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# Consumer diversity mediates invasion dynamics at multiple trophic levels

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Theory and recent experiments, mostly focused on plants, indicate that biodiversity can reduce invasion success, but diversity effects on mobile animal invasion have received little attention. We tested effects of mobile crustacean grazer diversity (species richness) on the establishment of invaders at multiple trophic levels in flow-through seagrass mesocosms. On average, increasing diversity of resident grazers reduced population growth and biomass of experimentally introduced grazers. This increase in invasion resistance was concurrent with reductions in food and habitat availability and increases in resident density, paralleling previous results with plants. In many cases, mixtures of resident species resisted invasion better than did any single resident species, arguing that interactions among residents, rather than a sampling mechanism, explained diversity effects on invasion. Higher grazer diversity also generally reduced biomass of naturally recruiting invertebrates and algae and shifted epiphytic community dominance from algae to sessile invertebrates. Exploitation competition, then, appears to contribute to the diversity effect on invasion in both plant and animal systems. Our results further suggest that resident competitive advantage may also be at work in multi-trophic level systems. Thus, negative effects of local diversity on invasion appear general, and trophically mediated processes can also strongly influence invader success and identity in multi-trophic level systems.

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Invasions are one of the primary threats to endangered species, community structure, and ecosystem functioning (Vitousek et al. 1996, Wilcove et al. 1998, Mack et al. 2000, Pimentel et al. 2000). Several community properties, including species richness and species composition, can influence a community's resistance to invasion (Levine and D'Antonio 1999, Alpert et al. 2000, Miller et al. 2002, Brown and Fridley 2003). Elton (1958) originally proposed that communities with higher species richness are more stable and therefore less vulnerable to invasions. Recent theory has built on Elton's arguments, suggesting that species-rich communities should be less invasible than depauperate communities because niche differences among resident species result in greater overall resource use, leaving fewer resources for invaders (MacArthur 1970, Naeem et al. 2000, Tilman 2004). The relationship between diversity and invasibility has, however, continued to resist generalization. For example, while most local-scale experiments have found that invasibility decreases with plot richness, the opposite relationship has been found in both models and larger-scale observational studies (Levine and D'Antonio 1999, Levine 2000, Hector et al. 2001, Fridley et al. 2004).

Despite strong interest in the relationship between biodiversity and invasibility, empirical research has been conducted in a limited number of systems, primarily terrestrial plant assemblages and aquatic microcosms. Although pioneering experiments on this problem were

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conducted in a marine fouling community (Stachowicz et al. 1999, 2002), work in marine systems is otherwise extremely limited. This is despite widespread invasion pressure on marine ecosystems from ballast water exchange, ship hulls, and aquaculture (Ruiz et al. 2000, Naylor et al. 2001, Wonham et al. 2001). Furthermore, most studies have focused on plants or other sessile organisms at basal trophic levels (but see Shurin 2000, Miller et al. 2002). Effects of consumer diversity on ecosystem structure and function, however, may be different from those of plant diversity (Duffy 2002, Holt and Loreau 2002, Naeem 2002). For example, competitive exclusion may be less frequent in mobile consumers than in sessile organisms (Peterson 1979), whereas interference competition may be more prevalent. Finally, like plants, consumers can affect habitat structure and resource availability for organisms at other trophic levels, which might mediate invasion dynamics at those levels via indirect effects. Yet few studies have examined effects of diversity at one trophic level on invasion success at other levels (McGrady-Steed et al. 1997, Duffy et al. 2003).

In this study, we examined how species richness and identity of native crustacean grazers affects establishment success of other native grazers and organisms at lower trophic levels in *Zostera marina* (eelgrass) mesocosms. Our experiment tested consumer effects on establishment by other native species both to explore processes of community assembly and as a model of diversity effects on invasion by non-natives. Several lines of evidence suggest that our approach using native “invaders” can also inform understanding of diversity effects on non-native invasion. First, the search for consistent ecological differences between “natives” and “non-natives” has been largely inconclusive (reviewed by Mack et al. 2000). In fact, regional-scale studies frequently find positive relationships between native and non-native richness (reviewed by Levine and D’Antonio 1999, Sax and Gaines 2003). These patterns suggest that the processes governing community structure in native species assemblages are often similar, on average, to those governing the incorporation of introduced species into native assemblages. A second line of support for our approach is that experiments testing plant diversity effects on invasion have found comparable results when using native and non-native species as experimental invaders (Crawley et al. 1999, Hector et al. 2001, Troumbis et al. 2002). Indeed, a long-term study of old-field succession concluded that “invasions by native and exotic species did not fundamentally differ” (Meiners et al. 2004). Consequently, “invasion dynamics” may be thought of as a specific subset of community assembly processes, and study of native species community assembly should help inform studies of exotic species invasion dynamics.

We employed two novel design components to examine the effects of biodiversity on invasion success. First, by using all possible resident: invader pairs drawn from a pool of four species, we tested the potential role of differing assembly sequence (priority effects, or resident competitive advantage) in mediating invasion dynamics. Second, by measuring success of both experimentally stocked grazer invaders and “volunteer” invaders that naturally recruited into the flow-through mesocosms, we tested the effects of mobile consumer diversity on invasion and establishment of a wide range of sessile and mobile taxa at different trophic levels.

## Methods

### Study system and experimental design

*Zostera marina* (eelgrass) is the most widespread and abundant marine macrophyte in the northern hemisphere, and it supports many commercially important species (Hemminga and Duarte 2000). The dominant primary consumers in many eelgrass beds are small crustacean mesograzers, which feed preferentially on epiphytic micro- and macroalgae and can have important indirect, positive effects on eelgrass (Neckles et al. 1993, Duffy et al. 2001). Numerous sessile invertebrates also frequently grow on eelgrass blades, and can have negative effects on the host macrophytes. Early settlement stages of some of these sessile invertebrates are consumed by mesograzers (Duffy and Harvilicz 2001, Duffy et al. 2003).

The experiment was conducted in outdoor, flow-through seagrass mesocosms on the VIMS Ferry Pier, York River estuary, Gloucester Point, Virginia, USA. The mesocosms were semi-transparent buckets filled with 13.5 l of water, fitted with 250-μm mesh drain holes and covered with a layer of neutral-density plastic screen to approximate natural light levels. The submerged mesocosm wall surface area available for colonization by invertebrates was approximately 0.2 $m^2$. Fifteen pre-weighed *Z. marina* shoots were planted in 8 cm of sand within the mesocosms. This eelgrass shoot density falls within the range observed locally (Orth and Moore 1986). Prior to planting, the shoots were spun 20 times in a salad spinner and then massed to determine an initial grass wet mass for each mesocosm.

