

GRAZER DIVERSITY, FUNCTIONAL REDUNDANCY, AND PRODUCTIVITY IN SEAGRASS BEDS: AN EXPERIMENTAL TEST

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Abstract. Concern over the accelerating loss of biodiversity has stimulated renewed interest in relationships among species richness, species composition, and the functional properties of ecosystems. Mechanistically, the degree of functional differentiation or complementarity among individual species determines the form of such relationships and is thus important to distinguishing among alternative hypotheses for the effects of diversity on ecosystem processes. Although a growing number of studies have reported relationships between plant diversity and ecosystem processes, few have explicitly addressed how functional diversity at higher trophic levels influences ecosystem processes. We used mesocosm experiments to test the impacts of three herbivorous crustacean species (*Gammarus mucronatus*, *Idotea baltica*, and *Erichsonella attenuata*) on plant biomass accumulation, relative dominance of plant functional groups, and herbivore secondary production in beds of eelgrass (*Zostera marina*), a dominant feature of naturally low-diversity estuaries throughout the northern hemisphere. By establishing treatments with all possible combinations of the three grazer species, we tested the degree of functional redundancy among grazers and their relative impacts on productivity.

Grazer species composition strongly influenced eelgrass biomass accumulation and grazer secondary production, whereas none of the processes we studied was clearly related to grazer species richness over the narrow range (0–3 species) studied. In fact, all three measured ecosystem processes—epiphyte grazing, and eelgrass and grazer biomass accumulation—reached highest values in particular single-species treatments. Experimental deletions of individual species from the otherwise-intact assemblage confirmed that the three grazer species were functionally redundant in impacting epiphyte accumulation, whereas secondary production was sensitive to deletion of *G. mucronatus*, indicating its unique, nonredundant role in influencing this variable. In the field, seasonal abundance patterns differed markedly among the dominant grazer species, suggesting that complementary grazer phenologies may reduce total variance in grazing pressure on an annual basis. Our results show that even superficially similar grazer species can differ in both sign and magnitude of impacts on ecosystem processes and emphasize that one must be cautious in assuming redundancy when assigning species to functional groups.

Key words: biodiversity; ecosystem function; eelgrass; *Erichsonella attenuata*; estuaries; functional redundancy; *Gammarus mucronatus*; grazing; *Idotea baltica*; mesograzers; productivity; *Zostera marina*.

INTRODUCTION

The relationships between species diversity and ecosystem stability and function have been central topics in ecology for decades (MacArthur 1955, Elton 1958, May 1974, McNaughton 1977, Jones and Lawton 1995). In recent years, however, concern over the accelerating loss of biodiversity has intensified both theoretical and empirical interest in untangling the complex relationships between community composition, species richness, and functional processes (Huston 1997, Schlöpfer and Schmid 1999, Tilman 1999). Species richness may influence ecosystem function in three fundamental ways (Chapin et al. 1997, Tilman 1999).

First, more diverse systems have a higher probability of containing a particular species with important traits influencing ecosystem function, the “sampling effect” (Tilman et al. 1997b, Huston 1997). Second, the greater diversity of functional traits represented in a larger species pool may lead to more efficient use of resources in a variable environment, the “niche complementarity effect.” Third, presence of multiple, functionally similar species in diverse assemblages may provide “biological insurance” against changes in ecosystem processes when individual species are deleted from the system (Naeem and Li 1997).

Proposed general relationships between species richness and ecosystem function, such as the widely discussed “rivet,” “redundant species,” and “idiosyncratic species” hypotheses (Lawton 1994), are statistical models in that they predict an *average* relationship between the number of species—whose individual

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characteristics are unspecified—and the magnitude of the variable. At a mechanistic level, however, the characteristics of individual species are fundamental to explaining the existence and form of such relationships (Aarssen 1997, Hooper and Vitousek 1997, Huston 1997, Tilman et al. 1997a, Wardle et al. 1997). Specifically, the relationship will depend on the degree of functional redundancy vs. complementarity among co-existing species (Lawton and Brown 1993). For example, in an assemblage where multiple species play similar roles, ecosystem processes should be less vulnerable to disturbance or random species extinctions than in an assemblage where each species has a unique role (Walker 1995). Thus, the degree of functional redundancy among co-occurring species is critical to testing the effects of species richness on ecosystem processes (Lawton 1994), and is of general interest.

A growing number of experimental studies has reported significant relationships between species richness and productivity, nutrient retention, drought resistance, or invasibility (reviewed in Schlöpfer and Schmid 1999 and Tilman 1999). Despite this intense interest, however, empirical studies have been highly skewed in terms of the types of ecosystems, trophic levels, and response variables considered. A recent review of empirical studies of diversity effects on ecosystem processes found that the great majority have focused on primary producers in grassland and old-field communities or aquatic microbial communities (Schlöpfer and Schmid 1999). In contrast, no published study has explicitly tested the effects of primary-consumer diversity on plant productivity or biomass, and, in general, “‘top-down’ effects have rarely been specifically examined” (Schlöpfer and Schmid 1999:904). As herbivores and predators have profound impacts on plant communities and functional processes in many ecosystems (McNaughton et al. 1988, Huntly 1991, Carpenter and Kitchell 1993, Menge 1995, Bigger and Marvier 1998), there is a clear need for controlled experimental studies addressing the effects of species richness at higher trophic levels on ecosystem processes.

In this study we used mesocosm experiments to test for functional redundancy among herbivore species in influencing ecosystem processes in a vegetated estuarine ecosystem. By establishing all possible combinations of three grazer species, we also explored relationships between grazer species richness, over a narrow range (0–3 species), and functional processes. Our study focused on the community associated with eelgrass (*Zostera marina*), beds of which are a major feature of shallow estuaries throughout the northern hemisphere. A key process in maintaining the health of seagrass and other macrophyte beds is the interaction among grazing invertebrates (mostly amphipods, isopods, and gastropods in temperate waters), epiphytic algae, and the macrophytes that support them (Orth and van Montfrans 1984, van Montfrans et al. 1984, Braw-

ley 1992, Jernakoff et al. 1996, Heck et al. 2000). Epiphytic algae are generally competitively superior to macrophytes where light and nutrients are abundant, and if unchecked by grazing they can rapidly overgrow their hosts (e.g., Neckles et al. 1993), with detrimental consequences for seagrasses (Cambridge et al. 1986, Silberstein et al. 1986, Williams and Ruckelshaus 1993, Short et al. 1995) and, presumably, the larger community that depends on them. Because most grazers feed preferentially on epiphytic algae (but see Valentine and Heck [1999] for exceptions), grazing appears vital to maintaining the dominance of eelgrass over epiphytes, and thus the health of seagrass ecosystems. Historically, the small invertebrate grazers in marine vegetation have been considered, often implicitly, to be a relatively homogeneous functional group in terms of impacts on plants (e.g., Steneck and Watling 1982, Bell 1991). Because there is strong spatial and seasonal variation in grazer assemblage structure in natural seagrass beds (Edgar 1990b, Thom et al. 1995), however, any functional differentiation among grazers is likely to have important consequences for the plant community. There is growing evidence that such grazer species-composition effects are important to marine plant assemblages (e.g., Paine 1992, Duffy and Hay 2000; Duffy and Harvilicz, *in press*). In addition to their top-down grazing effects on plants, the small crustaceans that dominate herbivore guilds in many estuarine and coastal marine ecosystems also play an important role in nutrient cycling (Taylor and Rees 1998), and they are critical links in the food chain to higher trophic levels. Their production often regulates population size and production of fishes (Kikuchi 1974, Edgar and Moore 1986, Edgar and Shaw 1995, Taylor 1998).

