Grazer diversity effects in an eelgrass–epiphyte–microphytobenthos system

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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 · Mesograzier · 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 (Jonson 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).
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 microalgal 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 μmol l⁻¹ ± 2.7, ammonium 3.7 μmol l⁻¹ ± 1.2, phosphate 0.8 μmol l⁻¹ ± 0.3 and silicate 18.4 μmol l⁻¹ ± 1.2. The nutrient concentrations in the Kiel Fjord were as follows: nitrate 1.6 μmol l⁻¹, ammonium 1.3 μmol l⁻¹, phosphate 0.2 μmol l⁻¹ and silicate 5.1 μmol 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 μmol s⁻¹ 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 (mm²) = AFDM (g) × 588.88 (R² = 0.97, P ≤ 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-Gamma-rus, Idotea-Littorina, Gammarus-Littorina,Idotea-Gamm-arus-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).
Grazer species richness (Table 1) and species identity showed significant effects; *Idotea* and *Gammarus* reduced epiphyte biomass significantly more effectively than *Littorina* (*P* ≤ 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 crustacean species (*P* ≤ 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* ≤ 0.001). Microphytobenthos 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.

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

| Grazer richness effects | 7 Days | 21 Days |
|-------------------------|--------|---------|
|                         | *F*    | *P*     | *F*    | *P*     |
| 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).
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* ≤ 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* < 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

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**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 (mean 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.
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, $F = 1.9$, $P = 0.012$). 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 microalgal 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
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 Kahler (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 hydrobid 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; Wom 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 by stream fungi. Oikos 101:247–252

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