

Genotypic diversity and grazer identity interactively influence seagrass and grazer biomass

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ABSTRACT: Despite experimental evidence for effects of primary producer diversity and consumer species diversity on population and community processes, little is known about how diversity at these multiple trophic levels may interact. We conducted a mesocosm experiment to examine the independent and interactive effects of seagrass *Zostera marina* genotypic diversity and grazer species diversity on seagrass, epiphyte, and grazer responses. There were no interactions between seagrass genotypic diversity and grazer species diversity, per se; however, the effects of seagrass genotypic diversity on both seagrass and grazer biomass depended on grazer species identity. In particular, seagrass biomass was higher in polyculture than in monoculture, but only when the sea hare *Phyllaplysia taylori* was the only grazer present. This enhanced growth was due to complementarity among genotypes in the presence of *P. taylori*. Seagrass genotypic diversity effects on grazer biomass and fecundity were small and/or idiosyncratic, yet grazer species composition had a large impact on grazer reproductive effort. Only grazer species identity, and not seagrass genotypic diversity or grazer species diversity, affected epiphyte biomass, consistent with other findings of the importance of species identity. Our results confirm the effects of seagrass genetic diversity on the plant itself as well as the grazer species that utilize it for both food and habitat. Furthermore, they emphasize the importance of grazers for controlling epiphyte and seagrass biomass.

KEY WORDS: Biodiversity-ecosystem function · Eelgrass · Epiphytes · Genetic diversity · Herbivory · *Zostera marina*

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INTRODUCTION

With increasing losses in species numbers and abundance, understanding the ecological effects of biodiversity has become a central theme in ecology. Although there are certainly exceptions, experimental increases in species diversity tend to have an overall positive effect on ecosystem processes like productivity (Balvanera et al. 2006, Cardinale et al. 2007). In addition, a growing body of evidence points to the importance of diversity within species (i.e. genetic diversity) for population-, community-, and ecosystem-level processes (Hughes et al. 2008). The majority of biodiversity studies have manipulated species or genetic diversity at the plant/producer level, revealing effects on producer productivity, nutrient cycling, and

community structure (Balvanera et al. 2006, Hughes et al. 2008). In particular, genetic diversity can have strong effects on the diversity, abundance, and distribution of species associated with habitat-forming plants in marine and terrestrial systems (Hughes & Stachowicz 2004, Reusch et al. 2005, Crutsinger et al. 2006, Johnson et al. 2006, Crawford et al. 2007), analogous to the effects of producer species diversity (Balvanera et al. 2006). However, in most, if not all, of these studies only genetic diversity was manipulated, and thus we have little sense of the strength of the effects of genotypic diversity relative to other factors (Hughes & Stachowicz 2009).

Consumer presence or abundance can also have strong effects on primary producer diversity (Lubchenco 1978) and biomass (Hairston et al. 1960,

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Schmitz et al. 2000). Although not as commonly manipulated as either consumer presence or producer diversity, consumer diversity and trophic level diversity (i.e. the number of trophic levels) can also be important for community- and ecosystem-level processes (Duffy et al. 2007). For example, predator diversity in kelp communities decreases foraging of intermediate consumers and results in increased kelp biomass via a trophic cascade (Byrnes et al. 2006). Further, the addition of a trophic level can alter the outcome of diversity manipulations at a different trophic level: increased seagrass grazer diversity led to increased grazer biomass and seagrass biomass only when predators were present (Duffy et al. 2005).

Although there have been significant advances in our understanding of the unidirectional impacts of diversity at one trophic level on another, we have relatively little information regarding how diversity at multiple trophic levels interacts to influence population and community processes (but see Fox 2004, Aquilino et al. 2005, Gamfeldt et al. 2005, Bruno et al. 2008, Douglass et al. 2008). The evidence to date suggests that, although not universal (e.g. Aquilino et al. 2005), significant interactions between levels of diversity can occur. For example, prey richness and consumer richness interactively affected total community biomass in a marine microbial system: differences among levels of prey diversity were only apparent at the highest consumer diversity (Gamfeldt et al. 2005). Similarly, increased herbivore diversity decreased macroalgal growth in experimental mesocosms, and this difference was exacerbated at higher algal diversity because of positive effects of algal diversity on growth (Bruno et al. 2008).