We tested the impacts of three common grazing crustacean species on three processes fundamental to function of seagrass ecosystems: (1) epiphyte accumulation, (2) eelgrass biomass accumulation, and (3) grazer secondary production. We concentrate on productivity and trophic transfer because they are fundamental functional processes within ecosystems (MacArthur 1955, McNaughton 1977, 1993, Lawton and Brown 1993, Naeem et al. 1994, Tilman et al. 1996). By establishing treatments with each of the three grazers alone and in all possible combinations, we assessed the importance of grazer species composition and the degree of functional redundancy among grazers to ecosystem processes. We addressed the following questions: (1) Are common grazer species functionally redundant in their impact on plant functional-group composition, biomass accumulation, and secondary production? (2) What are the mechanistic bases of grazer effects in terms of differences in feeding biology and population dynamics? (3) Do ecosystem processes in eelgrass communities correlate with grazer species richness?

METHODS

Natural history of the system

As in many shallow coastal areas worldwide, beds of submerged vascular plants once carpeted shallow sediments throughout the Chesapeake Bay (USA), although their areal extent has declined drastically within the last few decades (Orth and Moore 1983, 1984). In polyhaline regions of the Bay deeper than 0.5 m, these beds are dominated by eelgrass (Orth and Moore 1988), one of the most widespread and abundant marine plants in the northern hemisphere (Stevenson 1988). Eelgrass supports a highly productive and economically important community, providing habitat for fast-growing epiphytic algae, small invertebrate grazers, waterfowl, and commercially important fish and shellfish (Penhale 1977, Heck and Thoman 1984, Thayer et al. 1984, Fredette et al. 1990). Most of the resident grazing invertebrates appear to be generalist epiphyte and detritus feeders (Orth and van Montfrans 1984, Jernakoff et al. 1996). Despite much attention to the potential importance of epiphyte grazers in enhancing seagrass fitness, however, there have been few rigorous experimental confirmations of such an effect under natural conditions (Jernakoff et al. 1996).

Our experiment focused on three grazing crustacean species that dominate the seagrass epifauna in our study area (Marsh 1973, Fredette et al. 1990; Parker et al., *in press*): the isopods *Erichsonella attenuata* and *Idotea baltica*, and the gammaridean amphipod *Gammarus mucronatus* (referred to hereafter by genus names). *Gammarus* is a grazer of microalgae, detritus, and associated microbes (Zimmerman et al. 1979, Smith et al. 1982), and often reaches very high densities in shallow habitats in Chesapeake Bay during spring (Fredette and Diaz 1986). *Idotea baltica* is a characteristic member of vegetated marine and estuarine habitats on both sides of the North Atlantic, grazing on microalgae, macroalgae, and seagrasses (Robertson and Mann 1980, Shacklock and Doyle 1983, Salemaa 1987, Hauxwell et al. 1998, Worm et al. 2000). *Erichsonella attenuata* occurs along the East and Gulf coasts of North America and appears to feed primarily on microalgae (Howard and Short 1986, Boström and Mattila 1999). The only other mesograzer abundant in the field at the beginning of our experiment was *Caprella penantis* (see *Results: Field abundance of grazers*, below). This species fared poorly in previous mesocosm experiments (Duffy 1990; J. E. Duffy, *personal observation*), possibly because of its partial dependence on suspended food, and thus was not included in our experiment. Moreover, *C. penantis* was absent at our field sites by the end of our experiment.

Experimental design

We conducted a mesocosm experiment in spring 1998 to test the impacts of three common grazer species, alone and in combination, on eelgrass-epiphyte

interactions. The experiment ran for most of the spring period of rapid growth for eelgrass in Chesapeake Bay, and terminated shortly before the period when eelgrass begins to senesce in late summer. The experiments were conducted in a series of 48 122-L mesocosms constructed from plastic garbage containers and located at the Virginia Institute of Marine Science (Gloucester Point, Virginia, USA). The outdoor mesocosms were supplied with a constant flow of sand-filtered estuarine water from the adjacent York River estuary and were exposed to ambient conditions of light, temperature, and weather. A 250- μ m-mesh filter bag was placed under each container's inflow valve to minimize colonization of the containers by unwanted animals. A submersible pump attached to the wall of each container enhanced circulation. Water flowed out of each container through four holes, 4.5 cm in diameter and covered with 1-mm plastic mesh.

The experiment included eight treatments: a grazer-free control, three single-species grazer treatments, three two-species grazer ("deletion") treatments, and a treatment with all three grazer species. Thus, the experiment included all possible combinations of species and the complete range in grazer diversity from 0 to 3 species. Each treatment was replicated in six independent mesocosms in a randomized-block design, with all treatments in a given block established on the same day, and stocked from the same collection of eelgrass and grazers.

This design allowed two complementary approaches to addressing the issue of functional redundancy among grazers. First, effects of individual species were compared with one another using the three single-species treatments, which we refer to as "isolation" treatments. Second, we examined effects of deleting individual species from the system by comparing each two-species treatment with the "complete" treatment containing all three species. This comparison mimicked extinctions of single species from natural systems and allowed us to address whether the remainder of the community compensated for the deletion (see Walker 1992, Lawton and Brown 1993). Thus, we refer to the two-species treatments as "deletion" treatments. As we have used all possible combinations of species in this design, we also examine the trend in response variables with grazer species richness. It is important to note, however, that because the three-species treatment contained only one combination of species (i.e., all three), the effects of species composition cannot rigorously be distinguished from those of species richness per se in this design (Huston 1997).

The experiment was initiated on 1 April 1998, when we planted 60 eelgrass shoots in each container of the first two statistical blocks. Eight days later, after a light coating of epiphytes had developed on the eelgrass blades, the mesocosms were stocked with grazers. Stocking the remaining four blocks of mesocosms with eelgrass and grazers was completed by 24 April. To

ensure that treatment effects were attributable to differences in grazer diversity and species composition, rather than differences in initial grazer biomass, we initiated the experiment with the same total estimated grazer biomass (~0.35 g ash-free dry mass [AFDM]) in each treatment; this biomass is well within the range found in Chesapeake Bay eelgrass beds in spring (Fredette et al. 1990). The number of grazers corresponding to 0.35 g AFDM was 115 for *Gammarus*, 33 for *Idotea*, and 91 for *Erichsonella*; mixed-species treatments used fractions of these numbers to achieve a total estimated grazer biomass of 0.35 g. Each experimental container was harvested ~6 wk after eelgrass planting.

Sampling epiphyte accumulation

We measured epiphyte accumulation, using chlorophyll *a* as a proxy for biomass, at ~2, 4, and 6 wk after grazers were added. Epiphytes were sampled by haphazardly selecting three eelgrass blades in each tank, detaching each blade at its base, and gently removing the blade from the water into a plastic bag. The three blades from a given tank were pooled and used as a single replicate. All fouling material was then scraped from the blades using the edge of a glass microscope slide and vacuum-filtered onto a glass-fiber filter. The filter containing the epiphytic material was frozen to disrupt algal cell walls, then extracted with 20 mL of methanol:acetone:deionized water (45:45:10) at -20°C for 24 h. After filtering the extract, absorbance was read at 480, 510, 630, 647, 644, and 750 nm on a Milton Roy 1001 spectrophotometer (Milton Roy Company, Rochester, New York, USA). Chlorophyll concentration was calculated according to the formulae of Parsons et al. (1984). The area of each of the cleaned blades was then measured, either manually as the product of length times width or using a LI-COR 3100 area meter (LI-COR, Lincoln, Nebraska), and epiphytic chlorophyll concentrations were normalized to unit blade surface area by dividing the measured chlorophyll concentration by the area of blade surface sampled.

Final harvest

The experiment was terminated in each block 6 wk after grazers had been added. At this time, the 6-wk epiphytic chlorophyll sample was taken (see last paragraph), after which all eelgrass was uprooted, shaken gently in the water to dislodge grazers, then placed in a plastic bag and frozen until sorting. After eelgrass was removed, the remaining water in the tank was decanted through a 500- μ m-mesh sieve. Sieve contents, including grazers, were rinsed with running York River water, drained, and preserved in 70% ethanol.

Eelgrass samples were separated into above- and belowground portions, and any macroalgae, larger sessile invertebrates, and grazers present were also separated and identified. Above- and belowground eelgrass tissues, algae, and sessile invertebrates were dried for

several days at 60°C and weighed. Any grazers present were added to the ethanol-preserved sample from that mesocosm.

