Ecology Letters, (2005) **8**: 301–309 doi: 10.1111/j.1461-0248.2005.00725.x

LETTER

Ecosystem consequences of diversity depend on food chain length in estuarine vegetation

J. Emmett Duffy*, J. Paul Richardson and Kristin E. France
School of Marine Science and Virginia Institute of Marine Science, The College of William and Mary, Gloucester Point, VA 23062-1346, USA
**Correspondence: E-mail: jeduffy@vims.edu*

Abstract

Biodiversity and food chain length each can strongly influence ecosystem functioning, yet their interactions rarely have been tested. We manipulated grazer diversity in seagrass mesocosms with and without a generalist predator and monitored community development. Changing food chain length altered biodiversity effects: higher grazer diversity enhanced secondary production, epiphyte grazing, and seagrass biomass only with predators present. Conversely, changing diversity altered top-down control: predator impacts on grazer and seagrass biomass were weaker in mixed-grazer assemblages. These interactions resulted in part from among-species trade-offs between predation resistance and competitive ability. Despite weak impact on grazer abundance at high diversity, predators nevertheless enhanced algal biomass through a behaviourally mediated trophic cascade. Moreover, predators influenced every measured variable except total plant biomass, suggesting that the latter is an insensitive metric of ecosystem functioning. Thus, biodiversity and trophic structure interactively influence ecosystem functioning, and neither factor's impact is predictable in isolation.

Keywords

Biodiversity, ecosystem functioning, food webs, grazing, marine, response diversity, seagrass, trait-mediated indirect interactions, trophic cascade.

Ecology Letters (2005) 8: 301–309

INTRODUCTION

Understanding how community structure translates to ecosystem functioning is a central theme of ecology (Hairston *et al.* 1960; Odum 1969). Two of the most fundamental aspects of community structure are the number of trophic levels, or food chain length, and the number of species present, or diversity. Both aspects pervasively influence ecosystem properties. First, in a range of systems, predator impacts can cascade through food chains to cause major changes in plant biomass and composition, thereby modifying ecosystem structure and functioning (Pace *et al.* 1999; Shurin *et al.* 2002). Conversely, declining diversity within trophic levels often reduces aggregate biomass and resource use (Tilman 1999; Loreau *et al.* 2001). Both trophic cascades and links between biodiversity and ecosystem functioning have generated widespread attention in the last decade.

In complex natural ecosystems, these influences of biodiversity and trophic structure interact. Theory predicts that prey heterogeneity should dampen top-down control and enhance prey biomass accumulation in diverse food webs relative to simpler food chains (Leibold 1996; Thébault & Loreau 2003), and empirical data generally support this prediction (Leibold *et al.* 1997; Hulot *et al.* 2000; Steiner 2001). Yet both theoretical and experimental studies of how biodiversity influences ecosystem functioning (BD–EF) have focused primarily on interactions within single trophic levels. There is growing recognition that a robust framework linking biodiversity changes to ecosystem functioning requires incorporating the full range of interspecific interactions that operate within communities (Loreau *et al.* 2001; Naeem & Wright 2003; Worm & Duffy 2003; Petchey *et al.* 2004). In particular, grazing commonly modifies plant biomass and community composition (e.g. Paine 2002), and recent theory shows that relationships between biodiversity and ecosystem functioning depend critically on the strength of this top-down control (Thébault & Loreau 2003). Thus, assessing how food chain length interacts with changing diversity is a logical step in broadening the scope of BD–EF research. A few experiments have explicitly tested and confirmed the importance

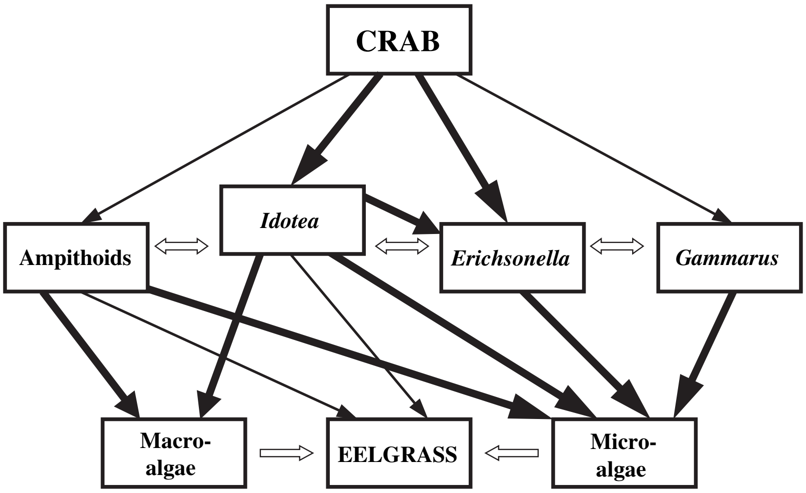

Figure 1 Interaction web for the experimental seagrass system. Arrows show the direction of influence, with thick and thin arrows representing strong and weak interactions, respectively. Solid arrows denote trophic interactions, and unfilled arrows competitive interactions. *Idotea* is raised slightly above the other grazers to indicate its higher position in the food web resulting from intraguild predation on *Erichsonella*.

of such interactions (Mulder *et al.* 1999; Naeem *et al.* 2000). Given the potential implications of diversity–function relationships for conservation and management, it is important to evaluate whether sensitivity of these relationships to consumers is a common phenomenon.