We used four native grazers in the experiment: ampithoid (a mixture of *Ampithoe longimana* and *Cymadusa compta*) and *Gammarus mucronatus* amphipods, and *Erichsonella attenuata* and *Idotea baltica* isopods. The relative abundances of these four taxa fluctuate markedly in time and space, but usually comprise a large fraction of the mesograzer assemblage in York River seagrass beds (Duffy et al. 2001, Parker et al. 2001), and therefore are likely to be the most important potential competitors influencing invasion of other grazer species. The same four grazer taxa were used as invaders in the experiment. All of these crustaceans have sexual reproduction, overlapping generations and direct development, and all feed on epiphytic algae and associated detritus (Duffy et al. 2003). At summer temperatures, generation times in our system can be as short as three weeks for amphipods (Fredette and Diaz 1986) and one month for isopods (Kouwenberg and Pinkster 1985, Jormalainen and Tuomi 1989). *A. longimana* and *C. compta* are in the same family, with similar life histories and feeding, and are difficult to distinguish when alive, so they were stocked as one taxonomic unit.

Our experimental design sought to test the influence of resident grazer presence, species identity, and species richness on establishment of invaders. To do so, we established four simultaneous experiments, with parallel designs, to test invasion success by each of the four grazer species into communities containing the remaining three species (Fig. 1). For each of the four invading grazer species, we established five treatments spanning a range in resident grazer richness, including no grazers (controls), each of the three remaining species alone (resident monocultures), and all three remaining species together (resident mixtures). Each of these five resident assemblage treatments was then experimentally invaded by the designated invader species. Consequently, there were a total of 20 treatments, each replicated five times (100 mesocosms total). Treatments were randomly assigned to one of ten large tanks and one of 12 positions (mesocosm) within that large tank.

Mesocosms were stocked with the resident communities on 23 July 2002. With the exception of the grazer-free controls, 30 individual reproductively mature adult grazers were placed in each mesocosm (30 of a given species for monocultures, and 10 of each species for mixtures). Since roughly half of the grazers stocked were adult females carrying embryos, populations began to grow immediately and rapidly. We allowed grazer populations to grow for four weeks, by which time a previous experiment showed that grazers reached carrying capacity (Duffy and Harvilicz 2001). At that point we "invaded" each mesocosm with ten reproductively mature adults of the designated invading species. After another month, all organisms retained by a 0.5-mm sieve were harvested. During this time, invader density increased by several- to 100-fold in controls, and some invasions failed completely (all invading individuals died, see Results). Nearly all of the planted eelgrass was consumed at the end of this 8-week period in a few mesocosms, so the experiment was terminated and harvested at this time to prevent population crashes. Note that the loss of grass biomass over the course of the experiment is not necessarily a mesocosm artifact; *Z. marina* often disappears during the late summer months in the York River estuary as well (pers. obs.).

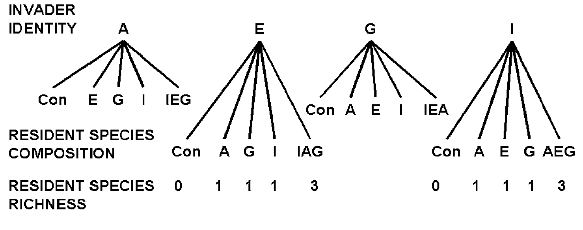

Fig. 1. Experimental design. A = ampithoids, E = *Erichsonella attenuata*, G = *Gammarus mucronatus*, I = *Idotea baltica*, Con = control (no residents). Each of the 20 treatments was replicated 5 times. Invaders were introduced one month after residents.

The mesocosms were continuously replenished with filtered York River water. The filtration system (pool sand filter +150 μm-mesh) excluded most juvenile amphipod and isopod grazers, but allowed passage of microscopic propagules of other invertebrates and algae. We refer to organisms that recruited into the tanks via the flow-through seawater system as "volunteer invaders". These were allowed to recruit throughout the experiment.

Prior to stocking experimental invaders (at 4 weeks) and at the end of the experiment (8 weeks), we estimated biomass of epiphytic algae by measuring epiphytic chlorophyll. Algae were negligible on the blades at the beginning of the experiment. Algae were scraped off of three haphazardly chosen blades from each mesocosm, pooled, collected on a glass fiber filter, and extracted in 20 ml of 90% acetone at −20°C for 24 h. Chlorophyll a was determined spectrophotometrically (Parsons et al. 1984) and normalized to leaf blade area.

At the end of the experiment, all epifaunal invertebrates, algae and eelgrass retained by a 0.5 mm mesh sieve were separated, identified, dried to constant mass, ashed at 450°C, and massed again. Amphipod and isopod grazers were separated into size classes using a stack of nested sieves, identified, and counted. Ash-free dry mass (AFDM) of amphipods was estimated using these size class data and empirically derived relationships between crustacean body size and biomass (Edgar 1990). Isopods did not uniformly size-fractionate through sieving, so were ashed and massed directly.

For stocked invaders, invasion success was measured as net invader population growth (final abundance/initial abundance) and final biomass. For volunteer invaders, invasion success was estimated as final abundance or final biomass.

## Statistical analyses

Our primary interest was testing the influence of resident diversity on invasion success. For statistical purposes, the five resident treatments invaded by a given grazer species were considered one experiment and analyzed with a

1-way, fixed-factor ANOVA. Thus, separate one-way ANOVAs were conducted for each of the four parallel experiments invaded by a different species. We could not use a single ANOVA design for the entire experiment because identity of resident species necessarily differed systematically and non-independently among invader treatments, and would have rendered such an analysis non-orthogonal. Each of the four ANOVAs tested the effects of resident grazer presence, identity, and species richness on invasion success as follows. Again, each experiment included five levels of resident community (Fig. 1): control (no grazer residents), three resident monocultures, and one resident mixture. For each of the four experiments, we partitioned the treatment sum of squares (SS) from the ANOVA into two orthogonal a priori contrasts, after Duffy et al. (2005): (1) the overall effect of resident grazers was tested as the contrast of grazer-free controls vs. the remaining four grazer treatments (three monocultures and one mixture, contrast $DF = 1$); (2) the effect of resident species richness was tested as the contrast of the resident mixture vs. the remaining three monocultures (contrast $DF = 1$); this tests whether or not the mixture of resident species was more resistant, on average, than the monocultures. Since the variances in our model are additive, after these two contrasts, the only variation remaining that is due to the treatment is variation among the monocultures. Consequently, we used this portion of the treatment SS remaining after accounting for the previous two contrasts to calculate an F-statistic ($DF = 2$) for the effect of resident identity. This identity F-statistic tests whether resident species differ in their ability to resist invasion. Once each of the four experiments had been analyzed, we obtained a single estimate, across all four experiments, of the overall influence of resident presence, richness, and identity on invasion success by combining the p-values for each contrast across the four experiments using the approach of Sokal and Rohf (1995, pp. 794–797).

The analyses above test whether richness and identity of residents affect invasion, but do not indicate which resident species are responsible, nor whether richness effects result from sampling or complementarity (Huston 1997, Hector 1998). To determine whether particular resident species dominated effects on invasion success (a "sampling effect"), we ran a separate multiple regression for each of the four stocked invader species, including all five treatments which that species invaded. Each regression modeled invader population growth as the response, and used the final abundance of each of the three remaining (resident) species as predictors. Both response and predictor variables were transformed by $\log_{10}(x)$ to meet the assumption of homogeneous variances. The predictors were not correlated (maximum absolute value of significant $r = 0.205$). To stringently assess whether richness effects derived from interactions among species, we calculated $D_{max}$ for invasion resistance. $D_{max,}$ the overyielding criterion, measures the difference between the observed total response in mixture (yield) and the maximal response in monoculture, as a proportion of the maximal response in monoculture (Loreau 1998).