Final ash-free dry biomass of the isopods was calculated by measuring the length of each isopod from rostrum to telson, and converting length to AFDM using equations derived from Fredette et al. (1990). For *Erichsonella* this was: AFDM (in milligrams) = $0.0056L^{2.41}$, and for *Idotea*: AFDM = $0.0110L^{2.17}$, where L = length in millimeters. Final biomass of the amphipod *Gammarus* was estimated using a variant of Edgar's (1990c) method: amphipods were sorted into size classes by rinsing the sample through a nested series of sediment sieves (5.6, 4.0, 2.8, 2.0, 1.4, 1.0, 0.71, 0.50 mm), amphipods retained on each sieve were counted, and their AFDM was calculated for each sieve size listed above using conversions in Edgar (1990c); these are 14.7, 5.8, 2.3, 0.91, 0.26, 0.143, 0.058, and 0.023 mg, respectively. As the approximate starting biomass of grazers in each treatment was known, and no known predators were present, grazer production can be estimated as the difference between initial and final biomasses. Because some juvenile grazers may have emigrated through the mesh drain holes during the experiment, secondary production estimates are conservative.

Calculation of effect strengths

To compare the impacts of different grazer species on eelgrass and epiphytes, we calculated grazer effects on both epiphyte biomass (chlorophyll *a*) and aboveground biomass of eelgrass at the conclusion of the experiment. For each grazer we estimated the "collective" grazing effect, i.e., the raw difference between grazer and control treatments resulting from the aggregate effects of all grazer individuals present, as well as the per capita and per biomass effects (see Berlow et al. [1999] and Duffy and Hay [2000] for further discussion). The per capita effect was estimated as the slope of the change in plant biomass with increasing grazer abundance across all replicates of the single-grazer and control treatments (see Paine [1992] for a similar approach). Per biomass effects were calculated analogously as the change in plant biomass with changing grazer biomass.

Field survey of grazer assemblages

To check the realism of grazer densities used in our mesocosm system, we measured density and species composition of eelgrass epifauna at two field sites approximately contemporaneously with the experiment. In late April, late May, and early July 1998 we sampled epifaunal assemblages near the inshore and offshore margins of eelgrass beds at Allen's Island (37°15' N, 76°26' W) and Goodwin Islands (37°12' N, 76°23' W) in the Lower York River, Virginia, USA. At each site we collected replicate samples of eelgrass with associated animals ($n = 9$ each at inshore and offshore

margins) from a bottom area of 0.0156 m² using a plexiglass core tube, 11.7-cm inside diameter, with a 250 μ m-mesh bag secured over its top end. The tube was placed gently over eelgrass blades with their associated fauna, blades were cut at the base with scissors, and the bottom of the tube was closed off. The tube was then inverted and its contents, including eelgrass, epifauna, and any associated algae, were rinsed into the bag, and stored frozen until processing. In the laboratory the sample contents were separated by taxon, and all plants and sessile invertebrates were identified to species or genus, dried for several days at 60°C, and weighed. All mobile epifaunal species were identified and counted.

As an estimate of the importance of grazer species composition to total grazing impact in the field, we multiplied the density of each grazer species in our field samples by its per capita grazing impact estimated in the mesocosm experiment (see *Results*, below) and summed these estimated impacts across grazer species. Because realized per capita grazing effects are unlikely to remain constant with increasing grazer density, we refer to the calculated estimates as "potential grazing impacts." Per capita grazing rate of *Cymadusa compta*, which was not included in the experiment, was assumed to be similar to that of *Gammarus mucronatus* based on other experiments (Duffy and Harvilicz, *in press*).

Statistical analysis

Our mesocosm experiment was designed to address two sets of hypotheses, one involving differences among individual species, and one involving the effects of deleting species from the system. We treated these as two separate experiments, one comparing the no-grazer and single-species treatments and one comparing the two- (i.e., deletion) and three-species (complete) treatments. Each was analyzed using a separate randomized-block ANOVA in which the different grazer treatments were considered fixed factors, reflecting our intent to draw conclusions about the specific sets of species involved. All analyses used the block \times treatment interaction mean square as the denominator in the *F* tests (see Newman et al. 1997). Within each experiment we tested two planned hypotheses, specified a priori, by partitioning the treatment sum of squares (Sokal and Rohlf 1981). In the single-species experiment, we tested the null hypotheses of (1) no average effect of grazers, i.e., no difference between the no-grazer treatment and the average of the single-grazer treatments, and (2) no difference among the single-grazer treatments. Similarly, in the deletion experiment we tested the null hypotheses of (3) no average effect of grazer deletion, i.e., no difference between the three-grazer treatment and the average of the two-grazer treatments, and (4) no difference among the two-grazer treatments. Where the *F* test of hypothesis 2 or 4 was significant, we identified differences among the three included treatments with Ryan's *Q* test (Day and

Quinn 1989), using as the denominator mean square the block \times treatment interaction from a separate ANOVA of the three treatments considered in that comparison. Heterogeneity of variances was tested using Cochran's test and variance was transformed by log (\times) where necessary. All statistical analyses were performed using SAS version 6.12 (SAS Institute 1988).

Our use of ANOVA reflects our imposition of treatments that initially differed discretely in absolute and relative abundances of grazer species. Final abundances of grazers varied considerably both within and among treatments, however, and we consequently used multiple regression as an additional means of assessing the relative impacts of different grazer species on final biomasses of epiphytes (i.e., chlorophyll) and eelgrass. This analysis employed stepwise (forward) multiple regressions to estimate the contribution of each grazer species, and of grazer species richness, to final biomass of epiphytes and eelgrass. To control for differences among blocks, we used the deviation from the block mean as the dependent variable. Separate multiple regressions were run using grazer abundance and grazer biomass as the independent variables.

RESULTS

Grazer impacts on epiphyte accumulation

Four of the 48 mesocosm units became contaminated by high densities (>500 individuals) of *Gammarus* during the experiment, probably as a result of incompletely defaunated eelgrass. Because of the blocked design, excluding these contaminated replicates from the analysis would require discarding other treatments within that block to preserve the balanced design, drastically reducing statistical power. Since the per capita grazing impact of *Gammarus* was so much lower than those of the two isopods (see *Grazer population growth and production*, below), these infections seem unlikely to have had a major effect on the grazing results, and visual inspection of data from these replicates corroborated this impression. Thus, we opted to retain the contaminated replicates in the analysis.

Overall, the presence of grazers tended to reduce the accumulation of epiphytic algae relative to grazer-free controls, although the strength and timing of this effect differed among grazer treatments (Fig. 1). In the single-species treatments, grazers significantly depressed epiphytic biomass (chlorophyll *a*) accumulation relative to grazer-free controls by week 4; this effect was mostly attributable to the strong reduction by *Erichsonella*, and differences among grazer species explained 26% of the variance in epiphyte biomass on this date (Fig. 1A, Table 1). By week 6, all three grazer species had reduced epiphyte accumulation to similarly low levels, averaging 65% lower than grazer-free controls (Fig. 1A). Statistical analyses of the data for week 6 were complicated because heavy grazing of eelgrass by *Idotea* eliminated both eelgrass and its epiphytic algae in