Despite the relative scarcity of experimental manipulations, we expect that interactions between changing diversity of producers and consumers are widespread for 2 reasons: (1) changes in biomass as a result of changing producer diversity can affect the quality and quantity of food or shelter for higher trophic levels (Balvanera et al. 2006), and (2) animals can affect the abundance and diversity of plants through many pathways (Schmitz et al. 2000, Bruno & Cardinale 2008). Given the parallels between ecological effects of species and genetic diversity (Hughes et al. 2008), similar interactions may occur between genetic diversity at one trophic level and species diversity at another. To examine these potential interactions, we simultaneously manipulated seagrass (*Zostera marina*) genotypic diversity and invertebrate grazer species diversity in a factorial replacement-series design in experimental mesocosms and examined their independent and interactive effects on (1) producer (seagrass and epiphyte) biomass and (2) grazer biomass and fecundity.

MATERIALS AND METHODS

Study system. Seagrasses, marine angiosperms that form critical habitat in coastal ecosystems worldwide, provide an ideal system for examining interactions between genetic and species diversity. First, seagrass genotypic diversity influences the productivity of the seagrass itself, as well as the community of organisms that depend on it. For example, seagrass genotypic diversity has positive effects on seagrass biomass, particularly in response to disturbances such as grazing (Hughes & Stachowicz 2004, Reusch et al. 2005). Seagrass genotypic diversity can also lead to increased species abundance and diversity of the community of invertebrates closely associated with seagrass habitat (Hughes & Stachowicz 2004, Reusch et al. 2005).

In addition to the effects of seagrass genotypic diversity on seagrass and community responses, grazer species identity and diversity can have strong impacts on the biomass of seagrass and the algal epiphytes that grow on the seagrass (Duffy et al. 2001, Duffy et al. 2003, Duffy et al. 2005). As grazer species vary in their preference for and ability to consume algal epiphytes or seagrasses (Duffy & Harvilicz 2001), the intensity of direct herbivory on seagrass versus the removal of epiphytes may vary between grazer monocultures and mixtures. The type and intensity of herbivory may then affect the rate at which seagrass genotypes grow and compete with each other and with epiphytes.

In this study, we utilized 6 genetically distinct clones of *Zostera marina* (hereafter *Zostera*) that exhibit considerable morphological and physiological variation when grown in a common environment (Hughes et al. 2009). This variation could contribute to effects of genotypic diversity on associated species through a variety of mechanisms, including greater food availability due to increased productivity in genetically diverse mixtures, lower susceptibility to predation due to enhanced habitat complexity in mixtures, or greater fitness due to the more diverse diet available in mixtures (Stachowicz et al. 2007). We also included 3 of the most commonly found grazers in seagrass beds in Bodega Harbor, California (R. Hughes unpubl. data): the isopod *Idotea resecata* (hereafter, *Idotea*), the sea hare *Phyllaplysia taylori* (hereafter, *Phyllaplysia*), and the gastropods *Lacuna/Lirularia* spp. (hereafter, *Lacuna*). These grazer species differ in feeding strategies: whereas they all prefer to consume epiphytic algae, both *Idotea* and *Lacuna* will also consume seagrass (Williams & Ruckelshaus 1993, R. Hughes unpubl. data). Due to the important role of epiphytes in this food web, and because of their contribution to seagrass declines (Hughes et al. 2004, Orth et al. 2006), we quantified epiphyte biomass in addition to seagrass and grazer responses.

Experimental set-up. We conducted a mesocosm experiment to examine the independent and interactive effects of *Zostera* genotypic diversity (2 levels: monoculture and polyculture) and invertebrate mesograzer diversity (2 levels: 1 species and 3 species) on epiphyte biomass, *Zostera* biomass and shoot density, and grazer biomass and reproductive effort. The 6 genetically distinct clones of *Zostera* (genotypes red, green, yellow, orange, purple, and blue from Hughes et al. 2009) were taken from stock propagated in separate outdoor mesocosms at Bodega Marine Laboratories since June 2004 (see Hughes et al. 2009 for more detail regarding propagation methods). We planted all experimental mesocosms with 4 *Zostera* terminal shoots: in genotypic monocultures all 4 shoots were from the same genotype, with 6 monocultures in total (1 for each genotype); in genotypic polycultures each terminal shoot was from 1 of 4 different genotypes, with 6 randomly generated unique 4-genotype combinations from all possible combinations of the 6 genotypes planted in monoculture. Thus, there were 12 genotypic identity treatments (6 unique monocultures and 6 unique polycultures).