Competition for food and substratum may mediate resident effects on invasion. To estimate the strength of exploitation competition among grazer species, we measured the loss of available habitat and surface area for growth of algal food as loss of eelgrass to grazer consumption. Final eelgrass AFDM was subtracted from initial AFDM, the latter estimated as $0.097 \times$ initial wet mass (g). We tested whether eelgrass biomass, resident grazer biomass, and resident grazer density differed in mixtures vs monocultures using one-way ANOVAs with a priori contrasts for each of the four invader experiments, as described above. As an index of resource limitation, resident density was calculated as mg resident grazers/(mg macroalgae + eelgrass).

Since the analyses just described treated the four invader species separately, they could not rigorously test the overall influence of invader identity, or the interaction of resident and invader identity, on community development. To do so, we conducted two-way ANOVAs, using only the resident monoculture treatments, with factors resident grazer identity (fixed factor, 4 levels) and stocked invader identity (fixed factor, 4 levels). There were five replicates of each treatment combination. Our experiment did not include treatments with residents and invaders of the same species (e.g. *Erichsonella* invading mesocosms with resident *Erichsonella*) because it would have been impossible to determine invasion success in such a combination. Therefore, we used data from the controls (e.g. *Erichsonella* invading a community initially free of grazers) for these treatment combinations in the ANOVAs. As invaders reached high population densities during their four weeks in the mesocosms (Results), we considered that these initially grazer-free controls should closely approximate the state of mesocosms that had had residents of the same species for the full eight weeks of the experiment. These two-way ANOVAs were conducted only for volunteer invaders and community-level responses (i.e. not for population growth of the stocked invader species or for density or biomass of the resident grazers).

Finally, we explored whether the sequence of community assembly influenced the outcome of competition by examining whether resident grazer species had a consistent competitive advantage over invaders. To do so, we used a continuous version of the Bradley-Terry paired comparison model that was developed to detect and estimate home field advantages in team competitions (Harville and Smith 1994). We considered each mesocosm with a single resident species and single invader species as a game (12 matchups, each replicated five times; Fig. 1), and used the difference in performance between the residents (home team) and the invaders (visiting team) as the difference in score. By comparing the fit of the following model to one without a home field advantage term using Akaike's information criterion (AIC), we were able to determine whether residents had a competitive advantage over invaders:

$$y_{ijk} = R_{resident\ j} - R_{invader\ i} + H_j + \varepsilon_{ijk}$$

$Y_{ijk}$ is the difference in net population growth between species j and species i. $R_{resident\ j}$ and $R_{invader\ i}$ are dummy variables for the resident competitive abilities ($R_j = 1$ when the species is a resident, $-1$ when it is an invader, and 0 when it is not present in a mesocosm; $R_i = 1$ when the species is an invader, $-1$ when it is a resident, and 0 when it is not present). $H_j$ is a dummy variable for the home field advantage of species j ($H_j = 1$ when species j is a resident, 0 otherwise). By assuming that the errors ($\varepsilon_{ijk}$ where k is the number of replicates of each resident:invader matchup) are normally distributed, this can be fit as an ordinary regression model (Harville and Smith 1994, Clarke and Norman 1995). We fit this regression model to several measures of differences in competitive ability between residents and invaders ($y_{ijk}$): difference in net population growth (final abundance/initial abundance), final biomass, final biomass with a handicap for residents (final biomass divided by 2), and final abundance. Using the sums of squares for the two models, we tested the null hypothesis that home field advantage = 0. The formula for the F-statistic for this hypothesis test is described in Harville and Smith (1994). We used SAS (SAS 2001) to fit the regression models (Agresti 2002, Weiss, pers. comm.).

## Results

The experimental gradient in resident grazer diversity was maintained in the final grazer abundances (mean Shannon-Weaver index: controls = 0.096; ampithoids = 0.171; *E. attenuata* = 0.310; *G. mucronatus* = 0.118; *I. baltica* = 0.204; mixtures = 0.354). This diversity gradient overlaps the range found in York River seagrass beds (mean = 0.378, range = 0.125–0.594) (Duffy et al. unpubl.). All four species of stocked invaders established populations in the initially grazer-free control treatments, indicating that the invading density was sufficient. Thirty-eight species of invertebrates, in addition to the stocked amphipods and isopods, invaded the mesocosms during the 8-week experiment, including anemones, bivalves, crabs, gastropods, nudibranchs, polychaetes, and tunicates. Seven species of macroalgae and two macroscopically different mixed microalgal assemblages (predominantly green or predominantly brown diatoms) colonized the experiment.

Both richness and identity of resident grazers strongly affected population growth and biomass of invading grazers (Fig. 2, Table 1). The overall effect of resident richness (i.e. combining the four experiments with different experimental invaders) was significant for both invader population growth ($p < 0.025$) and invader biomass ($p < 0.001$; Table 1). Resident richness also significantly reduced invasion success in the separate

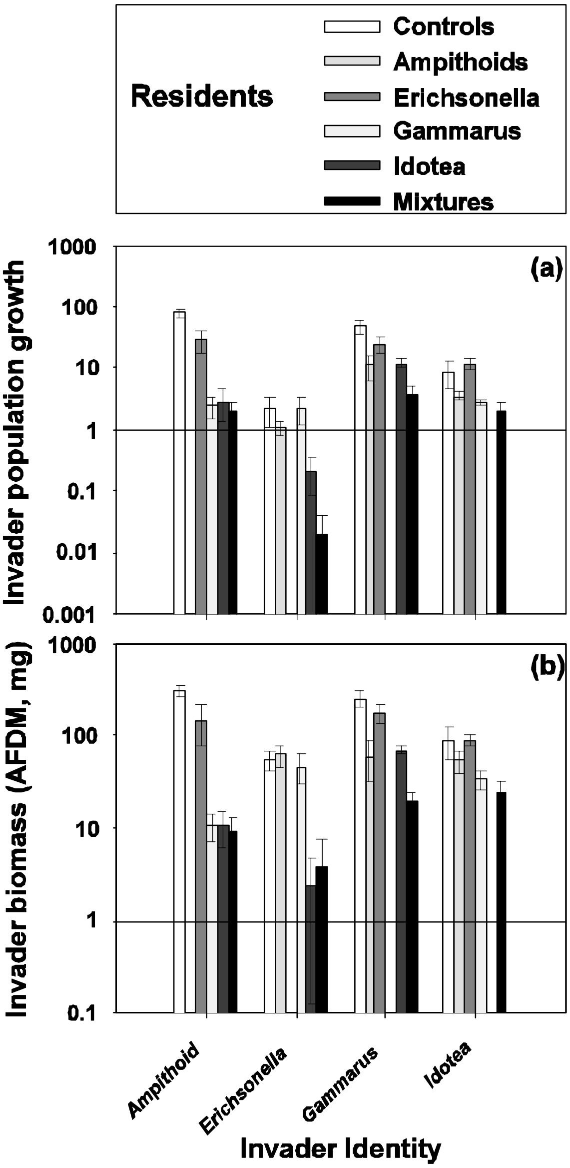

Fig. 2. Effects of resident grazer identity and richness on (a) population growth and (b) final biomass of experimentally stocked grazer invaders. Controls (white bars) had no stocked residents prior to invasion. Mixtures (black bars) contained all three species other than the invader. Population growth = $N_{final}/N_{initial}$. The line at $y = 1$ indicates the threshold of invasion failure (net negative population growth). Error bars show ±1 SE ($n = 5$). See Table 1 and 2 for statistical analysis.