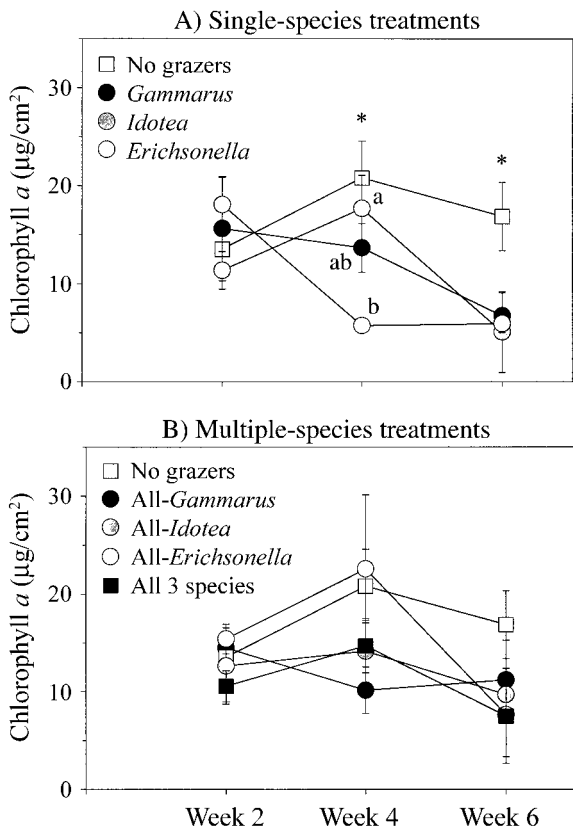


FIG. 1. Impacts of three grazer species, (A) alone and (B) in combination, on epiphytic algal biomass accumulation (measured as chlorophyll *a*; data are $\bar{X} \pm 1$ SE). Asterisks indicate that the contrast between the no-grazer and the mean of the single-species treatments was significant on that date. Means bearing the same lowercase letter at week 4 do not differ significantly ($P > 0.05$, Ryan's Q test following significant F test). Absence of letters in a given week means that the F test for difference among treatments was nonsignificant. See Table 1 for ANOVA results.

three of the six replicates. Thus, only three blocks had epiphytic chlorophyll data from all treatments at the end of the experiment. When the missing chlorophyll values from the heavily grazed blocks were counted as zeros, there was a highly significant effect of grazing, explaining 45% of the variance, but no significant difference among the three grazer species (Fig. 1A, Table 1). When the three blocks with missing data were omitted from the analysis, the grazer effect remained significant despite the low power of the test ($MS = 368$, $F_{1,6} = 6.06$, $P = 0.049$).

Surprisingly, there was no significant difference in epiphyte accumulation between the complete (three-species) and deletion (two-species) grazer treatments on any of the three-sampled dates (Fig. 1B, Table 1). Comparison of the no-grazer control vs. the mean of all two- and three-species grazer treatments at week 6 also revealed no significant reduction of epiphytes by grazing in the multi-species treatments ($MS = 169.9$,

$F_{1,12} = 1.86$, $P = 0.20$). At week 4 the *Erichsonella*-deletion treatment had the highest mean epiphyte accumulation of any of the grazer treatments (although they did not differ significantly), mirroring the strong reduction of epiphytes by *Erichsonella* in the single-species treatment at the same time (Fig. 1A).

Grazer impacts on eelgrass

Grazing had strong impacts on eelgrass both indirectly by reducing epiphyte loads and, in the case of *Idotea*, directly by consumption of eelgrass tissue. Final aboveground biomass of eelgrass was higher in the *Gammarus* and especially the *Erichsonella* treatments compared with the *Idotea* treatment (Fig. 2A, Table 2), reflecting the relatively rapid reduction of epiphytes by *Erichsonella* (Fig. 1A). Conversely, in the *Idotea* treatment, final aboveground biomass was similar or lower than in the grazer-free control (Fig. 2A) despite efficient grazing of epiphytes by *Idotea* (Fig. 1A). This result stems from direct grazing by *Idotea* on eelgrass blades in the mesocosms, which we observed as grazing scars and detached eelgrass blades by the end of the experiment. Differences among the three grazers explained 29% of the variance in aboveground biomass of eelgrass in this comparison (Table 2). Similar to the pattern seen in epiphyte accumulation (Fig. 1B), there was no significant difference among the multi-species grazer treatments in final aboveground eelgrass biomass (Fig. 2A, Table 2). Eelgrass biomass in the multi-species treatments also did not differ significantly, on average, from that in the no-grazer control ($MS = 0.064$, $F_{1,20} = 0.16$, $P = 0.69$). Surprisingly, the treatment excluding *Gammarus* had a higher belowground biomass of eelgrass than did the other deletion treatments, although this effect explained only 6% of variance in belowground biomass in the multi-species comparison (Fig. 2B, Table 2). Otherwise there was no difference among grazer treatments in belowground eelgrass biomass.

Grazer population growth and production

Population growth of *Gammarus* was much greater than that of the isopods, resulting in final *Gammarus* abundances one to two orders of magnitude greater than those of either isopod species (Fig. 3A). *Idotea* showed a trend toward reduced population growth rate in the three-species treatment, relative to the *Idotea*-only treatment ($P = 0.059$, one-tailed paired-sample t test, Fig. 3B), suggesting that it suffered from interspecific competition with the other grazers. Population growth rate of *Erichsonella* was not significantly reduced in the presence of the other two species ($P = 0.15$, one-tailed paired-sample t test). Paradoxically, population growth of *Gammarus* appeared marginally greater in the three-species treatment than in isolation ($P = 0.061$, two-tailed paired-sample t test), perhaps due to its lower initial abundance in the multi-species, compared with the single-species, treatment.

Accumulation of grazer biomass (i.e., secondary pro-

TABLE 1. Results of randomized-block ANOVAs testing differences among grazer treatments in impact on epiphyte biomass (chlorophyll *a*).

| Source of variation† | df | SS | MS | F | P‡ | Variance explained (%) |
|---|----|--------|-------|-------|------------------|------------------------|
| Single-species grazer treatments | | | | | | |
| Week 2 | | | | | | |
| Block | 5 | 140.7 | 28.1 | | | 16.8 |
| H ₀ 1: (Gam, Ido, Eri) < Control | 1 | 13.4 | 13.4 | 0.33 | 0.573 | 1.6 |
| H ₀ 2: Gam = Ido = Eri | 2 | 77.3 | 38.7 | 0.96 | >0.250 | 9.2 |
| Block × Treatment | 15 | 604.9 | 40.3 | | | 72.3 |
| Week 4 | | | | | | |
| Block | 5 | 417.5 | 83.5 | | | 24.0 |
| H ₀ 1: (Gam, Ido, Eri) < Control | 1 | 321.0 | 321.0 | 8.69 | 0.010 | 18.5 |
| H ₀ 2: Gam = Ido = Eri | 2 | 443.8 | 221.9 | 6.01 | <0.025 | 25.6 |
| Block × Treatment | 15 | 554.3 | 37.0 | | | 31.9 |
| Week 6 | | | | | | |
| Block | 4 | 126.2 | 31.5 | | | 11.9 |
| H ₀ 1: (Gam, Ido, Eri) < Control | 1 | 474.3 | 474.3 | 14.13 | 0.0027 | 44.7 |
| H ₀ 2: Gam = Ido = Eri | 2 | 58.3 | 29.2 | 0.87 | >0.25 | 5.5 |
| Block × Treatment | 12 | 402.7 | 33.6 | | | 37.9 |
| Multi-species grazer treatments | | | | | | |
| Week 2 | | | | | | |
| Block | 5 | 542.4 | 108.5 | | | 30.1 |
| H ₀ 1: (All-Gam, All-Ido, All-Eri) < ALL | 1 | 99.7 | 99.7 | 1.29 | 0.273 | 5.5 |
| H ₀ 2: All-Gam = All-Ido = All-Eri | 2 | 0.14 | 0.07 | 0.001 | >0.750 | 0.0 |
| Block × Treatment | 15 | 1156.7 | 77.1 | | | 64.3 |
| Week 4 | | | | | | |
| Block | 5 | 8.40 | 1.68 | | | 32.8 |
| H ₀ 1: (All-Gam, All-Ido, All-Eri) < ALL | 1 | 0.21 | 0.21 | 0.21 | 0.652 | 0.8 |
| H ₀ 2: All-Gam = All-Ido = All-Eri | 2 | 2.49 | 1.25 | 1.28 | <0.250 | 9.7 |
| Block × Treatment | 15 | 14.54 | 0.97 | | | 56.7 |
| Week 6 | | | | | | |
| Block | 3 | 106.5 | 35.5 | | | 9.9 |
| H ₀ 1: (All-Gam, All-Ido, All-Eri) < ALL | 1 | 1.2 | 1.2 | 0.01 | 0.916 | 0.1 |
| H ₀ 2: All-Gam = All-Ido = All-Eri | 2 | 68.9 | 34.5 | 0.34 | >0.500 | 6.4 |
| Block × Treatment | 9 | 900.9 | 100.1 | | | 83.6 |

Note: The treatment SS is partitioned into two components (Sokal and Rohlf 1981) to test the two listed null hypotheses (see *Methods: Statistical analyses*).