We tested 5 different grazer treatments in all, including a no grazer control, 3 single species treatments (*Phyllaplysia* only, *Idotea* only, and *Lacuna* only), and a 3-species treatment. To account for differences in grazer biomass as well as variation in natural densities in the field, the single species grazer treatments received either 9 individuals of *Idotea*, 9 individuals of *Phyllaplysia*, or 18 snails (9 *Lacuna*/9 *Lirularia*). These numbers are within the range observed in natural *Zostera* beds in our study area (R. Hughes unpubl. data). We utilized a substitutive design (i.e. the 3-species treatment contained 3 *Idotea*, 3 *Phyllaplysia*, and 3 *Lacuna*/3 *Lirularia*). Although this design can confound diversity with reduced intraspecific density, a combined design that also controlled for intraspecific density was not possible because of limits on the number of mesocosms available. As we were interested in the effects of grazer diversity or seagrass genotypic diversity on grazer reproductive effort, we included 5 and 2 brooding *Idotea* in the 1-species and 3-species treatments, respectively. We also removed all existing *Phyllaplysia* and *Lacuna* egg cases prior to the start of the experiment.

We crossed the 2 genotypic diversity treatments (represented by 6 monocultures and 6 polycultures, as described above) with the 5 grazer treatments (0, 1, and 3 species) to yield 60 experimental replicates. These treatments were randomly assigned to 60 individual 22.7 l flow-through outdoor mesocosms at Bodega Marine Laboratories (38° 19.110' N 123° 04.294' W). There was only 1 replicate of each grazer identity treatment for each particular seagrass monoculture or poly-

culture; replication was achieved across rather than within genotypic monoculture and polyculture combinations. The 60 mesocosms were placed in a fixed array of 15 larger tanks (i.e. 4 mesocosms per tank). Due to expected variation in environmental conditions (light, temperature) in our experimental array, we divided the tanks into 3 blocks of 20 mesocosms each.

In May 2008, we added 2 l of sieved field-collected sediment to each mesocosm and then transplanted 4 *Zostera* terminal shoots clipped to a standard shoot (30 cm) and rhizome (2.5 cm) length. We allowed epiphytes to accumulate for 5 d before adding invertebrate grazers to the tanks. At the end of 12 wk, we quantified the epiphytic algal biomass on *Zostera* shoots, seagrass shoot density and biomass (above-ground, belowground, and total), grazer density and biomass, and per capita grazer reproductive effort (number of juvenile *Idotea* or number of *Phyllaplysia* and *Lacuna* egg sacs). *Zostera* terminal shoots were removed from the sediment while keeping rhizomes intact, allowing us to assign new vegetative growth to the appropriate original terminal shoot.

Statistical analyses. We conducted 2 types of statistical analyses of our data. In the first, we examined whether genotypic diversity and grazer diversity independently or interactively affected (1) epiphyte or seagrass responses or (2) grazer responses using a multivariate analysis of variance (MANOVA) on all response variables with block, genotypic diversity, grazer treatment, and all possible interactions as fixed factors. As the MANOVA was significant, we then conducted separate analyses of variance (ANOVA) on individual response variables. We tested for effects of grazer diversity using planned independent contrasts to compare the 1-species grazer treatments to the 3-species grazer treatment. The proportion of variance explained by each factor was calculated by ω^2 (Olejnik & Algina 2003).

There was a significant interaction between grazer identity and genotypic diversity on seagrass biomass, with genotypic polycultures out-performing genotypic monocultures in the *Phyllaplysia* treatment (see 'Results'). To examine this interaction further, we first compared the observed biomass of each unique polyculture treatment (N = 6) in the presence of *Phyllaplysia* to that expected based on the performance of each of the component genotypes in monoculture with *Phyllaplysia*. Expected values were calculated by (1) dividing each monoculture yield by 4 (the initial number of transplants) to generate an average per transplant monoculture yield for each genotype, and (2) summing these values for each genotype in a given polyculture treatment. In addition to comparing observed and expected values, we also calculated the total biodiversity effect and partitioned it among dominance and complementarity mechanisms according to

standard methods (Fox 2005). The strength of trait-independent complementarity (TIC) varied widely among individual polycultures (see Results). We hypothesized that this variation may be due to differences in the degree of trait differentiation among individual genotypes in particular polyculture combinations. Using variation in monoculture biomass among the genotypes in a polyculture as a proxy for trait differentiation, we tested whether there was a relationship between the strength of TIC and the variance in monoculture biomass of the component genotypes.

In the second set of analyses, we evaluated the effects of genotypic and grazer diversity on grazer reproductive effort by conducting separate ANOVAs for each grazer species with block, seagrass genotypic diversity, grazer diversity (single species vs. all species), and all possible interactions as fixed factors. Statistical significance of differences among treatment means was assessed using Tukey's post-hoc tests. All analyses were conducted using JMP 5.0.