Here we test experimentally how food chain length interacts with changing grazer diversity to influence plant community biomass and composition. We use the latter as proxies for the primary production and habitat structure that support the functioning ecosystem. Our experiment focuses on beds of eelgrass (*Zostera marina*), the northern hemisphere's most widespread and abundant benthic marine plant (Fig. 1). Submerged macrophytes provide several important ecosystem services, stabilizing mobile sediments, creating essential three-dimensional habitat for fishery and forage species, and enhancing invertebrate secondary production (Klumpp *et al.* 1989; Williams & Heck 2001). Associated microalgae are the major source of primary production entering the food chain, but heavy algal growth can also create a nuisance by reducing habitat structure and associated fauna and fostering hypoxia (Valiela *et al.* 1997). Thus, healthy functioning of seagrass ecosystems depends on maintenance of low algal biomass. Grazing invertebrates are critical in maintaining this state as they facilitate macrophytes by preventing their overgrowth by algae (Valentine & Duffy 2005). Experiments show, moreover, that seagrass dominance depends on the identity and richness of grazers and predators (Heck *et al.* 2000; Duffy *et al.* 2003).

As coastal marine systems worldwide face pervasive anthropogenic impacts (Jackson *et al.* 2001), changes to both diversity and food web structure may have important and synergistic impacts on their structure and functioning (Duffy 2002, 2003). Thus, we tested how consumer diversity and food chain length interactively influence biomass accumulation of the major primary producers and grazers. Because different groups of primary producers often fulfil quite different functions, we also explored effects on the relative dominance of primary producer functional groups. We show that previously demonstrated ecosystem effects of grazer diversity in this system (Duffy *et al.* 2003) are altered by addition of a third trophic level, and we find partial support for the hypothesis that prey diversity reduces the strength of trophic cascades.

METHODS

Experimental design

We manipulated grazer diversity and food chain length in an array of 55 113-L outdoor mesocosm tanks supplied with flowing water from the York River estuary (Virginia, USA). Water was filtered with 0.15-mm mesh to minimize grazer invasion, but allowed passage of microscopic propagules of algae and sessile invertebrates, allowing their natural recruitment. Thus, the system was open at the bottom (Holt & Loreau 2002). We used a factorial design ($n = 5$ mesocosms per treatment), crossing two food chain lengths with five grazer treatments. The food chain treatments were two-level (plants, grazers) and three-level (plants, grazers, predator). Mesocosms assigned to three-level treatments received three juveniles of the blue crab (*Callinectes sapidus*, carapace width 2.0–4.0 cm), an important generalist predator in Chesapeake Bay eelgrass beds (Hines *et al.* 1990). Although blue crabs are omnivorous, they have little or no impact on algae in our system (JED, unpublished data). The five grazer treatments included each of four grazer taxa stocked alone, and all four taxa together, providing two levels of grazer richness and four compositions within the one-species level. Grazers included two amphipod taxa, ampithoids (a mixture of the morphologically similar *Cymadusa compta* and *Ampithoe longimana*) and *Gammarus mucronatus*; and two isopods, *Erichsonella attenuata* and *Idotea baltica*. These grazers, hereafter referred to by genus or family name, are among the most abundant epifaunal species in local eelgrass beds (Parker *et al.* 2001). Finally, we also included a control containing neither grazers nor predators ($n = 5$) as a baseline against which to evaluate effects of consumers.

In May 2002, in each mesocosm, we planted 75 defaunated eelgrass shoots in clean sand and added 80 grazers. This grazer density was below those typical in the field to allow grazer assemblages to adjust through growth and competition. Four-species treatments received 20 individuals of each grazer species. Crabs were added a few days later. The experiment ran for 6 weeks (one to three grazer generations), long enough for grazer relative abundances to adjust to natural levels and to approach carrying capacity, at least for the rapidly growing amphipods (Duffy & Harvilicz 2001). The experiment was terminated at 6 weeks to avoid contamination by non-target grazers entering via the flow-through seawater system, and because plants were entirely consumed in some treatments by that time.

As a measure of predator influence on grazer behaviour, we counted the number of *Idotea baltica* observed swimming during a 10-s period in each replicate *Idotea* mesocosm a few days after the experiment began. We focused on *Idotea* because it is relatively large and active and could be counted accurately. We compared the observed number swimming in crab and no-crab treatments with a paired-sample *t*-test.

Ecosystem properties were sampled at the end of the experiment because of the difficulty of obtaining accurate, non-destructive samples while underway. At 6 weeks, we sampled sediment-associated microalgae with a 2.6-cm diameter core, and measured algal biomass as chl *a* spectrophotometrically (see Duffy *et al.* 2003). Epiphytic algae were sampled from three eelgrass blades from each mesocosm and processed similarly. Then all non-grazer organisms ≥ 0.5-mm were harvested and identified, and ash-free dry mass (AFDM) of each taxon was measured. Grazer abundance and species composition were estimated in a sorted subsample (usually 1/4) of the mobile epifauna retrieved from each mesocosm, and biomass of each species was estimated using empirically derived relationships between body size and mass (Edgar 1990). Total grazer AFDM, pooled across all species present, was measured directly in the remainder of each sample by combustion. As an index of macrophyte dominance, we calculated [eelgrass biomass/(eelgrass biomass + macroalgal biomass)]. This index varies from zero when only algae are present to one when eelgrass alone is present.

Statistical analysis

We analysed the experiment using a fully factorial two-way ANOVA, with the fixed factors food chain length (i.e. presence/absence of crabs, d.f. = 1), grazer diversity (d.f. = 4) and their interaction. The grazer-free control was excluded from statistical analyses because absence of a corresponding control including only crabs would render this analysis non-orthogonal, and because our primary interest was how grazer diversity, rather than mere presence of grazers, influenced ecosystem properties. Numerous previous experiments in this system have documented the importance of grazers relative to grazer-free controls (cited in Duffy *et al.* 2003). As variance increased with the mean for most variables, ANOVAs were conducted on log-transformed data. From these ANOVAs we obtained both *F*-tests of significance and estimates of effect strength (i.e. ω^2, per cent variance explained) for both factors and their interaction. To distinguish effects of grazer species richness vs. grazer species composition, we partitioned the grazer diversity SS from the ANOVA into two orthogonal components: (1) a planned contrast comparing the four-species treatment against all single-species treatments (richness effect, d.f. = 1), and (2) the SS remaining after subtracting the richness contrast SS from the overall grazer diversity SS, which corresponds to the variance among single-grazer treatments (composition effect, d.f. = 3). Where grazer–crab interaction terms were significant, we conducted separate one-way ANOVAs for crab and no-crab treatments, again partitioning the grazer diversity effect into richness and composition components. ANOVAs were performed using SAS Version 8e (SAS 2001).

