three-grazer treatment against all single-grazer treatments were applied (richness effect).

Net biodiversity effects (ΔY) were calculated according to Loreau and Hector (2001) as an additional estimate of diversity effects. ΔY was tested against zero with a two-sided *t*-test. A significant net biodiversity effect shows that the effect in the combinations is higher than expected from the single-grazer treatments. To calculate the expected share of each species in the combinations (*Idotea-Gammarus*, *Idotea-Littorina*, *Gammarus-Littorina*, *Idotea-Gammarus-Littorina*), we used the means of the single-grazer treatments ($n = 3$). The increase in net biodiversity effects from two to three grazer species was tested with a linear regression.

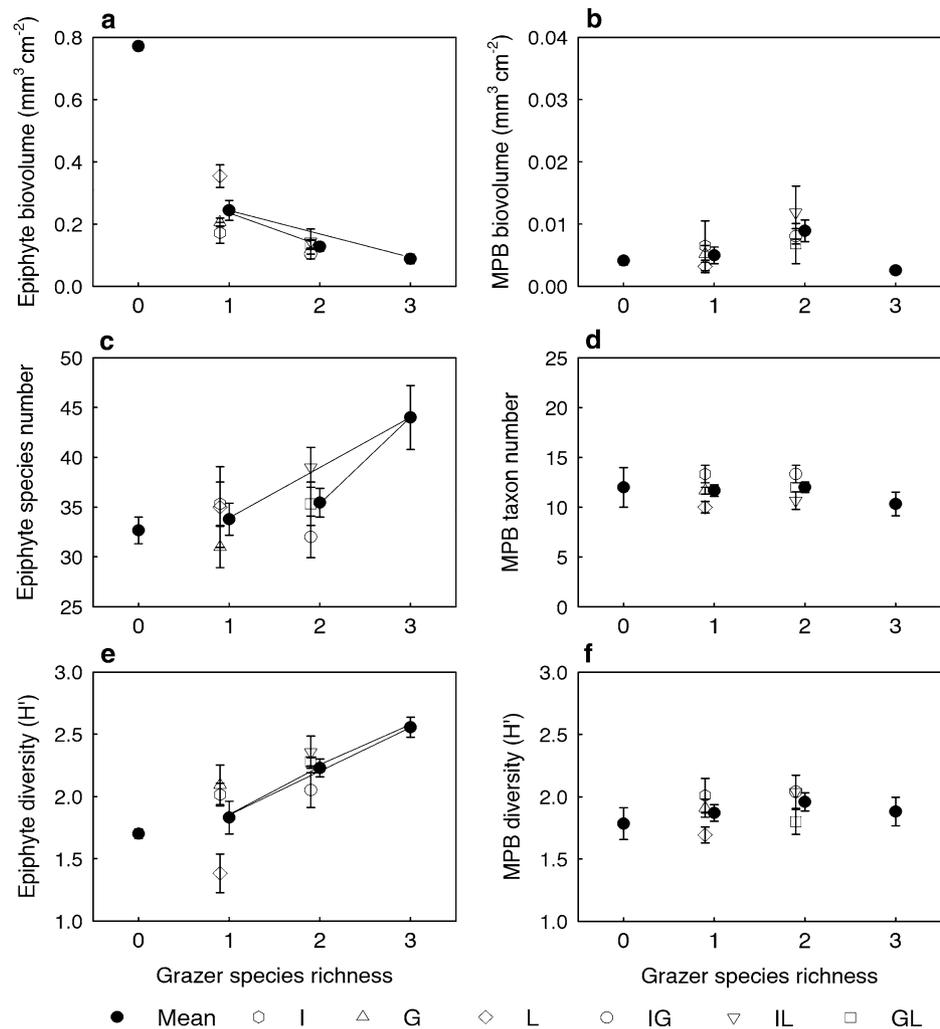
Multivariate ANOVAs were used to test the significant impact of grazer treatments on the proportional contribution of algal growth forms to epiphyte and microphytobenthos composition. Data were arcsine square root transformed. The analysis was performed with the Pillai's trace statistic (PT), recommended for interdependent response variables (Scheiner 1993).

Results

Consumer effects on ecosystem processes

After the first 7 days of the experiment, epiphyte biomass detected as biovolume was highest in the control treatment and decreased with consumer species richness (Fig. 1a).