RESULTS

Seagrass and epiphyte response

Seagrass genotypic diversity and grazer species identity interactively affected total seagrass biomass (Fig. 1a; see Table 1 for full statistics), primarily due to effects on aboveground biomass (Table 1). *Phyllaplysia* treatments resulted in higher seagrass biomass (Fig. 1a) and belowground biomass (Fig. 2) than any of the other grazer treatments. Differences in epiphyte biomass alone could not explain these effects: epiphyte biomass was comparably reduced in the presence of *Phyllaplysia*, *Idotea*, and the grazer polyculture (Fig. 1b), yet only the *Phyllaplysia* treatments yielded higher seagrass biomass. Despite significant differences among single-species grazer treatments, grazer species diversity did not affect plant biomass (Table 1), as the effects of combinations of grazers did not differ from that of the average grazer monoculture.

In addition to an effect of grazer identity on seagrass biomass, there was an interaction between grazer identity and genotypic diversity: genotypic polycultures with *Phyllaplysia* had higher biomass than any other treatment combination (Fig. 1a) despite equivalent reductions in epiphyte biomass in the *Phyllaplysia*, *Idotea*, and grazer polyculture treatments (Fig. 1b). Actual polyculture seagrass biomass (mean [SE] = 8.36 [0.51] g) was higher than the calculated expected value (mean [SE] = 6.28 [0.53] g; t -test $p = 0.02$; Fig. 3a) and also exceeded the biomass of the best-performing genotypic monoculture (7.95 g).

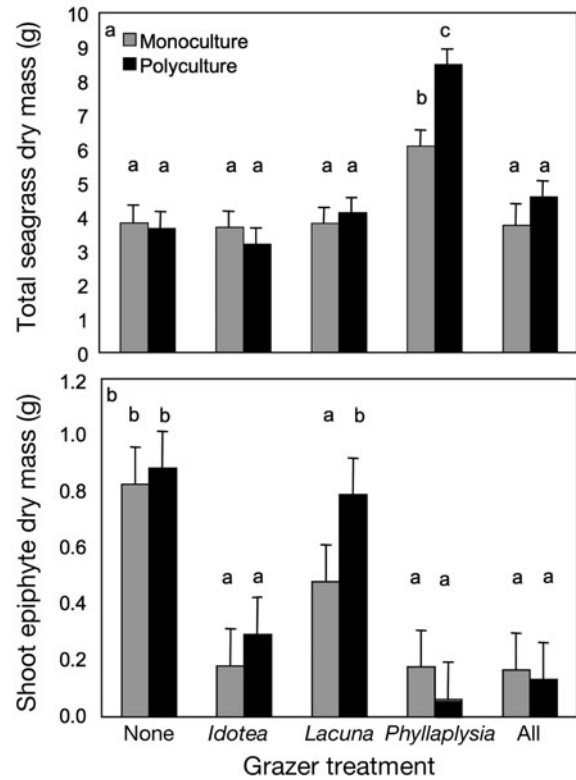


Fig. 1. Effects of grazer treatment and seagrass genotypic diversity on seagrass and epiphyte biomass. (a) Grazer identity and seagrass genotypic diversity interactively affect seagrass biomass. (b) Grazer identity affects epiphyte biomass. Statistical analysis by ANOVA. Letters indicate significant differences ($p < 0.05$) according to Tukey's posthoc tests. Error bars represent +1 SE

To understand better the mechanisms underlying the positive effect of genetic diversity in the presence of *Phyllaplysia*, we partitioned the biodiversity effect into 3 possible components (Fig. 3b) according to Fox (2005). TIC (equivalent to complementarity in the sense of Loreau & Hector 2001) was generally strong and positive (Fig. 3b), meaning that genotypes generally had higher biomass in mixture than expected, regardless of absolute monoculture biomass. The strength of TIC was highly correlated ($R^2 = 0.87$, $p = 0.007$; Fig. 3c) with the variance in monoculture biomass of the component genotypes in each polyculture (which could indicate variation in growth strategies); trait-dependent complementarity and dominance showed no relationship ($p > 0.05$; Fig. 3c).

Both trait-dependent complementarity (TDC) and dominance (together equivalent to selection sensu Loreau & Hector 2001) were negative but smaller in magnitude than TIC (Fig. 3b). This negative selection indicates a negative correlation between size in monoculture and relative increase in polyculture; it ap-

Table 1. Results of statistical analyses for genotypic diversity and grazer treatment. Values in parentheses are df. Bold indicates significant effect at $p < 0.05$. Italics indicate most important effect based on the proportion of the variance explained (ω^2). MSE = mean square error