† "Eri", "Gam", and "Ido" refer to *Erichsonella*, *Gammarus*, and *Idotea*, respectively. "ALL" = all three species together.

‡ P values ≤ 0.05 are in bold-face type.

duction) was also highest in the *Gammarus*-only treatment (Fig. 4), reflecting the rapid population growth of this species. When the experimental units that became contaminated with *Gammarus* were omitted from the analysis, it was clear that secondary production was considerably higher in all treatments containing *Gammarus* than in treatments lacking this species (Fig. 4). Because contaminated replicates from several blocks had to be excluded, however, this trend could not be confirmed formally with the randomized block ANOVA.

Per capita and per biomass impacts on plant biomass accumulation differed substantially among the three grazer species (Figs. 5 and 6). Regressions of plant biomass on grazer abundance approached significance only for *Idotea* and *Erichsonella* effects on epiphytic chlorophyll (Fig. 5), so per capita effects calculated from slopes of these regressions (Fig. 6) should be treated as rough estimates. Nevertheless, it is clear that a given density of isopods reduced epiphyte mass much more than a comparable density of *Gammarus* (Fig. 5).

Thus, the isopods had considerably higher per capita effects on epiphyte mass than *Gammarus* did, in contrast to the similar collective effects of these species (Fig. 6). Per capita impacts on final eelgrass biomass differed qualitatively as well as quantitatively among grazers: *Erichsonella* had a strong positive impact, *Gammarus* had essentially no effect, and *Idotea* had a negative effect on eelgrass (Fig. 6D). Differences among grazers in per biomass effects were similar but less marked (Fig. 6E and F), reflecting the somewhat larger body sizes of the isopods relative to *Gammarus*.

Grazer diversity effects on eelgrass and epiphytes

There was no clear relationship between the number of grazer species in the experiment and the effectiveness of epiphyte grazing, final eelgrass biomass, or secondary production (Fig. 7). Average (though not variance in) epiphyte accumulation (Fig. 7A) and final grazer biomass (Fig. 7C) were roughly similar at all grazer diversity levels, and eelgrass biomass was high-

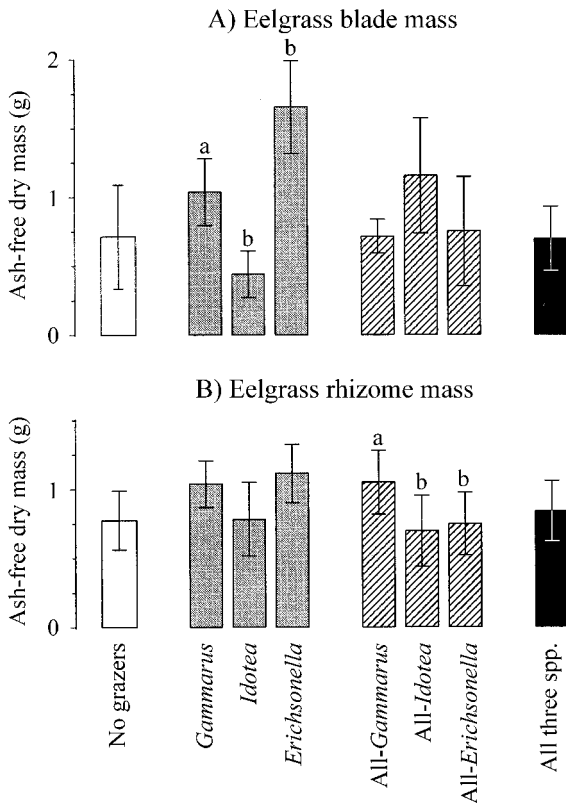


FIG. 2. Impacts of three grazer species, alone and in combination, on (A) eelgrass aboveground biomass and (B) belowground biomass, at the end of the experiment. Data are $\bar{X} \pm 1$ SE; means sharing the same lowercase letter do not differ significantly from other means within the same level of grazer diversity at $\alpha = 0.05$ (Ryan's Q test following significant F test of the among-treatment effect, see Table 2). $N = 6$ replicates for all treatments.

est, on average, in single-species treatments (Fig. 7B). Stepwise multiple regressions testing the relative importance of grazer species richness vs. abundances of individual grazer species consistently showed that effects of individual species were stronger than those of species richness (Table 3). Biomass of *Idotea* contributed most strongly to final epiphyte biomass ($r^2 = 0.19$, $P = 0.0037$), and no other variable was retained in the model after the effect of *Idotea* was included (Table 3). Aboveground eelgrass biomass was significantly influenced only by *Erichsonella* biomass at the $\alpha = 0.05$ level ($r^2 = 0.20$, $P = 0.0013$, Table 3). Similar results, with slightly lower r^2 , were obtained using grazer abundances as the independent variables (Table 3). The effect of grazer species richness never reached $P < 0.24$ or $r^2 > 0.034$ in any of the analyses.

Field abundance of grazers

Sampling of eelgrass-associated epifauna at Allen's and Goodwin Islands between April and July 1998 produced a total of 22 identified taxa; the three grazer species studied in our experiments, plus the amphipods

Cymadusa compta and *Caprella penantis*, were the five most abundant species found in the field collection and together comprised 90% of total epifaunal animals collected (Table 4). The three grazer species we studied together comprised 61–90% of total epifauna on the three sampling dates. The abundance of the top five species differed substantially both in time and among the four sites sampled (Fig. 8). *Gammarus* was by far the most abundant grazer, often exceeding abundances of the other species by an order of magnitude; its peak abundance during the sampling period was in May (87% of total). *Caprella penantis* was most abundant early in the season. The remaining three species increased through the summer. Because of these species-specific phenologies, both the absolute abundance and relative species composition of the grazer assemblage varied considerably in time and space. A two-way ANOVA testing differences in grazer abundance among species and dates yielded highly significant effects for species ($F_{4,525} = 181.9$, $P < 0.0001$), date ($F_{2,525} = 55.2$, $P < 0.0001$), and the interaction ($F_{8,525} = 65.7$, $P < 0.0001$); the species \times date interaction explained 28% of the total variance (i.e., ss), confirming that the major grazer species differed considerably in seasonal phenology.

Grazer abundances in the mesocosm experiment (three-species treatment) were generally similar to those found in the field at the same time (Fig. 8). When these field abundances were multiplied by the per capita grazing impacts of individual species estimated from the experiment, the spatial and seasonal pattern of potential grazing intensity differed from the pattern in total grazer abundance (Fig. 9). Whereas total grazer abundance peaked in May at all sites, estimated potential grazing impact remained similar or increased through July at all sites, and variation among sites in July was much more pronounced than for grazer abundance. These patterns reflect the changing species composition of the grazer assemblage (Fig. 8).