Fig. 1 Effects of grazer diversity on ecosystem properties after 7 days of incubation. Filled circles represent means with SE. Single-species treatments and two-species combinations are represented by unfilled symbols (means with SE, $n = 3$) [*Idotea* (I), *Gammarus* (G), and *Littorina* (L)]. Lines show significant responses to grazer species richness. Epiphyte biovolume (a), microphytobenthos (MPB) biovolume (b), epiphyte species richness (c), MPB taxon richness (d), epiphyte diversity (e), and MPB diversity (f)



Grazer species richness (Table 1) and species identity showed significant effects; *Idotea* and *Gammarus* reduced epiphyte biomass significantly more effectively than *Littorina* ($P \leq 0.001$). Neither grazer species richness nor species identity had significant effects on microphytobenthos biomass (Fig. 1b). The total algal biomass at the sediment surface was generally 1 order of magnitude lower than the epiphyte biomass.

Epiphyte species richness and diversity (H' , based on the Shannon–Wiener function) were lowest in the control treatment and increased with grazer species richness (Fig. 1c, e). We found significant effects of grazer species richness on epiphyte species richness and diversity (Table 1). The impact of *Littorina* differed significantly from *Idotea* and *Gammarus* as the periwinkle had a less positive effect on epiphyte diversity than the two crustacean species ($P \leq 0.001$), but there was no significant effect of grazer species identity on epiphyte species richness. Epiphyte evenness showed the same trend and was significantly affected by grazer species richness (Table 1) and grazer species identity ($P \leq 0.001$). Microphytobenthos

Table 1 Results of planned contrasts with the fixed factor grazer species richness. MPB Microphytobenthos

Grazer richness effects	7 Days		21 Days	
	<i>F</i>	<i>P</i>	<i>F</i>	<i>P</i>
MPB biovolume	0.62	0.4446	0.2	0.6572
Epiphyte biovolume	26.04	0.0002	1.32	0.2695
MPB taxon richness	2.21	0.1592	0.33	0.5729
Epiphyte species richness	11.22	0.0048	0.39	0.542
MPB diversity	0.01	0.9435	13.89	0.0023
Epiphyte diversity	27.29	0.0001	10.59	0.0058
MPB evenness	0.85	0.3728	14.65	0.0018
Epiphyte evenness	18.17	0.0008	11.26	0.0047
Eelgrass growth	0.94	0.3478	0.76	0.398
Secondary production	0.37	0.552	0.003	0.9576

Significant results are shown in **bold** ($P < 0.05$)

taxon richness and diversity provided similar values for the control and the grazer treatments after 7 days (Fig. 1d, f). The diversity increased slightly with increasing grazer

richness and *Littorina* had a more negative impact on microphytobenthos diversity than *Gammarus* and *Idotea*, but these differences were not significant ($P > 0.05$). We found no significant effects on microphytobenthos evenness.

After 21 days, the control treatment had the highest epiphyte biomass, but no significant effect of grazer species richness on epiphyte biomass was found (Fig. 2a; Table 1). Species identity significantly affected epiphyte biomass and *Littorina* showed the weakest impact on epiphyte biomass ($P \leq 0.001$). Neither grazer species richness nor species combination was significantly correlated with microphytobenthos biomass (Fig. 2b; Table 1). Epiphyte and microphytobenthos biomass increased in all treatments by as much as 2–20 times compared to the sampling after 7 days (Figs. 1, 2).