Table 1. Effects of grazer presence, species richness, and identity on invasion success and community development, pooled across all four invaders. Letters in last three columns indicate which invaders had significant effects in separate analyses by invader species (Appendix A), and correspond to the first letter of the invading genus or family. Letters in italics indicate marginally significant effects (p =approximately 0.05).

| Response variable | Chi square of combined p values | | | Significance of chi-square | | | Invader identity | | |
|---|---|---|---|---|---|---|---|---|---|
| | | ( −2 ΣIn(p)) | | | | | | | |
| | Grazers | Richness | Identity | Grazers | Richness | Identity | Grazers | Richness | Identity |
| Invader population growth | 19.16 | 19.55 | 27.60 | **<0.025** | **<0.025** | **<0.001** | A | E,I | E,I |
| Invader biomass | 35.27 | 31.58 | 19.79 | **<0.001** | **<0.001** | **<0.025** | A,G | E,G,I | G,I |
| Volunteer richness | 2.46 | 4.33 | 4.93 | NS | NS | NS | | | |
| Volunteer biomass | 17.28 | 15.44 | 24.75 | **<0.05** | NS | **<0.01** | E,G | E | A,E |
| *H. solitana* biomass | 40.32 | 23.39 | 43.57 | **<0.001** | **<0.01** | **<0.001** | A,E,I | E,I | *A*,E,G,I |
| *M. manhattensis* abundance | 43.91 | 34.39 | 27.07 | **<0.001** | **<0.001** | **<0.001** | A,E,G | A,E | E,G |
| Algae richness | 35.75 | 11.00 | 14.22 | **<0.001** | NS | NS | E,G,I | | *I* |
| Algae biomass | 31.79 | 20.45 | 20.10 | **<0.001** | **<0.01** | **<0.01** | E,G,I | *G*,I | *I* |
| Epiphytic chlorophyll | 44.26 | 4.46 | 35.41 | **<0.001** | NS | **<0.001** | A,G,*I* | | A,G |
| Resident biomass | NA | 23.33 | 9.35 | NA | **<0.01** | NS | | A,E | |
| Change in *Zostera* biomass | 12.84 | 23.46 | 28.62 | NS | **<0.01** | **<0.001** | A | A,E | A |
| Resident density | NA | 15.38 | 18.59 | **<0.0001** | NS | **<0.025** | E,I | E | *G*,I |

analyses for three of the four invaders (Appendix A). This negative effect of resident species richness on invasion was generally consistent despite clear variation in invasion success among the four stocked invader species (Fig. 2). All four mixtures overyielded, or resisted invasion better than the maximal monoculture ($D_{max}$ was greater than zero). Within the initially grazer-free controls, invading isopods (*E. attenuata* and *I. baltica*) reached significantly lower final biomass and population growth than the amphipods (ampithoids and *G. mucronatus*; one-way ANOVA $p < 0.001$, followed by Tukey's tests; Fig. 2).

The presence of grazers reduced the total biomass of volunteer epifaunal invertebrates (those invading through the seawater supply, Fig. 3a, Table 1). The aggregate biomass of these volunteer invaders was not significantly reduced at higher resident grazer species richness but was strongly affected by resident identity (Table 2). In contrast, the number of volunteer invertebrate species was unaffected by the presence, identity, or richness of resident grazers (Fig. 3c, Table 2).

Of the five most frequent volunteer invaders, all were significantly reduced by the presence of grazers, and two were affected by the characteristics of the resident grazer community. Invasion success (biomass) of the sea slug *Haminoea solitana*, the second most frequent volunteer and the only volunteer herbivore, was reduced by resident grazer richness and strongly affected by resident grazer identity (Fig. 3e, Table 1). The abundance of *Molgula manhattensis*, a solitary tunicate and the fourth most frequent invader, was significantly reduced by resident grazer richness and affected by resident grazer identity (Fig. 3f, Table 1). The first and third most frequent volunteers, *Hydroides dianthus*, a tube-dwelling polychaete, and *Corophium volutator*, a detritivorous amphipod, were unaffected by resident richness or identity (data not shown).

Grazers significantly reduced biomass and species richness of invading algae, relative to initially grazer-free controls, although resident *G. mucronatus* tended to increase algal biomass (Fig. 3b, 3d). Algal biomass was also significantly reduced by resident grazer richness and strongly affected by resident grazer identity (Fig. 3b, 3d; Table 1, 2, Appendix 1).

Identity of the invading grazer species significantly affected only two of the eight response variables examined: the invasion success of one of the volunteer invaders, *Molgula manhattensis* (Table 2) and the number of successfully invading algal taxa (Table 2). Interactions between resident and invader identity were highly significant for two of the volunteer invaders, *H. solitana* and *M. manhattensis* (Table 2).

Multiple regressions conducted separately for each of the four stocked invader species showed that reduced success of *E. attenuata* invasions was attributable primarily to *I. baltica* (overall regression $p < 0.001$,