Factor		Seagrass shoot production	Seagrass biomass	Seagrass aboveground biomass	Seagrass belowground biomass	Epiphyte biomass	Grazer biomass	Per capita grazer growth
Block (2)	<i>F</i>	0.48	0.63	1.50	0.42	0.41	8.25	4.92
	<i>p</i>	0.62	0.53	0.24	0.66	0.67	0.001	0.01
	ω^2	0.000	0.000	0.018	0.000	0.000	0.125	0.199
Genotypic diversity (1)	<i>F</i>	0.16	3.17	2.35	2.08	0.63	0.06	0.05
	<i>p</i>	0.69	0.08	0.13	0.16	0.44	0.81	0.82
	ω^2	0.000	0.019	0.006	0.002	0.000	0.000	0.000
Grazer identity (4)	<i>F</i>	5.76	22.17	14.75	18.25	12.29	29.75	1.61
	<i>p</i>	0.001	<0.001	<0.001	<0.001	<0.001	<0.001	0.19
	ω^2	<i>0.425</i>	<i>0.593</i>	<i>0.561</i>	<i>0.635</i>	<i>0.720</i>	<i>0.431</i>	0.119
Block × Genotypic diversity (2)	<i>F</i>	1.10	0.13	0.37	0.25	1.76	2.36	2.37
	<i>p</i>	0.34	0.88	0.69	0.78	0.19	0.11	0.11
	ω^2	0.005	0.000	0.000	0.000	0.039	0.028	0.07
Block × Grazer identity (8)	<i>F</i>	2.27	0.57	0.55	1.03	0.98	3.18	1.28
	<i>p</i>	0.05	0.79	0.81	0.44	0.47	0.009	0.29
	ω^2	0.363	0.044	0.047	0.118	0.155	0.194	0.226
Genotypic diversity × Grazer identity (4)	<i>F</i>	1.45	3.08	3.21	0.87	0.74	2.74	1.15
	<i>p</i>	0.24	0.03	0.03	0.49	0.57	0.05	0.35
	ω^2	0.097	0.149	0.176	0.029	0.026	0.086	0.072
Block × Genotypic diversity × Grazer identity (8)	<i>F</i>	0.75	1.92	1.63	1.82	0.52	2.06	1.75
	<i>p</i>	0.64	0.09	0.16	0.11	0.83	0.07	0.13
	ω^2	0.109	0.195	0.191	0.216	0.060	0.136	<i>0.315</i>
Grazer polyculture vs. monoculture contrast (1)	<i>F</i>	2.79	1.15	0.57	1.49	2.8	1.85	NA
	<i>p</i>	0.10	0.29	0.45	0.23	0.10	0.18	NA
MSE (30)		2.55	1.27	0.83	0.18	0.11	0.36	0.01

peared to result primarily from 3 genotypes that performed particularly poorly relative to others in seagrass monoculture with *Phyllaplysia* but had increased performance in seagrass polyculture with *Phyllaplysia* (Fig. 4). However, because there was only a single replicate of each genotypic monoculture for a given

grazer treatment, it is impossible to rule out the contribution of factors other than genotype (i.e. environmental variation among mesocosms).

Grazer response

Final grazer biomass varied with seagrass genotypic diversity and grazer species identity (Table 1). However, final biomass was largely a function of initial biomass, which varied between grazer species. There was also an interaction between block and grazer species identity (Table 1). Per capita change in biomass did not differ from zero for any treatment (Table 1), indicating that the interactive effect of genotypic diversity and grazer identity was slight.

Grazer fecundity differed between grazer monoculture and grazer polyculture for both *Idotea* (Fig. 5a) and *Lacuna* (Fig. 5b), though in opposing directions. *Idotea* fecundity was greater in grazer polyculture than monoculture, whereas snail fecundity declined in polyculture. In contrast, production of *Phyllaplysia* egg cases was consistent across grazer treatments (Fig. 5c). Seagrass genotypic diversity did not affect grazer reproductive output either independently or interactively with grazer treatment.

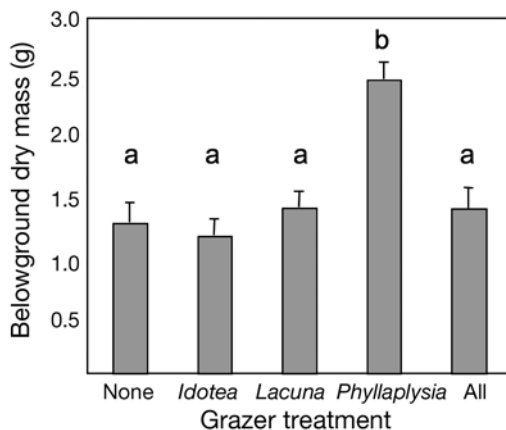


Fig. 2. Effects of grazer identity on seagrass belowground dry biomass. Statistical analysis by ANOVA. Letters indicate significant differences ($p < 0.05$) according to Tukey's post-hoc tests. Error bars represent +1 SE