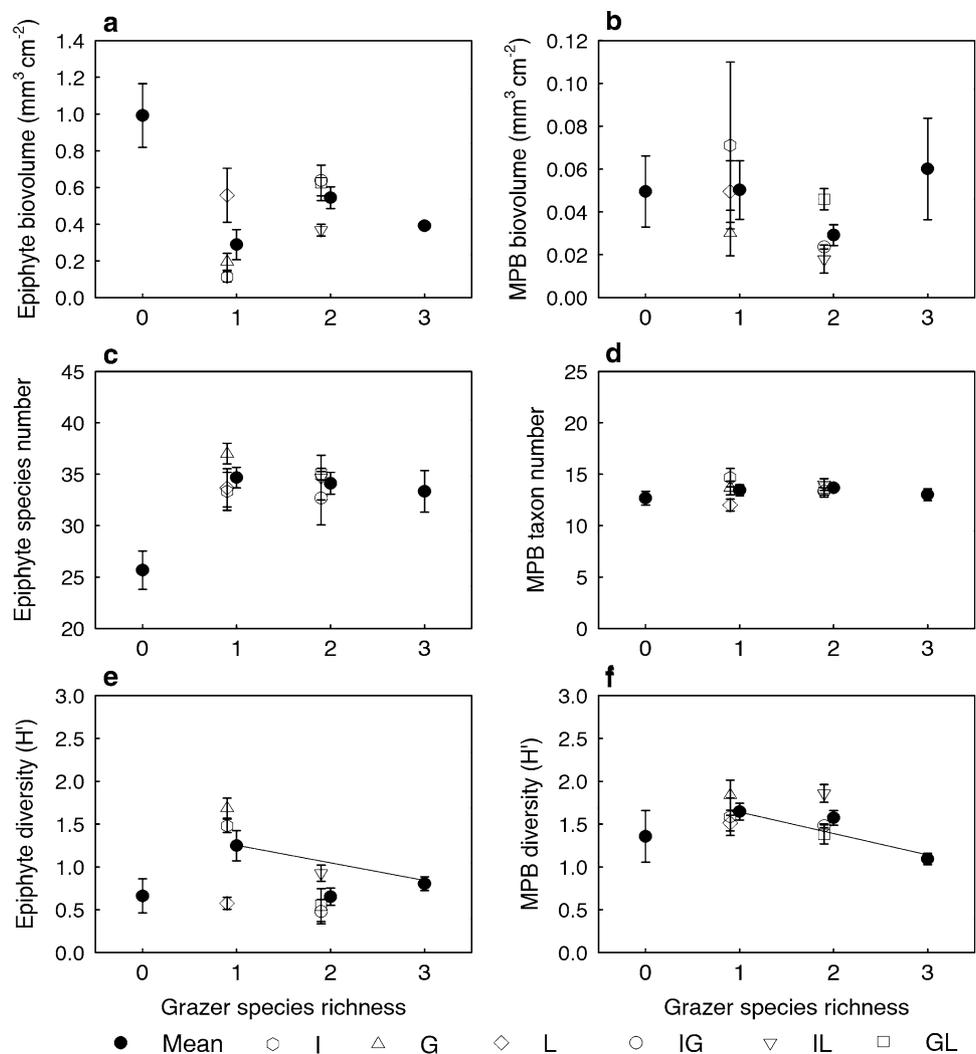
After 21 days, control treatments showed the lowest epiphyte species richness, and grazer richness had no significant impact on epiphyte species richness (Fig. 2c; Table 1). The H' of epiphytes was highest in the single grazer

treatments (Fig. 2e), whereas two- and three-grazer treatments were similar to the control treatment. Both crustacean species had a significantly more positive effect on epiphyte diversity than *Littorina* ($P \leq 0.001$). Grazer species richness and its combination did not significantly affect microphytobenthos taxon richness (Fig. 2d). However, we found a similar trend for diversity (Fig. 2f) as in the epiphyte assemblages. Overall, epiphyte and microphytobenthos diversity declined in all treatments after 21 days compared to the sampling after 7 days (Figs. 1, 2).

Net biodiversity effects

Significant net diversity effects of grazer richness were found for epiphyte biovolume and epiphyte diversity after 7 days (Fig. 3). Epiphyte biomass was significantly lower and epiphyte diversity was significantly higher in the combinations (two species and three species, respectively) than the expected values from the single-grazer treatments. We found no significant difference between the effect of the two

Fig. 2 Effects of grazer diversity on ecosystem properties after 21 days of incubation. Filled circles represent means with SE. Single-species treatments and two-species combinations are represented by unfilled symbols (means with SE, $n = 3$). Lines show significant responses to grazer species richness. Epiphyte biovolume (a), MPB biovolume (b), epiphyte species richness (c), MPB taxon richness (d), epiphyte diversity (e), and MPB diversity (f). For abbreviations see Fig. 1