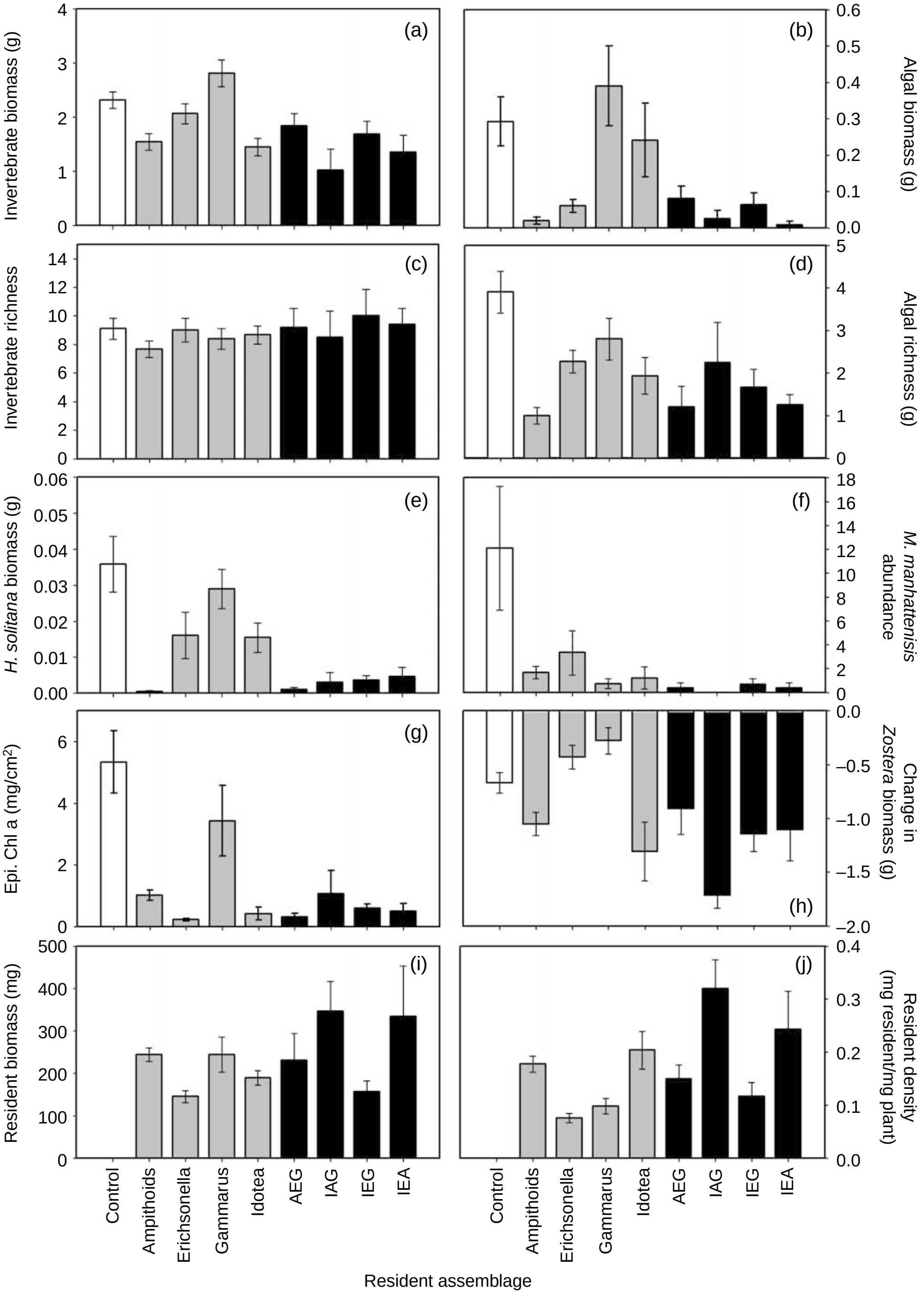

Fig. 3. Effects of resident grazer identity and richness on naturally recruiting ("volunteer") species and on resource availability. 1st row: Total ash-free dry biomass of naturally recruiting (a) invertebrates and (b) algae. 2nd row: Taxon richness of naturally recruiting (c) invertebrates and (d) algae. 3rd row: Two of the five most abundant naturally recruiting invertebrates, (e) *Haminoea solitana*, a gastropod grazer, and (f) *Molgula manhattensis*, a solitary tunicate. 4th row: Resource availability: (g) Final epiphytic chlorophyll a, normalized to leaf blade area and (h) loss of eelgrass biomass. 4th row: Resident grazer community (i) biomass and (j) density. Error bars show ±1 SE. Data for controls (n = 20) and resident monocultures (n = 15) are pooled across invader species while data for each resident mixture composition (and therefore each invader, n = 5) are presented separately to allow the reader to compare a response in the monoculture of a given resident to the response in the mixture missing that species. See Table 1 and 2 for statistical analysis.

Table 2. Interactive effects of resident identity and invader identity. Data from monocultures only (Fig. 1). MS and p-values are from 2-way ANOVAs of resident and invader identity. Bold values denote significance at the 0.05 level.

| Response variable | Resident identity (df = 3) | | Invader identity (df = 3) | | Resident × invader (df = 9) | | Overall model | | |
|---|---|---|---|---|---|---|---|---|---|
| | MS | P | MS | P | MS | P | MS | P | MSE |
| Volunteer richness | 3.79 | 0.7347 | 3.52 | 0.7562 | 3.99 | 0.9026 | 3.85 | 0.9626 | 8.88 |
| Volunteer biomass | 0.21 | **0.0012** | 0.01 | 0.8938 | 0.07 | 0.0638 | 0.09 | **0.0084** | 0.04 |
| *H. solitana* biomass | 3.09 | **0.0001** | 0.45 | 0.0897 | 1.17 | **0.0001** | 1.41 | **0.0001** | 0.20 |
| *M. manhattensis* abundance | 9.49 | **0.0001** | 31.42 | **0.0001** | 31.42 | **0.0001** | 14.01 | **0.0001** | 0.81 |
| Algae richness | 2.00 | **0.0348** | 3.36 | **0.0031** | 1.05 | 0.1341 | 1.70 | **0.0043** | 0.66 |
| Algae biomass | 6.23 | **0.0001** | 1.01 | 0.2258 | 1.61 | **0.0214** | 2.41 | **0.0002** | 0.68 |
| Epiphytic chlorophyll | 85.04 | **0.0001** | 0.21 | 0.9957 | 17.08 | 0.0893 | 27.30 | **0.0019** | 9.59 |
| Change in *Zostera* biomass | 3.33 | **0.0001** | 0.43 | 0.3174 | 0.49 | 0.2165 | 1.05 | **0.0014** | 0.36 |

adjusted $R^2 = 0.556$; *I. baltica* $p < 0.001$; other residents $p > 0.716$), and ampithoid invasion was marginally negatively affected by *G. mucronatus* (overall regression $p = 0.080$, $R^2 = 0.159$; *G. mucronatus* $p = 0.056$; other residents $p > 0.172$). There were no significant effects of any particular species on *G. mucronatus* and *I. baltica* invasions.

Summed biomass of all resident grazers, i.e. potential competitors for the invaders, was significantly higher, on average, in grazer mixtures than in monocultures (Fig. 3i, Table 2). Habitat and substrate availability were reduced at high resident richness, as eelgrass lost significantly more biomass, on average, in mixtures than in the monocultures. In contrast, eelgrass mass loss did not differ, on average, between monocultures and controls (Fig. 3h, Table 2). As an index of resource limitation for invading grazers, we examined density of resident grazers per gram plant. Resident density was marginally non-significantly greater in mixtures than in monocultures on average (Fig. 3j, Table 2), and was also affected by resident species identity. The resident densities measured in our mesocosm experiment are comparable to those found in the field if grazer abundance is normalized to all available surface area, including mesocosm walls (mean across treatments = 0.067 mg residents $cm^{-2}$ area, field mean = 0.11 mg $cm^{-2}$ eelgrass), but are higher than the maximum observed field density if only plant surface area is considered (mean across treatments = 0.328 mg $cm^{-2}$; field max = 0.20 mg $cm^{-2}$; field data from Duffy and Harvilicz 2001).