To test the specific hypothesis that grazer species richness dampened cascading predator effects, we calculated cascade strength as $\ln[(1000\ B_{\mathrm{C}} + 1)/(1000\ B_{\mathrm{NC}} + 1)]$, where B_{C} and B_{NC} are values of the response variable in the presence and absence of crabs, respectively; these variables were multiplied by 1000 to reduce any effect of the added constant. Cascade strength was calculated for the four-grazer treatment and for the average of all one-grazer treatments, with 95% CI of each obtained by bootstrapping. Grazer richness significantly affected cascade strength where the 95% CI for four-grazer species and one-species treatments did not overlap.

RESULTS

In five of the 55 mesocosms, unstocked grazer species invaded and reached > 500 mg AFDM by the end of the experiment; these contaminated replicates were excluded from analysis.

Food chain length, i.e. presence vs. absence of predators, strongly affected the absolute and relative abundances of

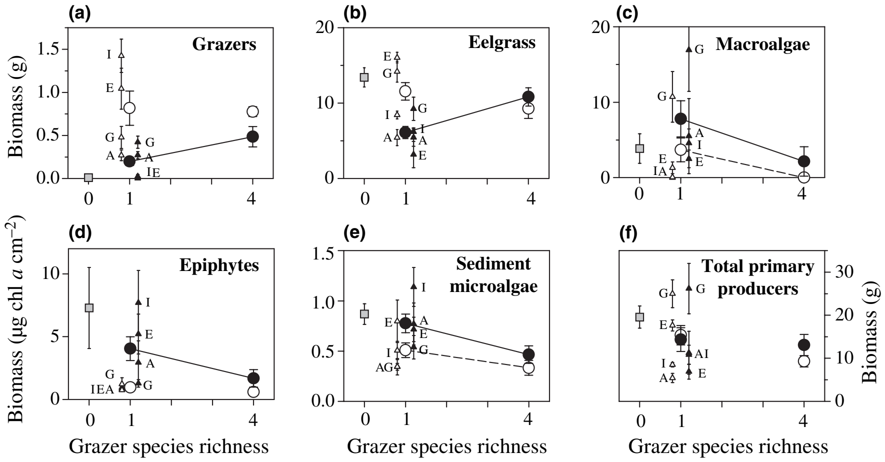

Figure 2 Influence of grazer diversity and food chain length on mean (± 1 SE) biomass of major benthic functional groups. Triangles show treatment means for individual grazer species ($n = 5$), accompanied by first letter of grazer genus name. Circles show means for single-grazer treatments (averaged across species, $n = 20$) and four-species treatments ($n = 5$). Filled and unfilled symbols represent treatments with and without predatory crabs, respectively. Lines connecting one- and four-species symbols indicate significant effects of grazer species richness (solid = with crabs, dashed = without crabs). See Table 1 for statistical analyses.

grazers (Figs 2a and 3). Among single-grazer treatments, the large-bodied isopod grazers (*Idotea* and *Erichsonella*) reached greater final biomass than amphipods did in the absence of crab predators, but those isopods were essentially eliminated when crabs were present. In contrast, biomasses of the smaller amphipods were unaffected by crabs (Fig. 2a). In the four-species grazer treatments, differential predation by crabs resulted in compensatory changes in density among grazer species. Specifically, crabs facilitated ampithoids, which reached fourfold higher density in the presence of crabs than in their absence; this facilitation of ampithoids compensated partially for the loss of *Idotea* to crabs, such that total grazer abundance was little affected by predation (Fig. 3), although total grazer biomass was reduced (Fig. 2a). *Erichsonella* was essentially eliminated from the four-species assemblages, even in the absence of crabs, by competition and/or intraguild predation. Presumably because of these compensatory responses of grazer species to predation, aggregate grazer biomass was significantly enhanced by grazer species richness only in the presence of crab predators (Fig. 2a, Table 1).

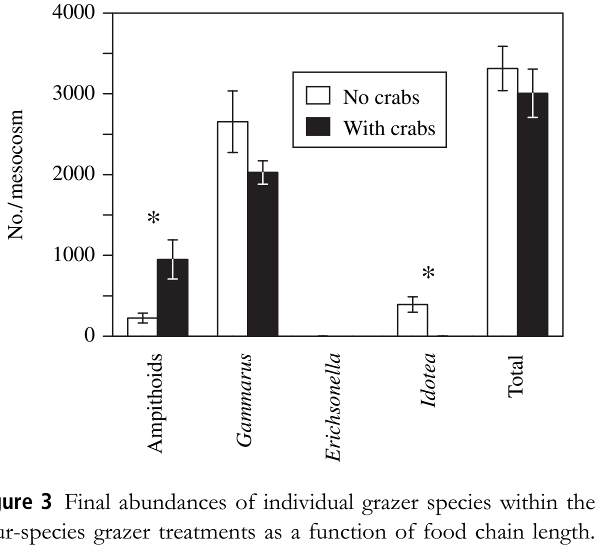

Figure 3 Final abundances of individual grazer species within the four-species grazer treatments as a function of food chain length. Total epifauna = sum of all preceding bars. *Significant difference in abundance between treatments with vs. without predators ($P < 0.05$, Wilcoxon test).