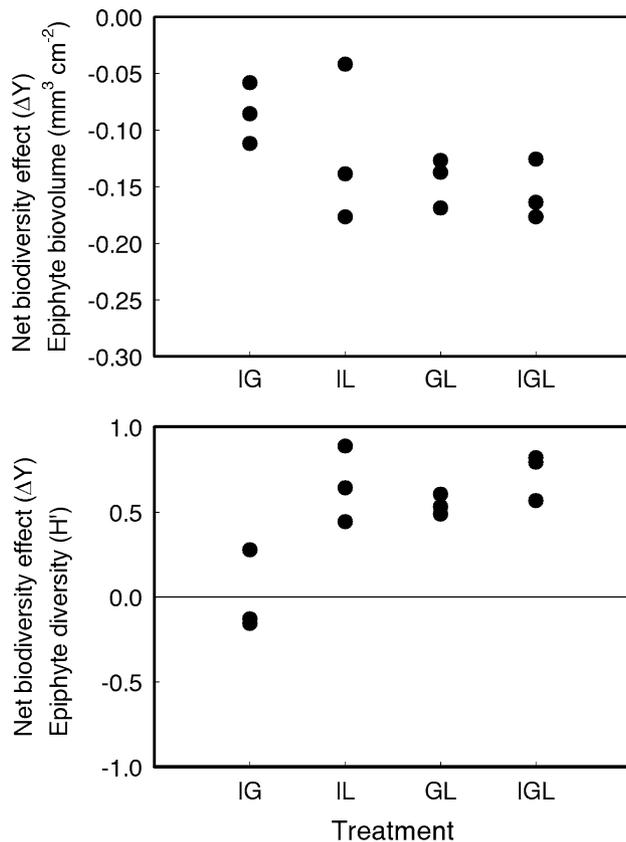


Fig. 3 Net biodiversity effects for the different grazer combinations after 7 days of incubation. Shown are the significant values with a higher grazer effect in the combinations than expected from the single-grazer treatments. For abbreviations see Fig. 1

species and the three species mixtures on net diversity effects.

Algal growth forms and taxonomic composition

Both microalgal assemblages were dominated by diatoms at the beginning of the experiment (microphytobenthos, 99%; epiphytes, 80% with 20% small brown algae mostly *Acrochaetium secundatum*). The diatoms in the epiphyte community mostly consisted of stalked forms (37%). Prostrate diatoms and diatom chains contributed roughly equal shares (20 and 22%, respectively). Tube-dwelling forms represented 1% of the total algal biovolume. In contrast, the microphytobenthos community was dominated by prostrate forms (over 90%) with only 7% comprising chain forming, and 0.4% stalked diatom genera.

After 7 days, a significant impact of the different grazer treatments on epiphyte composition was seen (Fig. 4a; $PT = 2.27$, $F = 1.94$, $P = 0.012$). The effect on microphytobenthos composition was not significant (Fig. 4b; $PT = 1.82$, $F = 1.33$, $P = 0.16$). Significantly different impacts on algal growth forms between all single-grazer

treatments were found in the epiphyte assemblage for stalked forms ($P \leq 0.04$) and diatom chains ($P \leq 0.05$). In the microphytobenthos assemblages, *Idotea* had a significant different impact on prostrate ($P \leq 0.02$) and *Littorina* on stalked diatoms ($P \leq 0.04$). The effect on green algae differed significantly between all three grazer species ($P = 0.0003$).

After 21 days, clear composition changes were detected in all treatments and an overall dominance of chain-forming diatoms appeared in both microalgal assemblages (Fig. 4c, d). *Melosira*, present initially in small amounts in the epiphyte assemblages, dominated both communities and made up between 60 and 92% and between 45 and 77% of epiphytes and microphytobenthos, respectively. Macroalgae were almost eliminated in most treatments. We found a significant impact of the different grazer treatments on epiphyte composition ($PT = 2.23$, $F = 1.9$, $P = 0.016$). The effect on microphytobenthos composition was not significant ($PT = 1.45$, $F = 0.95$, $P = 0.55$). *Littorina* had a different impact on epiphytes than *Idotea* and *Gammarus*. Significant effects on prostrate ($P \leq 0.015$) and stalked ($P = 0.025$) and chain-forming diatoms ($P \leq 0.005$) were observed. *Gammarus* had a significantly different impact on tube-living diatoms ($P \leq 0.0004$). For the microphytobenthos assemblages, we found no significant differences between the three grazers.