DISCUSSION

Grazer functional diversity and ecosystem processes in seagrass beds

The extent to which co-occurring species differ in functional characteristics fundamentally determines the relationship between diversity and functional processes (Lawton and Brown 1993, Chapin et al. 1997, Tilman et al. 1997b, Tilman 1999). In seagrass beds, previous research has shown that invertebrate grazers often exert strong top-down influence on the plant assemblage (Orth and van Montfrans 1984, van Montfrans et al. 1984, Jernakoff et al. 1996), and our findings corroborate this generalization. The novelty in our results is the experimental demonstration that individual species strongly influence seagrass-bed processes in different ways. Despite their superficial similarity, the co-occurring grazer species we studied differed substantially

TABLE 2. Results of randomized-block ANOVAs testing differences among grazer treatments in impact on eelgrass biomass.

| Source of variation | df | SS | MS | F | P | Variance explained (%) |
|--|----|--------|--------|------|--------|------------------------|
| Single-species grazer treatments | | | | | | |
| Eelgrass aboveground biomass | | | | | | |
| Block | 5 | 5.74 | 1.15 | | | 37.6 |
| H_0 1: (Gam, Ido, Eri) < Control | 1 | 0.49 | 0.49 | 1.62 | 0.227 | 3.2 |
| H_0 2: Gam = Ido = Eri | 2 | 4.44 | 2.22 | 7.25 | <0.010 | 29.1 |
| Block \times Treatment | 15 | 4.58 | 0.31 | | | 30.0 |
| Eelgrass belowground biomass | | | | | | |
| Block | 5 | 4.11 | 0.82 | | | 65.8 |
| H_0 1: (Gam, Ido, Eri) < Control | 1 | 0.19 | 0.19 | 1.74 | 0.207 | 3.0 |
| H_0 2: Gam = Ido = Eri | 2 | 0.36 | 0.18 | 1.69 | >0.100 | 5.8 |
| Block \times Treatment | 15 | 1.60 | 0.11 | | | 25.6 |
| Multi-species grazer treatments | | | | | | |
| Eelgrass aboveground biomass | | | | | | |
| Block | 5 | 6.10 | 1.22 | | | 47.1 |
| H_0 3: (All-Gam, All-Ido, All-Eri) < ALL | 1 | 0.14 | 0.14 | 0.36 | 0.557 | 1.1 |
| H_0 4: All-Gam = All-Ido = All-Eri | 2 | 0.72 | 0.36 | 0.91 | >0.250 | 5.6 |
| Block \times Treatment | 15 | 5.97 | 0.40 | | | 46.1 |
| Eelgrass belowground biomass | | | | | | |
| Block | 5 | 5.89 | 1.18 | | | 84.1 |
| H_0 3: (All-Gam, All-Ido, All-Eri) < ALL | 1 | 0.0002 | 0.0002 | 0.00 | 0.951 | 0.0 |
| H_0 4: All-Gam = All-Ido = All-Eri | 2 | 0.43 | 0.22 | 4.78 | <0.025 | 6.1 |
| Block \times Treatment | 15 | 0.68 | 0.05 | | | 9.7 |

Notes: The treatment SS is partitioned into two components (Sokal and Rohlf 1981) to test the two listed null hypotheses. Abbreviations and format are as in Table 1.

in their impacts on two central ecosystem processes: biomass accumulation of the major structural species, eelgrass, and total production of grazer biomass. These effects result from a combination of qualitatively and quantitatively different grazing behaviors and different population growth rates among grazer species.

First and most importantly, per capita impacts on eelgrass were strongly positive for *Erichsonella attenuata*, essentially zero for *Gammarus mucronatus*, and negative for *Idotea baltica* (Fig. 6D). The latter effect reflects *Idotea*'s direct grazing on eelgrass, which was unique among the grazer species studied. Grazing scars on eelgrass were conspicuous in *Idotea* treatments but rare in those without *Idotea*. As a consequence, final aboveground biomass of eelgrass was lower in treatments with *Idotea* alone than with either of the other two grazers alone (Fig. 2A). *Idotea baltica* is known to graze living eelgrass (Robertson and Mann 1980), as are several of its congeners. Studies in eelgrass beds of the Netherlands showed that *I. chelipes* grazed on eelgrass when epiphyte levels were low (Hootsmans and Vermaat 1985), that it was the only one of five invertebrate species examined that grazed on living eelgrass (Nienhuis and van Ierland 1978) and that "many leaf edges in the seagrass beds showed shredding marks" caused by *I. chelipes* (Nienhuis and Groenendijk 1986:30). In the northeast Pacific, *I. resicata* also appears to graze significant quantities of eelgrass (Thom et al. 1995). We have observed similar scars, albeit at low frequency, on eelgrass at our field sites (especially where *Idotea* was conspicuously abundant;

J. D. Parker, *personal observation*) Population blooms of *I. baltica* have also been implicated in widespread destruction of intertidal bladder wrack (*Fucus vesiculosus*) beds in the Baltic (Kangas et al. 1982, Haahtela 1984). Interestingly, *Idotea*'s negative impact on eelgrass in our study was partially compensated for by its positive indirect effect mediated via epiphyte consumption, so that mean biomass of eelgrass in the *Idotea* treatment was comparable to that in grazer-free controls (Fig. 2A), and multiple regression revealed no significant effect of *Idotea* on eelgrass when other grazers were included in the model (Table 3). In contrast, *Erichsonella* more than doubled the final aboveground biomass of eelgrass relative to grazer-free controls (Fig. 2A). Thus, fitness of the foundation species (Dayton 1975) in this ecosystem—eelgrass—depends strongly on the species composition of the associated grazers.

The second major difference among grazer species was in secondary production. Crustacean mesograzers are responsible for a major fraction of total secondary production in many vegetated marine systems (Klump et al. 1989, Taylor 1998), and production by mesograzer prey is the most reliable predictor of production by higher trophic levels (Edgar and Shaw 1995). In our experiment, populations of the amphipod *Gammarus* grew much more rapidly and produced more biomass than either isopod species did (Figs. 3 and 4). This result is consistent with previous field studies in Chesapeake Bay (USA). Based on cohort analysis, *Gammarus mucronatus* was estimated to reach maturity in as little as three weeks in the field, and matured in the

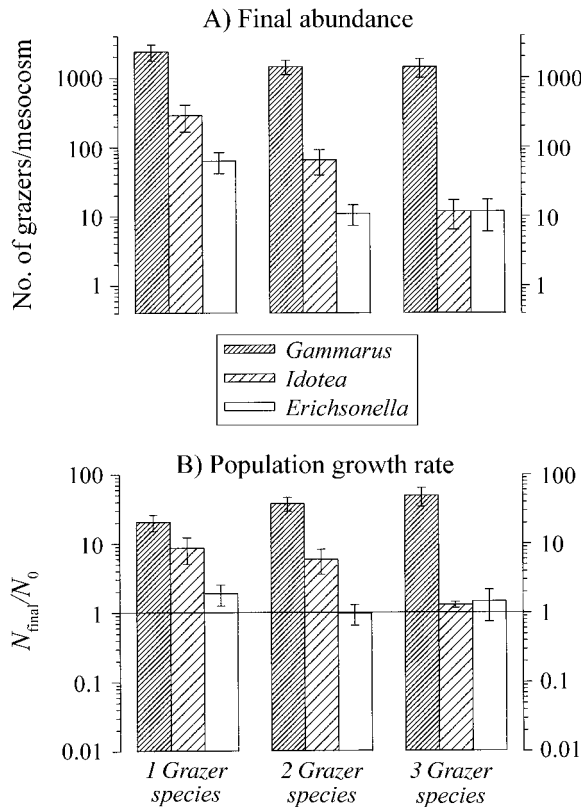


FIG. 3. (A) Final abundances and (B) rates of population growth for each of the three grazer species in treatments differing in grazer species richness. Data are $\bar{X} \pm 1$ SE; N_0 and N_{final} refer to the initial and final number of grazers per mesocosm. For the two-species treatments, data are pooled across both treatments containing a given species; thus, sample sizes for the two-species means are 12, whereas $N = 6$ mesocosms for the one- and three-species means. The line at 1.0 in (B) represents the transition point between declining and growing populations. Note the logarithmic scales.

laboratory in less than two weeks at 17°C (Fredette and Diaz 1986). Fredette et al. (1990) found that *Gammarus mucronatus* had the highest production: biomass ratio of the nine epifaunal species (seven crustaceans and two mollusks, including *Erichsonella* and *Idotea*) they studied in Chesapeake Bay. One factor potentially contributing to both the high productivity and low per capita grazing impact of *Gammarus* is its generalist feeding habits. *G. mucronatus* feeds on microbes and detritus (Zimmerman et al. 1979, Smith et al. 1982) in addition to epiphytic algae, and so may have had more food available than the herbivorous isopods did. Different seasonal reproductive cycles may also have contributed to the differences among grazer species in production; however, other experiments have shown that population growth rates of local amphipods greatly exceeded those of isopods in summer as well (J. E. Duffy and A. M. Harvilicz, *personal observations*).