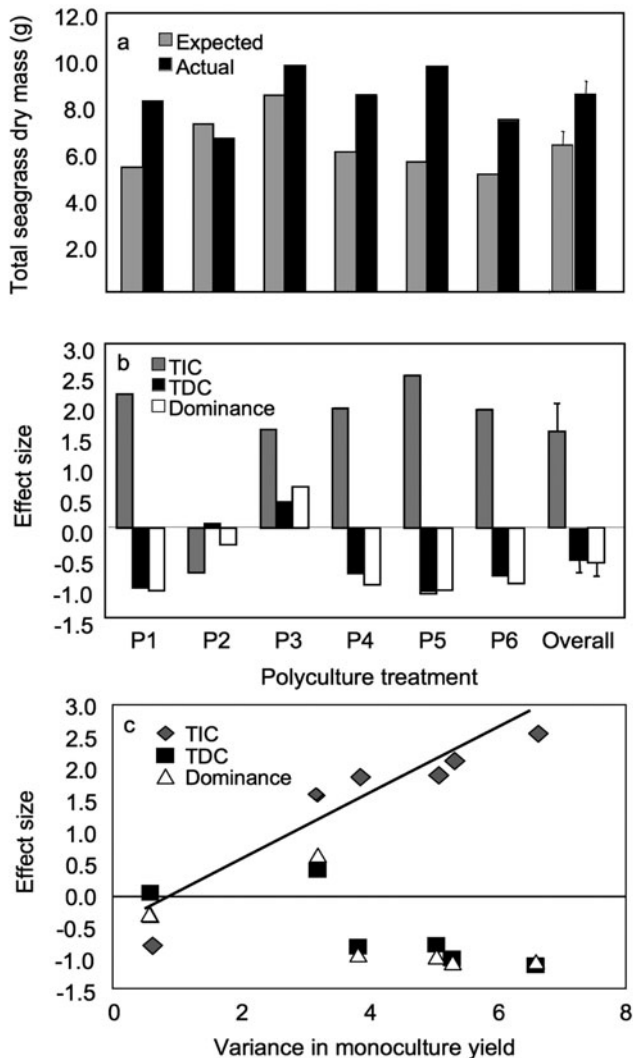


Fig. 3. Genotypic diversity mechanisms. (a) Actual versus expected seagrass polyculture biomass when grown with *Phyllaplysia*. Expected values are calculated based on the performance of component genotypes when grown in monoculture (see 'Materials and methods'). (b) Partitioning of the biodiversity effect into trait-independent complementarity (TIC), trait-dependent complementarity (TDC) and dominance. (c) Relationship between the variance in monoculture yield (as a proxy for phenotypic diversity) and the strength of TIC, TDC, and dominance. Effect sizes are square-root transformed with the original signs preserved as in Fox (2005). Error bars represent +1 SE

DISCUSSION

Our experiment reinforces other findings (e.g. Williams 2001, Hughes & Stachowicz 2004, 2009, Reusch et al. 2005) that positive effects of seagrass genetic diversity are contingent on specific abiotic or biotic conditions. As these previous experiments detected diversity effects in response to stress/distur-

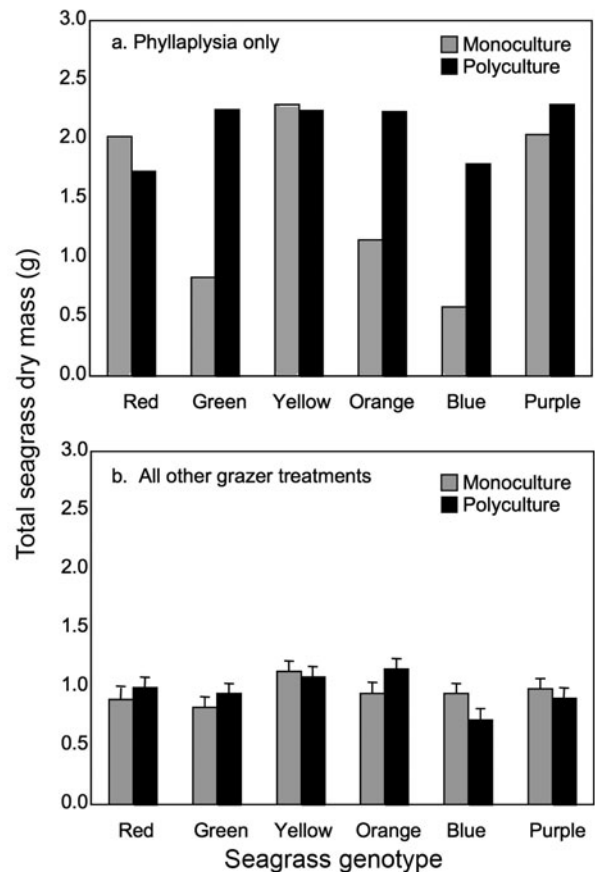


Fig. 4. Seagrass genotypic biomass per transplant in monoculture and polyculture. (a) Biomass of seagrass genotypes in the presence of *Phyllaplysia* only. Genotype color labels as in Hughes et al. (2009). (b) Biomass of seagrass genotypes in all other grazer treatments (no grazers, *Idotea* only, *Lacuna* only, and grazer polyculture)