The fit of the regression model including home-field advantage was highly significant, explained more than 50% of the variance in the competitive outcomes between residents and invaders, and was better than that of the model without home-field advantage, regardless of the competition measure used (Table 3). Residents had a significant competitive advantage over invaders (see F test for comparing model to null model without home field advantage, Table 3). In other words, for a given grazer species, performance against a given competitor was greater when the focal species was a resident than when it was an invader. We also compared invader biomass in controls (no competitors, 4 weeks of population growth) to resident biomass in monocultures (competitors for 4 weeks out of 8 weeks of population growth) to determine whether invader populations had time to reach carrying capacity in the absence of competitors. Amphipod populations that invaded control treatments reached population sizes equal to those of their conspecifics that had been residents in monocultures for 8 weeks (invader biomass, resampling two-tailed $p = 0.0896$ for ampithoids, $p = 0.8569$ for *G. mucronatus*), suggesting that the 4-week invasion period was sufficient for amphipods to reach carrying capacity in the absence of competitors. Isopods, however, had significantly lower population sizes in controls than in

Table 3. Regression models and hypothesis tests for resident competitive advantage. F tests for comparing models were calculated as: $F(\mathrm{I\ vs\ 0}) = (SSE_0 - SSE_1)/((SS_1 - SS_2 + SSE_2)/56)$ and $F(\mathrm{II\ vs\ 0}) = (SSE_0 - SSE_2)/((SSE_2)/53)$, after Harville and Smith (1994). Bold values denote significance at the 0.05 level.

| | Model | | | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | No resident advantage (0) (null hypothesis) | | | Resident advantage (I) same for all species | | | | | Resident advantage (II) diff. for each species | | | | |
| | Regression | | | Regression | | | F test (I vs 0) | | Regression | | | F test (II vs 0) | |
| Response variable | R2 | P | AIC | R2 | P | AIC | F (1,50) | P | R2 | P | AIC | F (?,?) | P |
| Population | | | | | | | | | | | | | |
| Growth | 0.438 | <0.0001 | 295.9 | 0.474 | **<0.0001** | 293.9 | 3.91 | 0.054 | 0.531 | **<0.0001** | 293 | 2.65 | **<0.05** |
| Biomass | 0.198 | 0.0053 | 630.9 | 0.753 | **<0.0001** | 562.3 | 125.68 | **<0.0001** | 0.761 | **<0.0001** | 566.2 | 31.23 | **<0.0001** |
| Biomass w/ resident handicap | 0.105 | 0.0935 | 567.8 | 0.702 | **<0.0001** | 504 | 111.83 | **<0.0001** | 0.776 | **<0.0001** | 497.9 | 35.32 | **<0.0001** |
| No. of indiv. | 0.164 | 0.0161 | 698.7 | 0.696 | **<0.0001** | 640.1 | 97.71 | **<0.0001** | 0.745 | **<0.0001** | 635.4 | 30.25 | **<0.0001** |

monocultures (resampling one-tailed *E. attenuata* p = 0.0004, *I. baltica* p = 0.0007), suggesting that they did not reach carrying capacity during the 4-week invasion period. Although these data advise caution in inferring resident competitive advantage, they suggest it is likely, at least for the amphipods.

## Discussion

We found that resident grazer species richness significantly decreased establishment of other mobile grazers, including both experimentally stocked amphipods and isopods as well as "volunteer" sea slugs that recruited naturally from planktonic larvae. This pattern was consistent for three of the four experimental grazer invaders analyzed separately, and was strongly significant when results were pooled across the four invader species. Moreover, multiple regressions revealed that no single resident species dominated the inhibitory effects on invaders, strongly suggesting that invasion resistance was a general effect of diverse resident assemblages rather than a sampling effect due to presence of a particularly strong interactor. This consistency is particularly noteworthy given the marked differences among invader species in potential population growth rates, as observed in competitor-free controls (Fig. 2a), and the differences among resident species in ability to resist invaders. Thus, our finding that mobile consumer diversity reduced invasion success of other species at the same trophic level appears robust.

A second line of evidence for the generality of diversity effects on invasion in our experiment comes from naturally recruiting "volunteer" invaders. Grazer species richness significantly reduced the success of two of the most frequent volunteer invaders, one of which (*H. solitana*) is a mobile grazer and therefore a potential competitor, and marginally reduced the aggregate biomass of all naturally recruiting invaders. Most of these volunteers were sessile organisms probably affected by grazers ingesting or disturbing their newly settled recruits. More diverse grazer assemblages tended to shift the system from algal dominance towards sessile invertebrate dominance, as seen before (Duffy et al. 2003).

The most straightforward explanation for reduced invasion success at high resident richness in our experiment appears to be stronger competition for resources, namely food and habitat. Several lines of evidence support this possibility. First, as expected, invasion success of stocked grazers was greater in the competitor-free controls (Fig. 2), suggesting that competition mediated invasion success, at least in part. Second, as in other studies where more diverse assemblages use resources more fully (Tilman 1997, Naeem et al. 2000, Duffy et al. 2003), food consumption tended to be greater in the grazer mixtures than in monocultures.

Specifically, algal biomass was significantly reduced by grazer richness, and both macro- and micro- algal biomass were quite low in all mixtures relative to controls, confirming that consumption pressure was high (Fig. 3b, 3g, Table 2). Intense consumption in grazer mixtures is further indicated by the significantly greater loss of eelgrass biomass in these treatments compared with monocultures (Fig. 3h, Table 2), since grazers usually only consume eelgrass when epiphytic algae, their preferred food source, is limited (Jernakoff et al. 1996, Valentine and Duffy in press). These results for mobile consumers parallel those from both plant and zooplankton assemblages, where species richness and aggregate biomass of native "invading" species decreased with increasing species richness of residents (Shurin 2000, Kennedy et al. 2002, Troumbis et al. 2002). Finally, habitat availability, i.e. eelgrass leaf area, was also reduced by grazer richness. Seagrass blades simultaneously serve as surfaces for feeding, resting, building tube dwellings, and reproducing as well as substrate for the mesograzers' main food source, epiphytic microalgae. There is some evidence for behaviorally mediated competitive exclusion among eelgrass-associated grazers when plant habitat is limiting (Nagle 1968), and both field experiments and energetic estimates suggest that mesograzer production often may be limited by diffuse competition in the field (Edgar 1990, 1993). Eelgrass biomass was lowest, and resident density tended to be highest, in mixtures (Fig. 3h, 3j, Table 2). This parallels findings of many plant studies that more diverse assemblages have more neighboring individuals or greater biomass (Naeem et al. 2000, Kennedy et al. 2002, Troumbis et al. 2002), presumably leaving less room and resources for invaders. Thus, the pattern emerging from our data on mobile consumers and previous studies is that resource limitation and competition are greater in more diverse assemblages.

The importance of resident density in influencing invasion success in our experiment is further supported by evidence of resident competitive advantage, or the advantage conferred simply by being there first. We suspected that residents might have such an advantage in our system because at least two of the grazers, *I. baltica* and *G. mucronatus*, consume juveniles of other grazer species as well as conspecifics (J. G. Douglass, unpubl.). We found that residents did have a competitive advantage: each species had significantly greater success as a resident than as an invader, regardless of which species it was paired with (Table 3). Although this apparent resident competitive advantage might be explained by invaders having insufficient time to reach their maximum population size, this seems unlikely. Only isopod invaders failed to reach carrying capacity in the absence of competition after four weeks of growth, suggesting that isopod invaders might be at a disadvantage. Yet half of the match-ups were isopod-isopod. Furthermore, our calculation of the difference between resident performance and invader performance could be considered biased (conservatively) towards invaders, since we divided final population size by initial population size (30 for residents and 10 for invaders) and populations increased by more than an order of magnitude. Finally, we found significant resident competitive advantage even when we "handicapped" residents by halving their final biomass (Table 3). Our demonstration of resident competitive advantage is consistent with considerable theoretical (Lotka 1932, Case 1990) and empirical (Shurin 2000, reviewed by Morin 1999) evidence that the outcome of competition and/or invasion can depend on initial conditions, including relative abundances and the order of arrival. This evidence of resident competitive advantage lends support to the idea that the diverse assemblages resisted invasion due to higher aggregate resident biomass and density, in keeping with Elton's (1958) original hypothesis.