The most direct test for functional redundancy involves deletion of species from an otherwise-intact

community (Walker 1992, Lawton and Brown 1993). Our grazer-deletion treatments allowed assessment of whether the strong differences we found among grazer species in isolation were compensated for by the other two common grazer species in the context of a larger community. The most marked impact of species deletion was the strong depression of total secondary production when *Gammarus* was removed (Fig. 4), reflecting the uniquely high rate of biomass production by this amphipod observed in the single-grazer treatment. *Gammarus* removal also slightly enhanced eelgrass rhizome mass (Fig. 2B), which we find difficult to explain. In contrast, deletions of single grazer species had no significant impact on epiphyte accumulation or eelgrass blade biomass (Tables 1 and 2), suggesting that the grazers studied here have largely redundant effects on these variables over the time scale of our experiment. Thus, the degree of redundancy among grazer species depends on the response variable considered, as found in many analogous tests of plant diversity effects (Schläpfer and Schmid 1999).

Functional differences among species, particularly niche complementarity, can potentially provide the raw material for relationships between species richness and ecosystem processes (Lawton and Brown 1993, Tilman 1999). The narrow range of species richness we used precludes a powerful test of diversity effects on functional processes (but see Stachowicz et al. 1999, Jonsen and Malmqvist 2000). Nevertheless, we found little evidence of niche complementarity among grazer species and no regular pattern in biomass accumulation of eelgrass, epiphytes, or grazers with increasing grazer species richness (Fig. 7). Instead, the greatest impacts of grazers on epiphyte accumulation, final biomass of the community dominant (eelgrass), and total secondary production all occurred in treatments with single grazer species. Multiple-regression analyses similarly

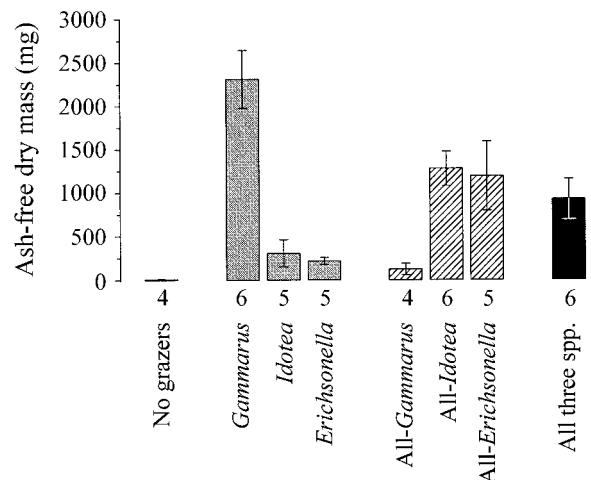


FIG. 4. Total biomass of grazers ($\bar{X} \pm 1$ SE) in each treatment at the end of the experiment. The number under each bar denotes the number of replicates used in the calculation.

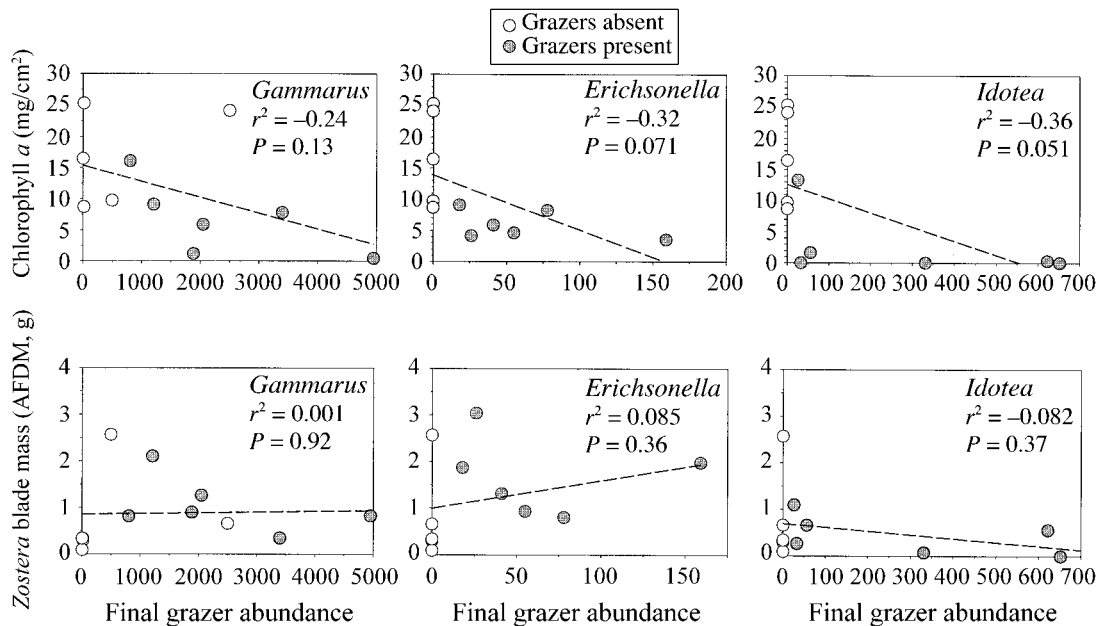


FIG. 5. Regressions of epiphytic chlorophyll *a* and eelgrass aboveground ash-free dry biomass on abundances of the three grazer species, using data from no-grazer and single-species treatments only.

confirmed that single grazer species had stronger effects on eelgrass and epiphytes than did grazer species richness (Table 3). Given the small range of grazer diversity in our experiments, the lack of a clear relationship between diversity and functional variables is not surprising. Theory suggests that the variance in ecosystem processes will be maximal at relatively low diversity (Tilman et al. 1997b), and empirical studies in this range of diversity have indeed produced mixed results (Schläpfer and Schmid 1999). Since grazer assemblages at our field site typically contain only a few common species (Table 4), however, responses of this ecosystem to changes in grazer diversity might be equally idiosyncratic in the field. It is puzzling that neither epiphyte (Fig. 1B) nor eelgrass (Fig. 2) biomass differed significantly between the multi-grazer treatments and the no-grazer control. We suspect that the trend toward lower epiphyte biomass in the three-species treatment (Fig. 1B) would have been significant with greater replication or longer duration of the experiment.

Two caveats may make our conclusions of functional differentiation among these grazer species conservative. First, since our mesocosms were designed to be environmentally as uniform as possible, opportunities for niche partitioning were probably more limited than they are in the field, biasing our design toward finding redundancy. A second important caveat involves the effects of timescale on interpretation of redundancy (Walker 1992, Lawton and Brown 1993): certain species may play important roles only seasonally, at irregular intervals, or under extreme environmental conditions (e.g., Tilman and Downing 1994) not encoun-

tered in short-term experiments. Hence such experiments generally will be biased, again, toward finding redundancy among species. In seasonal environments, a common manifestation of this timescale effect is in the differing phenologies of species. Abundance patterns of the grazers we studied differed markedly in both time and space in the field (Fig. 8). This seasonal and spatial complementarity likely results in more constant total grazing pressure and secondary production on an annual basis in the multi-species assemblage than with any one species alone. If so, this would be an example of the "portfolio effect" (Tilman et al. 1998), whereby more diverse systems have less variable properties simply because they statistically average the effects of several independently varying processes (in this case abundance trends of individual species, see Doak et al. 1998). The potential importance of the portfolio effect for trophic transfer in our system is illustrated by stomach contents of pipefish, which show that these predators track seasonal changes in grazer assemblages, feeding on the grazers that dominate at any given time (Ryer and Orth 1987). Both of the caveats discussed above suggest that redundancy among grazer species in eelgrass beds may be even lower than is evident from our data.