bance, it is interesting that the positive impacts of genotypic diversity found here occur only in the *Phyllaplysia* treatment, in which the perceived 'stresses' (epiphyte biomass and direct seagrass grazing) were lowest. In this case, *Phyllaplysia* presence does lead to higher seagrass biomass overall as expected given the reduction in epiphyte biomass and direct grazing (Fig. 1), but this increase is greater in genotypic polyculture. Partitioning this diversity effect revealed that TIC (Fox 2005, complementarity sensu Loreau & Hector 2001) was the dominant component of this effect (Fig. 3b). Complementary resource use could contribute to the increased growth in genotypic polyculture: because nutrient uptake rates and rooting depths are more similar among clonemates than non-clonemates (Hughes et al. 2009), it is likely that intra-genotypic competition for nutrients limits the growth of some genotypes in monoculture when total seagrass biomass is high.

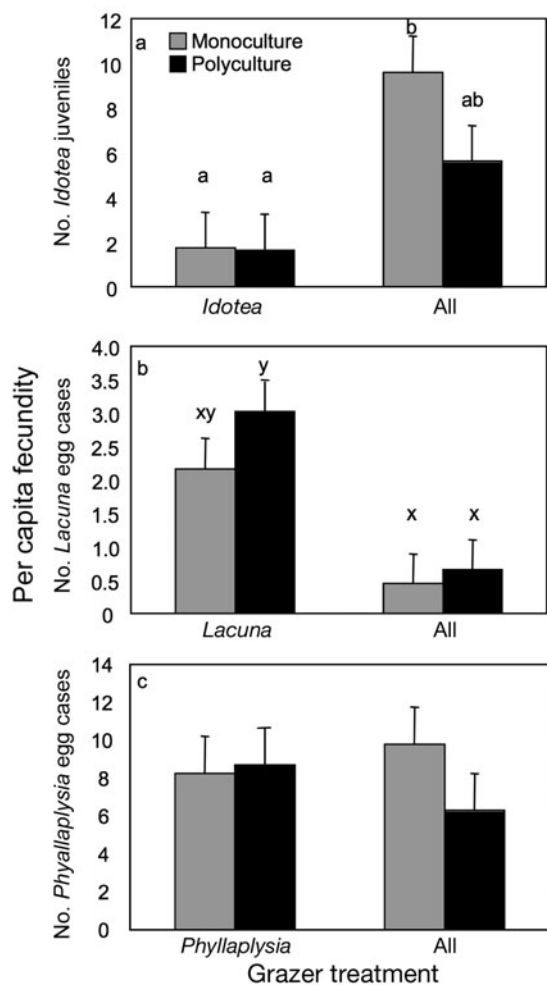


Fig. 5. Effects of seagrass genotypic diversity and grazer species diversity on per capita grazer reproductive effort. Data are presented as per capita because the initial number of grazers differed between grazer monoculture and grazer polyculture. (a) Number of newly produced juvenile *Idotea*. (b) Number of *Lacuna* egg cases. (c) Number of *Phyllaplysia* egg cases. Statistical analysis by ANOVA. Letters indicate significant differences ($p < 0.05$) according to Tukey's post-hoc tests. Error bars represent $+1$ SE

The positive TIC in polyculture was reduced by negative dominance and TDC (together equivalent to the selection effects of Loreau & Hector 2001), because those genotypes least abundant in monoculture showed disproportionate increases in biomass in genotypic polyculture. Though negative, these effects were less consistent and weaker than those of TIC, resulting in a positive net diversity effect that was strongly affected by the combination of genotypes present in a polyculture, rather than just the presence of particular genotypes. Similar counteracting effects of complementarity and selection have been found in other seagrass genetic (Reusch et al. 2005) and algal species (Bruno et al. 2006) diversity experi-

ments, though the net balance between these components varies among studies.