Food chain length also strongly influenced primary producer biomass accumulation and composition. Crabs produced a trophic cascade that consistently increased algal biomass across most grazer species and algal functional groups (Fig. 2). At low grazer diversity, crabs also generally reduced eelgrass biomass, probably both indirectly by facilitating competing algae and directly by disturbing the sediment and damaging the grass itself (Fig. 2b). Consequently, at low grazer diversity, cascading impacts of crab predation shifted dominance from eelgrass towards macroalgae and epiphytes (Table 1, eelgrass dominance), while aggregate primary producer biomass remained unchanged by crabs (Fig. 2f). Both grazers and predators had strong negative impacts on total benthic diversity (number of macroscopic species or taxa recorded from a given mesocosm, Table 1).

Changing grazer diversity (species richness and composition) strongly influenced primary producer biomass and composition (Fig. 2, Table 1). First, grazer species differed

Table 1 Tests of significance and estimated magnitudes of effect (ω^2) of within-trophic level diversity (grazer), food chain length (crab), and their interaction, on community and ecosystem properties

	Grazer					Crab (d.f. = 1)			Grazer × crab (d.f. = 4)			Error (d.f. = 34)	
	Richness (d.f. = 1)		Composition (d.f. = 3)										
Response†	MS	P	MS	P	ω^2	MS	P	ω^2	MS	P	ω^2	MS	ω^2
Grazers (log)	1.492	<0.0001*	0.488	>0.500	0.14	6.721	<0.0001*	0.34	1.964	<0.0001*	0.39	0.049	0.13
Eelgrass	19.066	0.105	63.552	<0.001*	0.20	149.830	<0.0001*	0.16	67.008	<0.0001*	0.27	6.860	0.38
Epiphytes	16.787	0.090	14.091	<0.01*	0.08	89.511	0.000*	0.19	16.674	0.031*	0.10	5.507	0.62
Macroalgae (log)	16.691	0.000*	12.785	<0.001*	0.41	22.818	<0.0001*	0.17	2.327	0.066	0.04	0.958	0.38
Sediment algae	0.482	0.020*	0.281	<0.05*	0.17	0.680	0.007*	0.10	0.138	0.175	0.04	0.081	0.69
Total plants (log)	0.004	0.793	1.561	<0.001*	0.33	0.003	0.809	0.00	0.133	0.052	0.08	0.051	0.61
Eelgrass dominance	0.924	0.001*	0.472	<0.001*	0.29	1.897	<0.0001*	0.26	0.081	0.300	0.01	0.064	0.45
Benthic diversity	0.774	0.001*	0.395	<0.001*	0.32	0.812	0.001*	0.14	0.123	0.086	0.05	0.055	0.50
Mean					0.24			0.17			0.12		0.47

*$P < 0.05$.

†Response variables are biomass (see Fig. 2 for units) except for eelgrass dominance and benthic diversity (see Methods). Data were analysed by two-factor model I ANOVAs. (log) indicates that data were transformed by $\log(1000X + 1)$ to reduce variance heterogeneity. The ω^2 values for 'grazers' are calculated for the overall grazer effect, combining richness and composition components. Negative estimates of ω^2 are reported as zeros.

widely in both magnitude and sign of their impacts on biomass of primary producers. In the absence of crab predation most grazers nearly eliminated algae, but *Gammarus* instead enhanced macroalgal biomass over ungrazed controls by a factor of 2 (without crabs) to 4 (with crabs, Fig. 2c) by facilitating the red macroalga *Polysiphonia* sp. Similarly, grazer effects on eelgrass ranged from strongly negative to moderately positive, relative to grazer-free controls, depending on species (Fig. 2b). Primary producers were also influenced by increasing grazer species richness, which reduced macroalgal (Fig. 2c) and sediment algal biomass (Fig. 2e) in both presence and absence of crabs. In contrast, increasing grazer richness significantly enhanced eelgrass biomass, and reduced epiphyte biomass, only in the presence of crabs (Fig. 2b,d Table 1). The effects of grazer richness on algal biomass cannot be explained solely by a sampling effect for larger grazers, as in the absence of crabs grazer biomass was no higher in the four-grazer treatment than in the average single-grazer treatment (Fig. 2a).

Our primary interest was in the interactive effects of diversity and food chain length on ecosystem properties. These interactions significantly influenced biomass of grazers, eelgrass and epiphytes (Fig. 2, Table 1). Separate ANOVAs conducted on crab and no-crab treatments showed that, in the presence of crabs, grazer species richness enhanced grazer biomass, eelgrass biomass and grazing impact on macroalgae, epiphytes and sediment microalgae. In contrast, in the absence of crabs, grazer richness affected only macroalgal and sediment microalgal biomass (Fig. 2, Table 1). Hence, grazer diversity effects were generally stronger in the three-level system. Our bootstrapped estimates of cascade strength showed that increasing grazer diversity significantly weakened effects of predatory crabs on grazer biomass, eelgrass biomass and eelgrass dominance, but not on algal or total plant biomass (Fig. 4).

Indirect evidence indicates that failure of enhanced grazer diversity to dampen cascading predator effects on algae reflects a behaviourally mediated cascade: in the three treatments where grazers remained abundant in the presence of crabs, the biomass ratio of algae to grazers was consistently greater in the presence of crabs than in their absence ($P = 0.015$, two-way ANOVA, Fig. 5), suggesting that grazers consumed less algae per capita when predators were present. Direct observations also indicated that predators changed grazer behaviour. The number of *Idotea* observed swimming within a 10-s period was more than an order of magnitude greater in crab treatments (mean ± SE = 7.4 ± 1.2) than in the absence of crabs (0.4 ± 0.2), a significant difference ($P < 0.001$, *t*-test on log-transformed data).