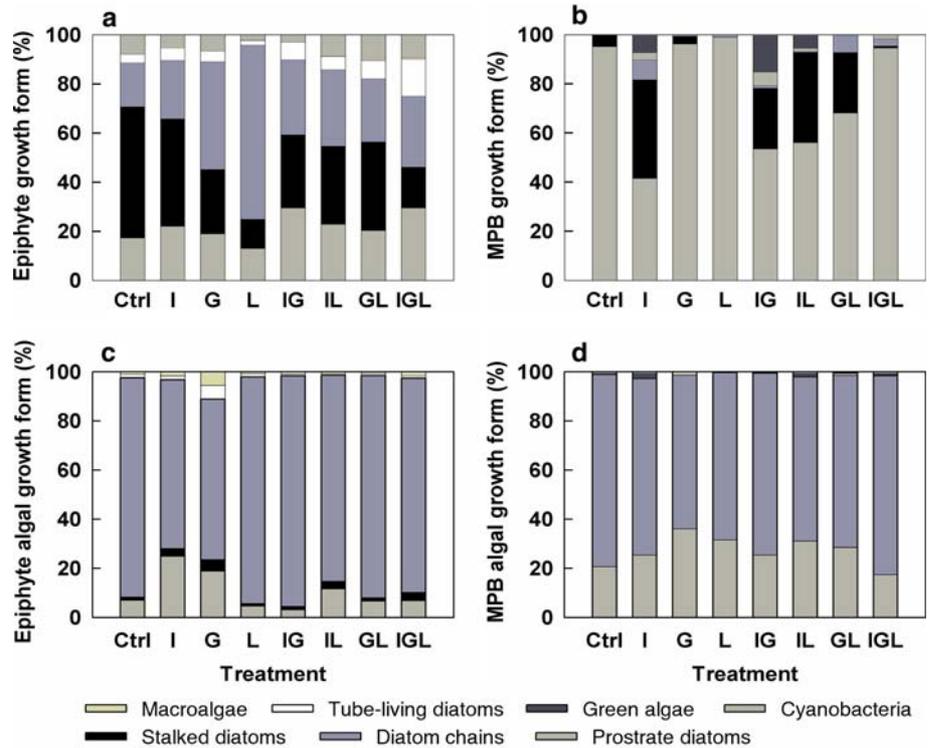
Discussion

We found diverse impacts of grazer richness on microalgal biomass, diversity, and taxonomic composition within the experimental seagrass communities. The studied consumers, the isopod *Idotea*, the amphipod *Gammarus*, and the periwinkle *Littorina*, showed a significant impact on biomass and diversity of the epiphytic assemblages only. Strong effects on algal growth forms and taxonomic composition occurred in both microalgal assemblages. The consumer richness effects on epiphyte biomass and species richness were not consistent with time under a high nutrient regime.

After 7 days, our results showed that even low consumer richness can affect primary production in an eelgrass community. Epiphyte biomass was significantly reduced with increasing consumer species richness after 7 days. Thus, our results corroborate the findings of recent studies in aquatic foodwebs. Higher diversity of protists had strong negative effects on microalgae biomass (Naeem and Li 1998; Gamfeldt et al. 2005) and higher diversity of snails increased the grazing impact on epiphyton and periphyton in a freshwater macrophyte system (Wojdak 2005).

A theoretical framework in the literature has proposed that biodiversity effects on ecosystem processes can be

Fig. 4 Effects of grazer richness and combination on algal composition. Shown are the proportional contributions of algal growth forms ($n = 3$). Epiphyte growth forms after 7 days of incubation (a), MPB growth forms after 7 days of incubation (b), epiphyte growth forms after 21 days of incubation (c), and MPB growth forms after 21 days of incubation (d). *Ctrl* Consumer-free controls; for other abbreviations see Fig. 1



grouped into two classes: the selection and the complementarity effect (Loreau and Hector 2001). The selection effect operates on the higher probability of dominance of species with strong effects, while the complementary effect includes resource partitioning via niche differentiation and facilitation. The diverse impact of the studied consumers on the taxonomic composition of the microalgal assemblages supported the possibility that niche differentiation played a role in our experiment. Facilitation may have been another mechanism that increased the grazing impact. The growth of *Littorina* was significantly higher in the presence of other grazers (Gohse-Reimann 2007).

The different qualitative grazing behaviour of co-occurring consumer species (specialists) seems to be fundamentally important to the relationship between consumer diversity and ecosystem function (Chapin et al. 1997; Duffy 2002; Gamfeldt et al. 2005). Consumers with identical feeding behaviour were not found to have a positive diversity–production relationship (Fox 2004). Our findings here of strong species effects on the composition of microalgal assemblages are in good correspondence with recent models (Thébault and Loreau 2003; Fox 2004). In these, it is predicted that a high degree of specialisation of consumers is necessary to cause significant effects of consumer diversity on prey biomass.