Seagrass genotypic diversity did not increase grazer reproductive output (Fig. 5), suggesting that the genotypes used are not complementary in nutritional content or secondary chemistry such that a benefit of a 'mixed' diet is realized for those species that directly consume seagrass (cf. Stachowicz et al. 2007). We did, however, find effects of grazer diversity on per capita reproductive effort (Fig. 5). *Idotea* reproduction was diminished in the monospecific treatment as compared to the grazer polyculture (Fig. 5a); such negative intraspecific effects could be due to either competition or cannibalism (Duffy et al. 2005). In contrast, *Lacuna* fecundity was reduced significantly by inter-specific interactions with *Idotea* and/or *Phyllaplysia* compared to when only snails were present (Fig. 5b). Because both *Lacuna* and *Phyllaplysia* utilize seagrass leaves for laying eggs, the larger *Phyllaplysia* egg cases may have preempted space needed by *Lacuna*. *Phyllaplysia* exhibited consistent reproductive effort regardless of grazer species diversity or seagrass genotypic diversity (Fig. 5c).

Overall, grazer identity was a key determinant of both epiphyte and seagrass biomass (Figs. 1 & 2), in keeping with other grazer manipulations in similar systems (Duffy & Harvilicz 2001, Duffy et al. 2001, 2003, 2005). Unlike some previous seagrass research (Duffy et al. 2003, 2005), we did not observe an effect of grazer species diversity on seagrass growth. The absence of such an effect could be the result of our experimental design (e.g. we tested a relatively small range in diversity; cf. Duffy et al. 2001 vs. Duffy et al. 2003; Stachowicz et al. 2007), yet it is also consistent with several key characteristics of this system. First, the diversity of epiphytic organisms on *Zostera* in our study system is relatively low, comprised mostly of diatoms and other microalgae, and relatively little macroalgae or fouling invertebrates (R. Hughes pers. obs.). Second, at least 2 of the dominant grazer species (*Phyllaplysia* and *Idotea*) are largely redundant in their ability to control these epiphytes, in that each alone can significantly reduce epiphyte biomass (Fig. 1b). Thus, there is little opportunity for complementarity among grazer species in their effects on epiphyte biomass, at least over the short term. However, variation in life history strategies (e.g. timing of reproduction) could result in important temporal diversity effects that have been demonstrated elsewhere (e.g. Stachowicz et al. 2002); studies of longer duration are needed to test for such effects in this system.

The importance of grazer identity (and not diversity) in this experiment likely stems from differences in feeding strategies among species, as has been shown in other mesograzer studies (Duffy & Harvilicz 2001):

whereas all of the species included in our experiment prefer to consume epiphytes, both *Idotea* and *Lacuna/Lirularia* spp. will also consume seagrass (Williams & Ruckelshaus 1993, R. Hughes unpubl. data). In this experiment, seagrass leaves in treatments with *Idotea* frequently showed evidence of grazing, with either holes or entire ends of blades missing. The tendency of *Idotea* to consume both epiphytes and seagrasses may explain why seagrass biomass did not increase in the presence of *Idotea*, despite reduced epiphyte biomass. In contrast, equivalently low epiphyte biomass was associated with significantly higher seagrass biomass in the presence of *Phyllaplysia* alone. Consumption of seagrass by *Idotea* when epiphyte biomass is low may also explain the absence of a seagrass response to grazer polyculture, despite the presence of *Phyllaplysia*. Alternatively, the positive effect of *Phyllaplysia* on seagrass biomass may be absent in grazer polyculture because of lowered *Phyllaplysia* densities in these treatments due to our substitutive experimental design. Overall, our results highlight that although the effects of individual grazer species vary, collectively grazers exhibit strong top-down control of epiphyte biomass.

Our mesocosms did not include predators of grazers, so we did not test the possibility that increased refuge (e.g. due to higher shoot density or biomass) would lead to greater abundance or biomass of grazers in seagrass polycultures. Differential susceptibility to or tolerance of predation among grazer species could also lead to grazer species diversity effects that were not tested for here (e.g. Duffy et al. 2005). Further studies including higher trophic levels are needed to test additional mechanisms by which seagrass genotypic identity/diversity and grazer species diversity interact to influence seagrass communities.

This study was motivated by a lack of information regarding the reciprocal effects of diversity at multiple trophic levels. Although there was no interaction between grazer species diversity and seagrass genotypic diversity in our experiment, the effects of genotypic diversity on overall seagrass and grazer biomass did vary depending on the grazer species present. This result underscores the need to consider multiple trophic levels in diversity manipulations, as has been stressed by others (Duffy et al. 2007). Further, it confirms that genotypic diversity as well as identity can be important for key population- and community-level parameters such as seagrass and grazer biomass. Given the predominance in marine systems of habitat-providing species similar to seagrasses (e.g. kelps, corals, salt marsh grasses), the strong role of consumer control of producer biomass (Paine 2002), as well as changes in consumer abundance and diversity in these systems (Jackson et al. 2001, Duffy 2002, Byrnes et al. 2007), the phenomena we describe here may be widespread.

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