Overall, changing diversity and changing food chain length had comparably strong effects on the eelgrass system (Table 1). The proportion of total experimental variance explained (ω^2) by grazer diversity ranged from 8 to 41% (mean = 24%) across the eight response variables, whereas magnitude of the predator effect ranged from 0 to 34% (mean = 17%). Interactions between grazer diversity and food chain length explained about half as much variance as

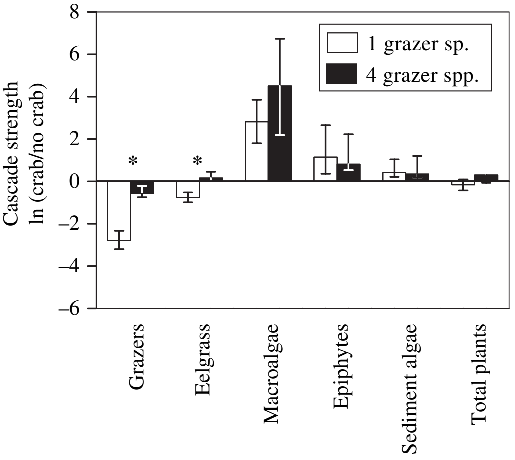

Figure 4 Influence of grazer species richness on strength of cascading predator impacts. Cascade strength, expressed as impact of crabs on biomass of each major group (mean ± 95% CI), obtained by bootstrapping (see text). *Significant difference ($P < 0.05$) in cascade strength between treatments with four grazer species vs. the average of one-species treatments, determined by non-overlapping 95% CI.

did either main effect, ranging from 1 to 39% (mean = 12%, Table 1). Importantly, because of the partially compensatory responses of algae vs. eelgrass in crab treatments, grazer species composition was the only significant influence on total plant biomass, explaining 33% of the variance, whereas presence of crabs had no effect (Table 1). Unexpectedly, total plant biomass was in fact the only response variable we measured that was not affected by food chain length.

DISCUSSION

Humans are fundamentally altering both diversity and food web structure, particularly in aquatic systems (Jackson *et al.* 2001; Duffy 2003), and thus the question of how diversity and food chain length affect ecosystem functioning has important practical implications. Our experimental results demonstrate that biodiversity and food chain length interact in influencing ecosystem functioning, such that neither factor's effects can be understood in isolation. Grazer diversity – both species composition and richness – altered the strength and nature of cascading predator impacts and, conversely, food chain length altered the influence of diversity on ecosystem properties. These results support recent theoretical predictions that food web structure interacts with changing diversity to influence patterns of ecosystem biomass accumulation (Holt & Loreau 2002; Thébault & Loreau 2003). Two previous experiments have also demonstrated such interactions, finding that relationships between primary producer species richness and productivity were eliminated by consumers (Mulder *et al.* 1999; Naeem *et al.* 2000). Interestingly, we found the opposite pattern, i.e. that species richness affected several ecosystem properties only in the *presence* of a higher-level consumer (Fig. 2). In essence, the principal effect of increasing within-level diversity in this system was to increase that trophic level's control of ecosystem processes. Specifically, higher diversity of grazers both enhanced grazer pressure on resources below, and dampened responses to predators above them in the food web.

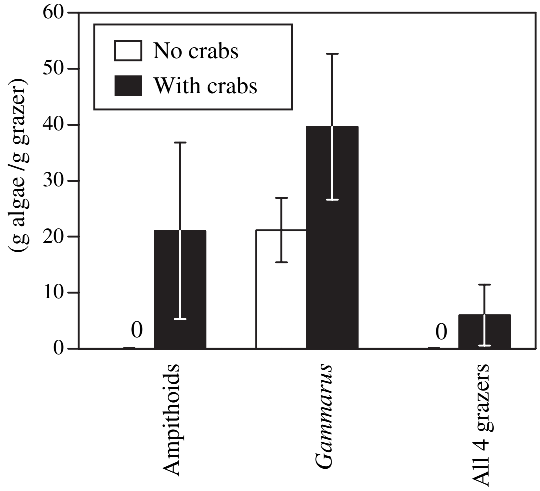

Figure 5 Influence of predators on estimated interaction strength (grazing impact per unit grazer biomass) of grazers on algae in the three treatments in which grazers survived crab predation. Interaction strength is estimated as B_A/B_G, where B_A and B_G are final biomasses of algae and grazers, respectively, in a given mesocosm. The test could not be conducted for *Erichsonella* and *Idotea* treatments as these grazers were essentially eliminated from mesocosms with predators. Interaction strengths differ among grazer treatments ($P < 0.001$) but are consistently lower (i.e. algal biomass is greater) in the presence of crab predators ($P = 0.015$, two-way ANOVA on log-transformed data), supporting a behaviourally mediated trophic cascade.