The biomass of the microphytobenthos community was not affected by grazer richness, species identity or combination in this study. Such an insusceptibility of microphytobenthos biomass to grazing impacts by macrofauna

organisms is in good agreement with studies conducted by Hillebrand and Kahlert (2002). These authors found that in contrast to epilithic algae, the effect of grazing on the microphytobenthos was negligible. Although grazers like *Idotea*, *Gammarus* and *Littorina* are known to graze on microphytobenthos, their effect is considered less strong than the impact of very effective microphytobenthos grazers such as hydrobiid snails and *Corophium* sp. (Gerdol and Hughes 1994). Additionally, the epiphyte biomass was 10–20 times higher than the microphytobenthos biomass, and thus greater availability of epiphytes could have partially neutralized the negative impact of macrofauna grazing on microphytobenthos biomass in our study.

In our experiment, high consumer diversity caused increasing epiphyte species richness at first. This positive effect of consumer diversity on prey diversity is in good agreement with theoretical predictions (Dunne et al. 2002; Thébault and Loreau 2003; Petchey et al. 2004) and with results from a field study in an eelgrass bed, where macroalgae diversity was positively related to animal diversity (Parker et al. 2001). A plausible explanation for such top-down diversity effects is the capability of consumers to mediate coexistence of their prey by feeding on the competitive dominant prey species, and thus confine competitive exclusion at the prey level (Paine 1966; Hillebrand 2003; Petchey et al. 2004). Consumer effects show a unimodal relationship with prey diversity, with the highest prey diversity related to “intermediate” mortality (Huston 1979). In our study, the grazing efficiency increased with growing

mesograzers richness and this effect had the adequate strength and was directed towards the dominant algae species, such that it positively affected epiphyte diversity. In contrast, Duffy et al. (2003) reported a negative effect of growing mesograzers richness on benthic diversity. The mesograzers abundance in this study was about double compared to our experiment. The strong grazing pressure may have prevented a positive effect. Positive top-down effects of diversity have also been reported in a terrestrial endophytic community, but not in a detrital food web (Dyer and Letourneau 2003). Some authors have argued that the likelihood of top-down effects declines from aquatic to terrestrial and decomposer food webs (Polis and Strong 1996; Shurin et al. 2002). More tests of cascading effects of consumer diversity in different ecosystems and under different consumer pressures and nutrient supplies are necessary to obtain a conclusion which is applicable overall.

After 3 weeks of incubation, we found a drastic change in our experimental units: the consumer richness effects on epiphyte biomass and species richness disappeared, although the effect of consumer species identity remained constant. An explanation for this change in impact of consumer richness with time is the high nutrient availability. The counteracting processes of herbivore grazing and nutrient enrichment on autotrophic biomass and diversity have received a lot of attention recently (Hillebrand and Kahlert 2002; Hillebrand 2003; Hughes et al. 2004). These studies reported that grazing pressure and nutrient availability can have strong antagonistic effects on prey biomass and diversity. Some studies focus on the influence of nutrient availability and accordingly productivity on the relationship between consumers and prey diversity (Proulx and Mazumder 1998; Hillebrand 2003). Multivariate models and empirical studies show that these factors have interactive effects on prey diversity (Kondoh 2001; Worm et al. 2002).

The influence of resource availability on consumer diversity effects has so far only been tested in a freshwater gastropod-macrophyte system (Wojdak 2005). In contrast to our results, the consumer diversity effects were stronger than the nutrient effects and remained constant under high nutrient supply. However, Bärlocher and Corkum (2003) found that nutrient enrichment overwhelms diversity effects in leaf decomposition. This result agrees with Huston (1994) who concluded that the effects of plant diversity are small compared to the strong effects of nutrient availability.