The invasion resistance that we observed was not primarily mediated by the presence of a single species – that is, by a sampling effect – as it has been in some studies (McGrady-Steed et al. 1997, Hodgson et al. 2002). Several pieces of data confirm that no one resident species dominated the inhibition of invasion in our study. First, although *I. baltica* was the resident species most resistant to grazer invasion in monoculture (Fig. 2), it did not dominate the mixtures where it was present. Second, every resident species used in the experiment was absent from one of the 3-species resident mixtures. If invasion resistance was primarily conveyed by one species, then the mixture lacking that species should have lower invasion resistance relative to the other three mixtures. This was not the case for most variables (Fig. 3). Perhaps most importantly, multiple regressions examining the dependence of invader population growth on the abundance of each resident species were only significant for two of the four stocked grazer invaders, and the resident species with the greatest effect was different in these two cases. Finally, $D_{max,}$ a stringent index for overyielding, was positive for all four mixtures.

Experiments such as ours have potential implications for understanding how native biodiversity influences exotic invasion. These implications depend, however, on the assumption that the native species used as "invaders" are suitable proxies for exotic invaders. The course of any particular real invasion will of course be influenced by the idiosyncratic traits of both residents and invader. Nevertheless, several lines of evidence suggest that native and non-native species often establish in communities by similar mechanisms, and thus that using non-natives as invaders would not have changed the outcome of our experiment dramatically. First, searches for consistent trait differences between natives and non-natives, with the exception of organisms that invade unaccompanied by predators or pathogens, have been largely unsuccessful (reviewed by Mack et al. 2000). Second, the mechanisms apparently responsible for the richness effect on invasion in our experiment, reduced food and habitat availability and increased density of competitors, should similarly reduce success of native and non-native grazers. Third, our four native grazer invaders had different population growth rates and degrees of omnivory, but were similarly deterred by richness of co-occurring native grazers. Finally, most small marine crustaceans, in contrast to terrestrial insects, are generalists, and, at least in seagrass beds, are readily consumed by most predators (Edgar and Shaw 1995). Although we appreciate the importance of studying how specific non-native invaders infiltrate communities, these considerations suggest that studying invasion dynamics of native species can provide important insights into the more logistically and ethically difficult questions of non-native invasions.

More generally, our experiment suggests that some mechanisms hypothesized to explain diversity effects on invasibility and community assembly in plants also apply to mobile consumers, and thus may be general. Our results suggest that three mechanisms of diversity effects may be important in mediating invasion success. First, species richness can reduce invasion success of some invaders by decreasing resource availability at a given point in time through complementary resource use (in our experiment, food and habitat availability, Table 1). Second, species-rich communities can reduce invasion success of a diverse suite of invaders because they contain species that are better at deterring a particular invader (the sampling effect). For example, in our experiment, *H. solitana* was primarily deterred by ampithoid residents (Fig. 3e, Table 1). Across the whole experiment, the proportion of variance in invasion success explained by different components of the resident community (grazer presence, richness, and identity) also varied widely for the different invaders, suggesting that the best defense against invasion is a species-rich, intact community (data not shown). Finally, species-rich communities may stand a better chance of reducing invasion success through time by increasing average resource utilization through time (Davis et al. 2000, Davis and Pelsor 2001, Stachowicz et al. 2002). While our experiment does not test this, we note that our grazers show different seasonal abundance patterns (Duffy et al. 2001, Parker et al. 2001), which should produce more complete resource use through time as shown for space use by sessile invertebrates (Stachowicz et al. 2002). Our demonstration of resident competitive advantage highlights the importance of having competitors present, regardless of their size or competitive ability, to impede invasion.

In summary, as resident grazer diversity increased in the eelgrass system, food and habitat availability decreased, aggregate grazer biomass increased, and invasion success of both experimentally introduced grazers and naturally recruiting mobile (*H. solitana*) and sessile organisms was reduced. These effects could not be attributed to any particular resident species by way of a sampling effect. We found these significant effects of consumer species richness on invasibility despite using a low (albeit near natural) level of maximum diversity, studying invaders with different population growth capacities, and allowing trophic interactions and some natural recruitment to occur. Further work is necessary to determine the importance of invasion resistance conveyed by biodiversity relative to other factors, such as disturbance, resource availability, and propagule supply (Elton 1958, Crawley 1987, Huston 1994, Levine and D'Antonio 1999, Stohlgren et al. 1999, Davis et al. 2000, Levine 2000, Brown and Peet 2003). Our results, however, argue for the generality of a negative relationship between diversity and invasibility at the neighborhood scale, and they support straightforward and common mechanisms of exploitative resource competition as producing these relationships.

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Appendix 1: Effects of grazer presence, species richness, and identity on invasion success and community development for each of the four experiments (one for each invader) conducted concurrently. SS and p-values are from one-way ANOVAs for each invader, partitioned as described in the text. The total SS is the total sum of squares for the whole model (model SS+error SS).

| Response variable | Invader = Ampithoids | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|
| | Grazers (df = 1) | | Richness (df = 1) | | Identity (df = 2) | | Total | | |
| | SS | P | SS | P | SS | P | SS | P | MSE |
| Invader population growth | 11.765 | **0.0041** | 0.000 | 0.9981 | 7.465 | 0.1685 | 41.657 | **0.0118** | 22.427 |
| Invader biomass | 11.792 | **0.011** | 0.000 | 0.9917 | 9.234 | 0.1873 | 51.093 | **0.0255** | 1.503 |
| Volunteer richness | 0.645 | 0.8179 | 14.933 | 0.2746 | 2.533 | 0.8514 | 267.115 | 0.8221 | 249.200 |
| Volunteer biomass | 0.027 | 0.834 | 2.044 | 0.0787 | 8.290 | **0.0251** | 22.264 | **0.0108** | 11.903 |
| *Haminoea* biomass | 1.483 | **0.0085** | 0.544 | 0.0931 | 1.429 | **0.0554** | 7.214 | **0.0054** | 3.693 |
| *Molgula* abundance | 5.550 | 0.0854 | 16.041 | **0.0058** | 3.463 | 0.392 | 61.509 | **0.0182** | 35.774 |
| Algae richness | 0.018 | 0.907 | 2.743 | 0.1584 | 4.933 | 0.178 | 34.615 | 0.2389 | 26.933 |
| Algae biomass | 0.609 | 0.3994 | 2.691 | 0.0849 | 4.240 | 0.0714 | 24.739 | 0.0964 | 17.284 |
| Epiphytic chlorophyll | 107.620 | **0.0001** | 1.844 | 0.5434 | 16.287 | 0.0033 | 228.337 | **0.0014** | 101.477 |
| Resident biomass | NA | NA | 0.190 | **0.0078** | 0.010 | 0.9607 | 0.547 | **0.0571** | 0.356 |
| Change in *Zostera* biomass | 0.464 | **0.0263** | 0.921 | **0.0029** | 7.441 | **0.0001** | 10.581 | **0.0001** | 1.707 |
| Resident density | NA | NA | 0.005 | 0.7959 | 0.647 | **0.0573** | 1.970 | 0.0709 | 1.556 |