In the context of such multi-trophic level systems, diversity is potentially important in two ways (Duffy 2002). First, a more diverse consumer assemblage can use available resources more efficiently, and thus exert stronger control on the resource (e.g. Tilman *et al.* 1997; Stachowicz *et al.* 2002). Second, prey diversity may foil the ability of higher predators to control aggregate prey biomass and activity (Strong 1992; Leibold 1996). Our experiment tested both of these hypotheses. With respect to the first, our results are generally consistent with previous findings in the two-level system (plants, grazers) that high grazer diversity maximized grazing pressure on algae (Duffy *et al.* 2003). Specifically, both macroalgae, which dominated total algal biomass in our experiment, and sediment microalgae were more effectively consumed at high grazer diversity in both absence and presence of predators (Fig. 2c,e). Moreover, increasing grazer species richness strongly enhanced dominance of eelgrass over algae in both the presence and absence of predation (Table 1). This pattern resulted in part from reduction of eelgrass biomass by crabs at low grazer diversity (Fig. 2b), an impact not easily explained by stronger competition from algae (Fig. 4). One possible explanation is that crabs had more prey available at high grazer diversity (Fig. 2a), and therefore caused less damage to eelgrass through foraging and burrowing in this treatment. Although the mechanism behind this eelgrass dominance appears complex, our results suggest that the greater grazing pressure of diverse assemblages is a relatively robust phenomenon in this system, apparent under different food chain lengths (two vs. three levels), for different algal functional groups (microalgae and macroalgae), and in different seasons. By shifting dominance from plant taxa considered detrimental to those considered beneficial to ecosystem services, the diverse grazer assemblage appears important to maintaining a healthy eelgrass ecosystem. In contrast to previous results (Duffy *et al.* 2003), however, grazer biomass production was not enhanced by high diversity in the absence of predators (Fig. 2a). This may reflect the larger range of grazer diversity used in the previous study (six species, compared with four here), the different traits of those species, or seasonal differences in grazer–algal interactions.

The second hypothesized role of diversity, in buffering against control by higher predators, has been cited widely as a factor reducing strength of trophic cascades (Strong 1992; Leibold *et al.* 1997; Duffy 2002 and references therein). The central argument is that a more diverse prey assemblage should contain a wider range of predator-resistant taxa, such that predation causes a shift towards dominance by resistant species ('species turnover', Leibold 1996) rather than a strong decline in aggregate prey biomass. This hypothesis is supported by a meta-analysis of periphyton-grazer experiments (Hillebrand & Cardinale 2004), and by a laboratory experiment comparing grazing on a natural assemblage vs. an edible monoculture of phytoplankton (Steiner 2001). To our knowledge, however, our experiment is the first to test the prey diversity hypothesis explicitly by manipulating prey species richness while controlling for composition. Our results provide mixed support for this hypothesis. In support of it, predator impact on grazer biomass was strongly reduced at high diversity relative to the average single-grazer treatment (Figs 2a and 4). Mechanistically, this effect results from density compensation among competing prey species, together with trade-offs between competitive ability and resistance to predation (Leibold 1996). Such trade-offs are well documented in phytoplankton (Agrawal 1998) and terrestrial plants (Strauss *et al.* 2002). Indeed, the exception supports the rule: protist assemblages that lacked a strong trade-off between prey competitive ability and resistance to predation showed no clear dependence of prey biomass on prey diversity (Fox 2004). Our results suggest a similar trade-off among animals at an intermediate trophic level: in the mixed-grazer treatment, densities of the two fastest growing species (thus, best competitors), *Gammarus* and *Idotea*, were reduced by crabs, whereas the relatively poorly competing ampithoids increased fourfold in the presence of crabs (Fig. 3), presumably because their cryptic tube-building habit protected them (Nelson 1979). Thus, crab predation produced compensatory shifts in abundance of predator-susceptible vs. predator-resistant species, a mechanism analogous to that buffering diverse phytoplankton against grazer control (Leibold 1996; Steiner 2001).

Despite the reduced predator impact on grazer abundance at high diversity, however, we found no corresponding weakening of cascading predator impacts on algal biomass, which were strong at both low and high grazer diversity (Figs 2 and 4). Two lines of evidence suggest that these results reflect a behaviourally mediated trophic cascade. First, we directly observed a change in behaviour of the grazing isopod *Idotea baltica* in the presence of crabs: *Idotea* swam much more actively in mesocosms with crabs than in those without them – presumably attempting to escape. Second, estimated per capita impacts of grazers on algae were significantly reduced in the presence of predators (Fig. 5), suggesting that crabs reduced amphipod grazing rates despite having little impact on their abundance. Such changes in prey behaviour are common responses to predator presence in a variety of systems. Indeed, Schmitz *et al.* (2004) argued that this trait-mediated trade-off between foraging and predator avoidance in species at intermediate trophic levels is a major source of the previously unexplained variation in strength of trophic cascades among systems. Our data support their conclusion that behaviourally mediated cascades can dramatically influence primary producer communities, and bolster evidence that trait-mediated cascades can be important in complex food webs (Schmitz 1998) as well as in simple food chains (Strong 1992). Finally, these results illustrate that the mechanisms mediating BD–EF relationships in multi-level food webs are more complex than those proposed for plant assemblages (Duffy 2002; Thébault & Loreau 2003).

Much research addressing biodiversity effects on ecosystem functioning has focused on the response variable of aggregate primary productivity, usually measured as net accumulation of plant biomass (Tilman 1999). Similarly, Polis *et al.* (2000) argued that community-wide plant biomass is the most appropriate response variable for identifying trophic cascades. This concentration on total plant production reflects its fundamental importance to structure and functioning of all ecosystems. Nevertheless, a narrow focus on this single variable may divert attention from consumer-induced shifts in plant community composition (Schmitz 2003), which can have major influences on ecosystem properties even when total plant biomass changes little. Our results illustrate this situation clearly: of the several community and ecosystem response variables we measured, total plant biomass was the single one that was unaffected by food chain length (predators). Thus, we found no community-wide trophic cascade. Yet cascading predator effects, or their interaction with grazer diversity, influenced biomasses of the major structural species, eelgrass; the algae that support the food web; sessile invertebrates; and the small crustacean grazers that transfer production to fish populations (Fig. 2, Table 1). Clearly, total plant biomass is a relatively insensitive metric of important functional attributes in this system. Our system, moreover, is not unique in this respect. Normal ecosystem functioning often depends more on the influence of particular taxa, such as foundation species or keystones than on gross, system-level production (Power *et al.* 1996; Grime 1998; Downing & Leibold 2002). This is particularly true in aquatic systems, where different groups of primary producers have fundamentally different roles and impacts on ecosystem functioning. In these systems high productivity can actually be injurious to ecosystem health as it is frequently manifested as 'nuisance blooms' of algae, and the appropriate index of healthy aquatic ecosystem functioning is widely considered to be the relative performance of macrophytes, rather than of aggregate primary producers (e.g. Dennison *et al.* 1993). Hence, dominance of macrophytes – and the existence of the ecosystems based on them – depends on factors that maintain low biomass of algae. We have shown that a diverse grazer assemblage is one such factor.