The nutrient concentrations in our experiment were in the range of moderate enrichment reported for estuaries in the case of anthropogenic eutrophication (Valiela 1992). However, the nitrogen and phosphorus concentrations were 4 times higher than the usual summer concentrations in the Kiel Fjord. During the experiment, we found an overall

increase in epiphyte and microphytobenthos biomass and a decrease in diversity in both microalgal assemblages. Such phenomena are usually found in communities under nutrient enrichment (Sundbäck and Snoeijs 1991; Hillebrand 2003; Hughes et al. 2004). Furthermore, effects on taxonomic composition were substantial in all treatments: both microalgal assemblages changed into monoculture-like communities consisting mainly of the highly productive filamentous diatom *Melosira nummuloides*. This species and its congener, *Melosira moniliformis*, are known for their ability to respond rapidly to nutrient enrichment, especially at high silicate concentrations as in our experiment (Hillebrand et al. 2000). Our results support the hypothesis that nutrient effects—resulting in a high productivity—can neutralize consumer diversity effects.

In general, our data supported the hypothesis that in a prey-consumer system higher consumer diversity can lead to a more efficient resource utilisation and consequently, to a stronger control of prey biomass. The importance of species identity and functional traits was emphasized. We showed that diversity at the prey level can be affected by diversity changes on the consumer level. The inconsistency of consumer diversity effects with time revealed the overall importance of collateral factors, e.g. nutrient conditions in a multitrophic system.

Acknowledgements We thank B. Matthiessen for her statistical advice and enthusiastic discussion of the manuscript. S. Flöder and R. Karez are thanked for their helpful comments on the manuscript. Financial support was provided by the German Research Foundation (So 145/20, Wi 1810/2, Br 1189/3). Our experiment complies with current German law.

References

- Aberle N, Wiltshire KH (2006) Seasonality and diversity patterns of microphytobenthos in a mesotrophic lake. *Arch Hydrobiol* 167:447–465
- Bärlocher F, Corkum M (2003) Nutrients enrichment overwhelms diversity effects in leaf decomposition by stream fungi. *Oikos* 101:247–252
- Chapin FS III et al (1997) Biotic control over the functioning of ecosystems. *Science* 277:500–504
- Duffy JE (2002) Biodiversity and ecosystem function: the consumer connection. *Oikos* 99:201–219
- 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
- Duffy JE, Richardson JP, France KE (2005) Ecosystem consequences of diversity depend on food chain length on estuarine vegetation. *Ecol Lett* 8:301–309
- Dunne JA, Williams RJ, Martinez ND (2002) Network structure and biodiversity loss in food webs: robustness increases with connectance. *Ecol Lett* 5:558–567
- Dyer LA, Letourneau D (2003) Top-down and bottom-up diversity cascades in detrital vs. living food webs. *Ecol Lett* 6:60–68