| Response variable | Invader = Erichsonella | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|
| | Grazers (df = 1) | | Richness (df = 1) | | Identity (df = 2) | | Total | | |
| | SS | P | SS | P | SS | P | SS | P | MSE |
| Invader population growth | 3.021 | 0.175 | 9.277 | **0.0232** | 11.825 | **0.0403** | 52.598 | **0.018** | 28.919 |
| Invader biomass | 8.575 | 0.0764 | 17.983 | **0.0138** | 8.780 | 0.2672 | 80.690 | **0.0263** | 2.442 |
| Volunteer richness | 6.422 | 0.4082 | 1.856 | 0.6545 | 0.133 | 0.9924 | 179.333 | 0.9102 | 170.600 |
| Volunteer biomass | 2.520 | **0.0354** | 3.179 | **0.0198** | 9.773 | **0.0019** | 24.567 | **0.0007** | 9.334 |
| *Haminoea* biomass | 0.703 | **0.0152** | 0.987 | **0.0052** | 4.365 | **0.0001** | 7.861 | **0.0001** | 1.878 |
| *Molgula* abundance | 23.849 | **0.0001** | 4.240 | **0.0001** | 40.275 | **0.0001** | 68.456 | **0.0001** | 0.927 |
| Algae richness | 41.408 | 0.0003 | 2.654 | 0.2753 | 0.933 | 0.4418 | 85.958 | **0.0042** | 39.950 |
| Algae biomass | 3.598 | **0.0457** | 1.560 | 0.1753 | 3.254 | 0.2287 | 23.166 | 0.0683 | 14.954 |
| Epiphytic chlorophyll | 8.249 | 0.3636 | 4.497 | 0.5002 | 36.743 | 0.2316 | 229.831 | 0.3104 | 180.855 |
| Resident biomass | NA | NA | 0.467 | **0.0013** | 0.125 | 0.1726 | 0.591 | **0.0047** | 0.445 |
| Change in *Zostera* biomass | 0.692 | 0.2329 | 3.347 | **0.0139** | 3.696 | 0.1078 | 16.263 | **0.0136** | 8.654 |
| Resident density | NA | NA | 0.260 | **0.0133** | 0.034 | 0.6022 | 0.788 | 0.0657 | 0.494 |

Appendix 1 (*Continued*)

| Response variable | Invader = Ampithoids | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|
| | Grazers (df = 1) | | Richness (df = 1) | | Identity (df = 2) | | Total | | |
| | SS | P | SS | P | SS | P | SS | P | MSE |
| Invader population growth | 0.354 | 0.5565 | 0.940 | 0.3414 | 0.618 | 0.1867 | 21.705 | 0.748 | 19.726 |
| Invader biomass | 1.593 | **0.0002** | 1.083 | **0.0011** | 0.935 | **0.0291** | 5.113 | **0.0001** | 0.075 |
| Volunteer richness | 0.010 | 0.9693 | 0.817 | 0.7283 | 8.533 | 0.4939 | 140.960 | 0.8371 | 131.600 |
| Volunteer biomass | 2.345 | **0.0299** | 0.404 | 0.3434 | 0.969 | 0.2795 | 12.302 | 0.11 | 8.583 |
| *Haminoea* biomass | 0.666 | 0.1357 | 0.047 | 0.6838 | 3.318 | **0.0092** | 9.539 | **0.0216** | 5.509 |
| *Molgula* abundance | 41.809 | **0.0001** | 1.405 | 0.3507 | 15.880 | **0.0338** | 89.852 | **0.0002** | 30.758 |
| Algae richness | 37.210 | **0.0014** | 3.750 | 0.2541 | 12.400 | 0.1519 | 107.760 | **0.0064** | 54.400 |
| Algae biomass | 8.060 | **0.0012** | 2.404 | **0.0536** | 4.084 | 0.095 | 25.978 | **0.0018** | 11.430 |
| Epiphytic chlorophyll | 188.376 | **0.0001** | 0.473 | 0.7483 | 5.439 | **0.0001** | 283.745 | **0.0001** | 89.456 |
| Resident biomass | NA | NA | 0.087 | 0.3596 | 0.677 | 0.0633 | 0.764 | 0.0878 | 1.564 |
| Change in *Zostera* biomass | 0.314 | 0.4657 | 0.992 | 0.2009 | 1.929 | 0.2972 | 14.580 | 0.2618 | 11.345 |
| Resident density | NA | NA | 0.134 | 0.1637 | 0.302 | 0.166 | 1.458 | 0.1184 | 1.286 |

| Response variable | Invader = *Idotea* | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|
| | Grazers (df = 1) | | Richness (df = 1) | | Identity (df = 2) | | Total | | |
| | SS | P | SS | P | SS | P | SS | P | MSE |
| Invader population growth | 0.174 | 0.1727 | 0.777 | **0.0072** | 1.014 | **0.0008** | 3.704 | **0.0033** | 1.739 |
| Invader biomass | 0.284 | 0.1307 | 0.950 | **0.0092** | 0.353 | **0.0346** | 3.874 | **0.0262** | 2.287 |
| Volunteer richness | 0.160 | 0.9035 | 0.267 | 0.8757 | 28.133 | 0.2042 | 240.960 | 0.6189 | 212.400 |
| Volunteer biomass | 0.755 | 0.2006 | 0.021 | 0.8281 | 1.305 | 0.3161 | 10.697 | 0.3387 | 8.617 |
| *Haminoea* biomass | 5.203 | **0.0001** | 1.264 | **0.0252** | 5.095 | **0.0068** | 15.885 | **0.0001** | 4.323 |
| *Molgula* abundance | 0.757 | 0.341 | 1.634 | 0.1673 | 0.000 | NA | 18.302 | 0.5689 | 15.912 |
| Algae richness | 12.960 | **0.0452** | 2.400 | 0.3689 | 19.600 | 0.0685 | 91.760 | **0.0397** | 56.800 |
| Algae biomass | 4.800 | **0.0057** | 2.285 | **0.0454** | 6.221 | **0.0278** | 23.343 | **0.0014** | 10.035 |
| Epiphytic chlorophyll | 46.977 | 0.0674 | 5.174 | 0.5283 | 33.606 | 0.2683 | 336.990 | 0.188 | 251.232 |
| Resident biomass | NA | NA | 0.009 | 0.6521 | 0.008 | 0.8887 | 0.016 | 0.9403 | 0.664 |
| Change in *Zostera* biomass | 0.087 | 0.57 | 0.000 | 0.9955 | 0.890 | 0.1902 | 0.977 | 0.4622 | 5.205 |
| Resident density | NA | NA | 0.192 | 0.1247 | 0.770 | **0.0317** | 2.129 | **0.0195** | 0.073 |