Finally, our results illustrate that functional redundancy can be a misleading concept when function is considered under only a single set of conditions. Species with apparently identical functions can respond quite differently to perturbations, or under different conditions, with important consequences for ecosystem functioning, a phenomenon termed response diversity (Elmqvist *et al.* 2003). For example, all four grazer species we studied had essentially identical, strong impacts on epiphyte biomass in the absence of predation, whereas epiphyte control differed widely among grazers in the presence of predation (Fig. 2d). Thus, these grazers showed response diversity to perturbations at upper levels of the food web, with the result that an important ecosystem function – grazing – was better buffered against top-down control in the diverse assemblage. In summary, our results support suggestions that the ecosystem impacts of biodiversity loss, and their implications for societally important ecosystem services, may often be trophically mediated (Duffy 2003; Thébault & Loreau 2003; Worm & Duffy 2003). They emphasize that healthy ecosystem functioning depends not only on species richness and composition but also on normal trophic interactions.

ACKNOWLEDGEMENTS

We are grateful to J. Douglass, M. Fitchett, M. Harris, L. Lau, R. Ríos, M. Roggero and A. Spivak for assistance with the experiment; J. Douglass, O. Schmitz, J. Stachowicz and two anonymous referees for comments on the MS; and the National Science Foundation (OCE 00-99226, OCE 03-52343) for support. This is VIMS contribution no. 2647.

REFERENCES

Agrawal, A.A. (1998). Algal defense, grazers, and their interactions in aquatic trophic cascades. *Acta Oecologica*, 19, 331–337.

Dennison, W.C., Orth, R.J., Moore, K.A., Stevenson, J.C., Carter, V., Kollar, S. *et al.* (1993). Assessing water quality with submersed aquatic vegetation. *BioScience*, 43, 86–94.

Downing, A.L. & Leibold, M.A. (2002). Ecosystem consequences of species richness and composition in pond food webs. *Nature*, 416, 837–840.

Duffy, J.E. (2002). Biodiversity and ecosystem function: the consumer connection. *Oikos*, 99, 201–219.

Duffy, J.E. (2003). Biodiversity loss, trophic skew, and ecosystem functioning. *Ecol. Lett.*, 6, 680–687.

Duffy, J.E. & Harvilicz, A.M. (2001). Species-specific impacts of grazing amphipods in an eelgrass-bed community. *Mar. Ecol. Prog. Ser.*, 223, 201–211.

Duffy, J.E., Richardson, J.P. & Canuel, E.A. (2003). Grazer diversity effects on ecosystem functioning in seagrass beds. *Ecol. Lett.*, 6, 637–645.

Edgar, G.J. (1990). The use of the size structure of benthic macrofaunal communities to estimate faunal biomass and secondary production. *J. Exp. Mar. Biol. Ecol.*, 137, 195–214.

Elmqvist, T., Folke, C., Nyström, M., Peterson, G., Bengtsson, J., Walker, B. *et al.* (2003). Response diversity, ecosystem change, and resilience. *Front. Ecol. Environ.*, 1, 488–494.

Fox, J.W. (2004). Effects of algal and herbivore diversity on the partitioning of biomass within and among trophic levels. *Ecology*, 85, 549–559.

Grime, J.P. (1998). Benefits of plant diversity to ecosystems: immediate filter and founder effects. *J. Ecol.*, 86, 902–910.

Hairston, N.G., Smith, F.E. & Slobodkin, L.G. (1960). Community structure, population control, and competition. *Am. Nat.*, 94, 421–425.

Heck, K.L., Pennock, J.R., Valentine, J.F., Coen, L.D. & Sklenar, S.A. (2000). Effects of nutrient enrichment and small predator density on seagrass ecosystems: an experimental assessment. *Limnol. Oceanogr.*, 45, 1041–1057.

Hillebrand, H. & Cardinale, B.J. (2004). Consumer effects decline with prey diversity. *Ecol. Lett.*, 7, 192–201.

Hines, A.H., Haddon, A.M. & Wiechert, L.A. (1990). Guild structure and foraging impact of blue crabs and epibenthic fish in a subestuary of Chesapeake Bay. *Mar. Ecol. Prog. Ser.*, 67, 105–126.

Holt, R.D. & Loreau, M. (2002). Biodiversity and ecosystem functioning: the role of trophic interactions and the importance of system openness. In: *The Functional Consequences of Biodiversity. Empirical Progress and Theoretical Expectations* (eds Kinzig, A.P., Pacala, S.W. & Tilman, D.). Princeton University Press, Princeton, pp. 246–262.

Hulot, F.D., Lacroix, G., Lescher-Moutoué, F. & Loreau, M. (2000). Functional diversity governs ecosystem response to nutrient enrichment. *Nature*, 405, 340–344.

Jackson, J.B.C., Kirby, M.X., Berger, W.H., Bjorndal, K.A., Botsford, L.W., Bourque, B.J. *et al.* (2001). Historical overfishing and the recent collapse of coastal ecosystems. *Science*, 293, 629–638.

Klumpp, D.W., Howard, R.K. & Pollard, D.A. (1989). Trophodynamics and nutritional ecology of seagrass communities. In: *Biology of Seagrasses* (eds Larkum, A.W.D., McComb, A.J. & Shepherd, S.A.). Elsevier, Amsterdam, pp. 394–397.