- Edgar GJ, Shaw C (1995) The production and trophic ecology of shallow-water fish assemblages in southern Australia. III. General relationships between sediments, seagrasses, invertebrates and fishes. *J Exp Mar Biol Ecol* 194:107–131
- Fox JW (2004) Modelling the joint effects of predator and prey diversity on total prey biomass. *J Anim Ecol* 73:88–96
- Gamfeldt L, Hillebrand H, Jonsson PR (2005) Species richness changes across two trophic levels simultaneously affect prey and consumer biomass. *Ecol Lett* 8:696–703
- Gerdol V, Hughes RG (1994) Feeding behaviour and diet of *Corophium volutator* in an estuary in southeastern England. *Mar Ecol Prog Ser* 114:1–2
- Gohse-Reimann S (2007) Untersuchungen zur Ernährungsökologie benthischer Invertebraten im Makrophytensystem: ein marin-limnischer Ansatz. In: *Limnology*. PhD dissertation, Christian-Albrechts-University, Kiel
- Hillebrand H (2003) Opposing effects of grazing and nutrients on diversity. *Oikos* 100:592–600
- Hillebrand H, Cardinale BJ (2004) Consumer effects decline with prey diversity. *Ecol Lett* 7:192–201
- Hillebrand H, Kahlert M (2002) Effect of grazing and water column nutrient supply on biomass and nutrient content of sediment microalgae. *Aquat Bot* 72:143–159
- Hillebrand H, Dürselen C-D, Kirschtel D, Pollinger U, Zohary T (1999) Biovolume calculation for pelagic and benthic microalgae. *J Phycol* 35:403–424
- Hillebrand H, Worm B, Lotze HK (2000) Marine microphytobenthic community structure regulated by nitrogen loading and grazing pressure. *Mar Ecol Prog Ser* 204:27–38
- Hooper DU et al (2005) Effects of biodiversity on ecosystem functioning: a condensus of current knowledge. *Ecol Monogr* 75:3–35
- Hughes AR, Jun Bando K, Rodriguez LF, Williams SL (2004) Relative effects of grazers and nutrients on seagrasses: a meta-analysis approach. *Mar Ecol Prog Ser* 282:87–99
- Hunter MD, Price PW (1992) Playing chutes and ladders: heterogeneity and the relative roles of bottom-up and top-down forces in natural communities. *Ecology* 73:724–732
- Huston MA (1979) A general hypothesis of species diversity. *Am Nat* 113:81–101
- Huston MA (1994) *Biological diversity*. Cambridge University Press, Cambridge
- Jackson JBC et al (2001) Historical overfishing and the recent collapse of coastal ecosystems. *Science* 293:629–638
- Jaschinski S, Sommer U (2008) Functional diversity of mesograzers in an eelgrass-epiphyte system. *Mar Biol* 154:475–482
- Jonsson M, Malmquist B (2000) Ecosystem process rate increases with animal species richness: evidence from leaf-eating, aquatic insects. *Oikos* 89:519–523
- Kondoh M (2001) Unifying the relationship of species richness to productivity and disturbance. *Proc R Soc Lond B* 268:269–271
- Loreau M, Hector A (2001) Partitioning selection and complementarity in biodiversity experiments. *Nature* 412:72–76
- Matthiessen B, Gamfeldt L, Jonsson PR, Hillebrand H (2006) Effects of grazer richness and combination on algal biomass in closed and open marine systems. *Ecology* 88:178–187
- Naeem S, Li S (1998) Consumer species richness and autotrophic biomass. *Ecology* 79:2603–2615
- O'Connor NE, Crowe TP (2005) Biodiversity loss and ecosystem functioning: distinguishing between number and identity of species. *Ecology* 86:1783–1796
- Paine RT (1966) Food web complexity and species diversity. *Am Nat* 100:65–75
- Parker JD, Duffy JE, Orth RJ (2001) Plant species diversity and composition: experimental effects on marine epifaunal assemblages. *Mar Ecol Prog Ser* 224:55–67
- Petchey OL et al (2004) Species loss and the structure and functioning of multitrophic aquatic systems. *Oikos* 104:467–478
- Polis GA, Strong DR (1996) Food web complexity and food web dynamics. *Am Nat* 147:813–846
- Proulx M, Mazumder A (1998) Reversal of grazing impact on plant species richness in nutrient-poor vs. nutrient-rich ecosystems. *Ecology* 79:2581–2592
- Scheiner SM (1993) MANOVA: multiple response variables and multisppecies interaction. In: Scheiner SM, Gurevitch J (eds) *Design and analysis of ecological experiments*. Chapman and Hall, London, pp 94–112
- Shurin JB, Borer ET, Seabloom EW, Anderson K, Blanchette CA, Broitman B (2002) Cross-ecosystem comparison of the strength of trophic cascade. *Ecol Lett* 5:785–791
- Sundbäck K, Snoeijis P (1991) Effect of nutrient enrichment on microalgal community composition in a coastal shallow-water sediment system: an experimental study. *Bot Mar* 34:341–358
- Terborgh J (1992) Maintenance of diversity in tropic forests. *Biotropica* 24:283–292
- Thébault E, Loreau M (2003) Food-web constraints on biodiversity-ecosystem functioning relationships. *Proc Natl Acad Sci USA* 100:14949–14954
- Tilman D (1999) The ecological consequences of changes in biodiversity: a search for general principles. *Ecology* 80:1455–1474
- Valiela I (1992) Coupling of watersheds and coastal waters: an introduction to the dedicated issue. *Estuaries* 15:429–430
- Wiltshire KH (2000) Algae and associated pigments of intertidal sediments, new observations and methods. *Limnologica* 30:205–214
- Wiltshire KH, Blackburn J, Paterson DM (1997) The Cryolander: a new method for fine-scale in-situ sampling of intertidal surface sediments. *J Sed Res* 67:977–981
- Wojdak JM (2005) Relative strength of top-down, bottom-up, and consumer species richness effects on pond ecosystems. *Ecol Monogr* 75:489–504
- Worm B, Duffy JE (2003) Biodiversity, productivity and stability in real food webs. *Trends Ecol Evol* 18:628–632
- Worm B, Lotze HK, Hillebrand H, Sommer U (2002) Consumer versus resource control of species diversity and ecosystem functioning. *Nature* 417:848–850