Leibold, M.A. (1996). A graphical model of keystone predators in food webs: trophic regulation of abundance, incidence, and diversity patterns in communities. *Am. Nat.*, 147, 784–812.

Leibold, M.A., Chase, J.M., Shurin, J.B. & Downing, A.L. (1997). Species turnover and the regulation of trophic structure. *Annu. Rev. Ecol. Syst.*, 28, 467–494.

Loreau, M., Naeem, S., Inchausti, P., Bengtsson, J., Grime, J.P., Hector, A. *et al.* (2001). Biodiversity and ecosystem functioning: current knowledge and future challenges. *Science*, 294, 804–808.

Mulder, C.P.H., Koricheva, J., Huss-Danell, K., Hogberg, P. & Joshi, J. (1999). Insects affect relationships between plant species richness and ecosystem processes. *Ecol. Lett.*, 2, 237–246.

Naeem, S. & Wright, J.P. (2003). Disentangling biodiversity effects on ecosystem functioning: deriving solutions to a seemingly insurmountable problem. *Ecol. Lett.*, 6, 567–579.

Naeem, S., Hahn, D.R. & Schuurman, G. (2000). Producer–decomposer co-dependency influences biodiversity effects. *Nature*, 403, 762–764.

Nelson, W.G. (1979). Experimental studies of selective predation on amphipods: consequences for amphipod distribution and abundance. *J. Exp. Mar. Biol. Ecol.*, 38, 225–245.

Odum, E.P. (1969). The strategy of ecosystem development. *Science*, 164, 262–270.

Pace, M.L., Cole, J.J., Carpenter, S.R. & Kitchell, J.F. (1999). Trophic cascades revealed in diverse ecosystems. *Trends Ecol. Evol.*, 14, 483–488.

Paine, R.T. (2002). Trophic control of production in a rocky intertidal community. *Science*, 296, 736–739.

Parker, J.D., Duffy, J.E. & Orth, R.J. (2001). Plant species diversity and composition: experimental effects on marine epifaunal assemblages. *Mar. Ecol. Prog. Ser.*, 224, 55–67.

Petchey, O.L., Downing, A.L., Mittelbach, G.G., Persson, L., Steiner, C.F., Warren, P.H. *et al.* (2004). Species loss and the structure and functioning of multitrophic aquatic systems. *Oikos*, 104, 467–478.

Polis, G.A., Sears, A.L.W., Huxel, G.R., Strong, D.R. & Maron, J. (2000). When is a trophic cascade a trophic cascade? *Trends Ecol. Evol.*, 15, 473–475.

Power, M.E, Tilman, D., Estes, J.A., Menge, B.A., Bond, W.J., Mills, L.S. *et al.* (1996). Challenges in the quest for keystones. *BioScience*, 46, 609–620.

SAS (2001). *SAS Version 8e*. SAS Institute, Cary, NC, USA.

Schmitz, O.J. (1998). Direct and indirect effects of predation and predation risk in old-field interaction webs. *Am. Nat.*, 151, 327–342.

Schmitz, O.J. (2003). Top predator control of plant biodiversity and productivity in an old-field ecosystem. *Ecol. Lett.*, 6, 156–163.

Schmitz, O.J., Krivan, V. & Ofer, O. (2004). Trophic cascades: the primacy of trait-mediated indirect interactions. *Ecol. Lett.*, 7, 153–163.

Shurin, J.B., Borer, E.T., Seabloom, E.W., Anderson, K., Blanchette, C.A., Broitman, B. *et al.* (2002). A cross-ecosystem comparison of the strength of trophic cascades. *Ecol. Lett.*, 5, 785–791.

Stachowicz, J.J., Fried, H., Osman, R.W. & Whitlatch, R.B. (2002). Biodiversity, invasion resistance, and marine ecosystem function: reconciling pattern and process. *Ecology*, 83, 1575–2590.

Steiner, C.F. (2001). The effects of prey heterogeneity and consumer identity on the limitation of trophic-level biomass. *Ecology*, 82, 2495–2506.

Strauss, S.Y., Rugers, J.A., Lau, J.A. & Irwin, R.E. (2002). Direct and ecological costs of resistance to herbivory. *Trends Ecol. Evol.*, 17, 278–285.

Strong, D.R. (1992). Are trophic cascades all wet? Differentiation and donor control in speciose ecosystems. *Ecology*, 73, 747–754.

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.

Tilman, D., Lehman, C.L. & Thomson, K.T. (1997). Plant diversity and ecosystem productivity: theoretical considerations. *Proc. Natl Acad. Sci. USA*, 94, 1857–1861.

Valentine, J.F. & Duffy, J.E. (2005). The central role of grazing in seagrass ecosystems. In: *Seagrasses: Biology, Ecology and Conservation* (eds Larkum, A.W.D., Orth, R.J. & Duarte, C.M.). Springer, in press.

Valiela, I., McClelland, J., Hauxwell, J., Behr, P.J., Hersh, D. & Foreman, K. (1997). Macroalgal blooms in shallow estuaries: controls and ecophysiological and ecosystem consequences. *Limnol. Oceanogr.*, 42, 1105–1118.

Williams, S.L. & Heck, K.L. Jr (2001). Seagrass community ecology. In: *Marine Community Ecology* (eds Bertness, M.D., Hay, M.E. & Gaines, S.D.) Sinauer Associates, Sunderland, MA, USA, pp. 120–150.

Worm, B. & Duffy, J.E. (2003). Biodiversity, productivity, and stability in real food webs. *Trends Ecol. Evol.*, 18, 628–632.

Editor, Oswald Schmitz
Manuscript received 2 November 2004
First decision made 30 November 2004
Manuscript accepted 16 December 2004