In summary, the composition of the grazer assemblage strongly influenced eelgrass biomass accumulation and secondary production, despite the superficial similarity of the three crustacean mesograzer species studied. These response variables were unrelated to grazer species richness over the narrow range used in our experiments. Indeed, the trend was toward reduced grazing impact in more diverse assemblages. That is,

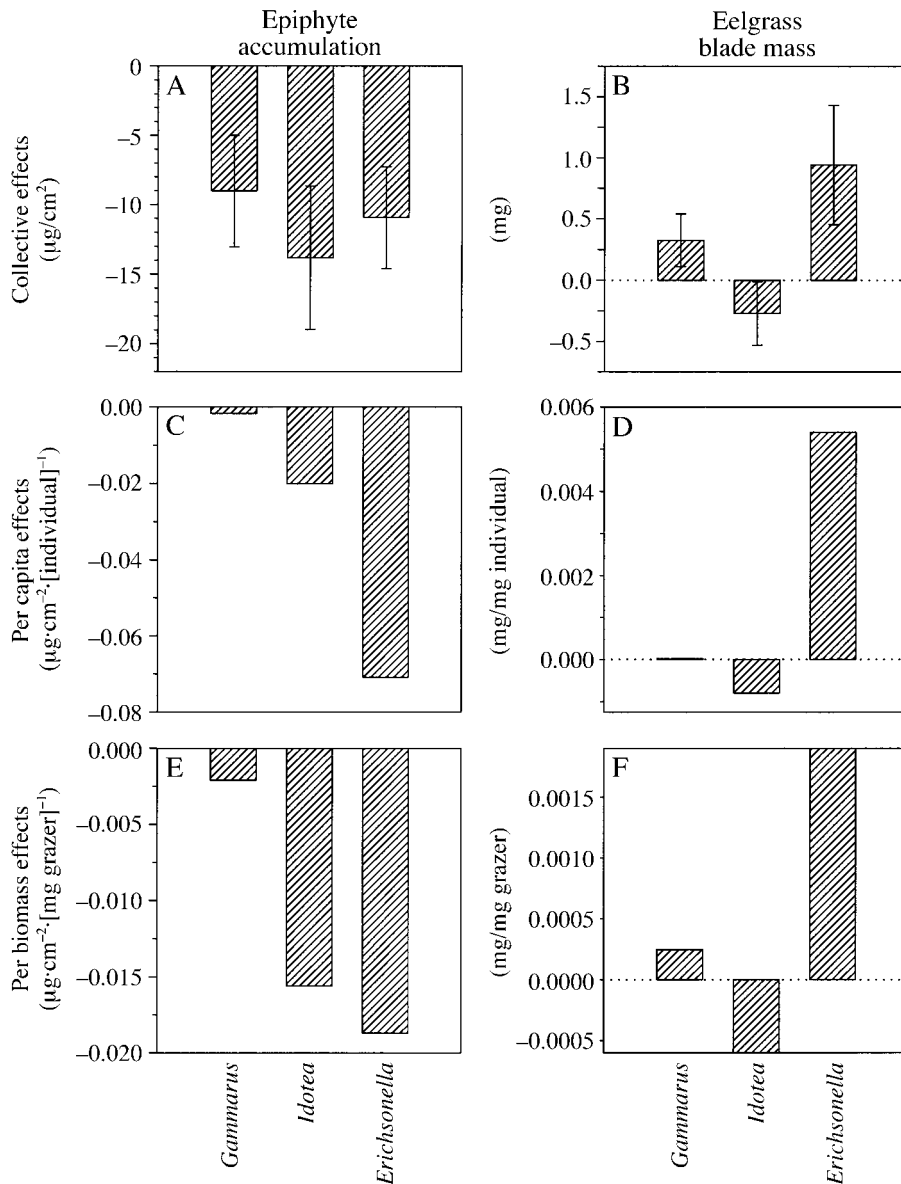


FIG. 6. Comparative impacts of different grazer species on biomass of epiphytic algae (A, C, E) and eelgrass (B, D, F). The collective effect of a grazer is the raw, arithmetic difference in plant biomass between the treatment containing only that grazer and the treatment containing no grazers. Per capita and per biomass effects are calculated as the slope of the change in plant biomass with increasing grazer density and grazer biomass, respectively (Fig. 5). Because only a single slope could be calculated for each grazer species, no estimate of variance is plotted for these effects. Effects were calculated using data from the final sampling (week 6).

each grazer species, when present alone, reduced epiphytes to similarly low levels, whereas epiphyte levels were not significantly different from grazer-free controls in any of the multi-species grazer treatments (Fig. 1). These trends may be related in part to interspecific competition among grazers. Specifically, the population growth rate of *Idotea*, the species with the overriding effect on epiphyte mass (Table 3), tended to be lower in the presence of the other two grazers (Fig. 3B). Other experimental studies have also demonstrat-

ed interference competition among grazing isopod species (Franke and Janke 1998), and we have found experimental evidence of interspecific competition among grazing amphipods in this system (Duffy and Harvilicz, *in press*), as have other authors for epifauna inhabiting both seagrasses (Edgar 1990A) and macroalgae (Edgar and Aoki 1993). In this regard our results are similar to those of Hooper and Vitousek (1997), who found that competition among plant species in a California grassland strongly reduced total

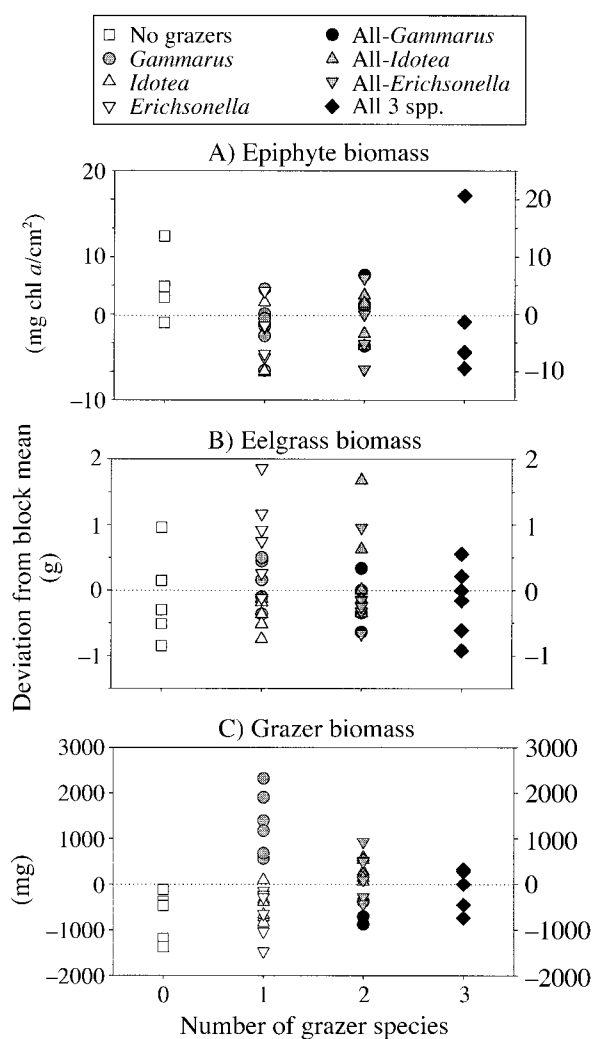


FIG. 7. Final biomass of (A) epiphytes, (B) eelgrass (aboveground), and (C) grazers, as a function of grazer species richness. Data are expressed as deviations from block means.

biomass production in multi-species treatments, and that total biomass was greatest in plots containing only a single species. Walker (1992) and Lawton and Brown (1993) consider such competition strong evidence of functional redundancy among species. Together with the absence of deletion effects on biomass of epiphytes, the primary food of our grazers, such competition points to functional redundancy among grazers with respect to epiphyte grazing. In contrast, the grazers were functionally different in impacts on eelgrass biomass and on secondary production.

Grazer diversity and the functional-group concept

Our results emphasize that, when grazer species composition differs among samples, aggregate grazer biomass (or abundance) is a poor predictor of both impact on the plant assemblage and production of an-

imal biomass available to higher trophic levels (see also Davis 1987, Lehman 1988, Polis and Strong 1991). The importance of grazer functional differentiation can be illustrated by comparing field abundances with potential grazing impacts estimated from per capita grazing rates (Fig. 9). The three grazer species studied here make up the majority of epifaunal animals (78% of the total collected during our study, Table 4) in local eelgrass beds. Since macrograzers such as herbivorous fishes, sea urchins, and larger gastropods are absent from our sites, the mesograzer species we studied (plus *Cymadusa compta* and *Caprella penantis* in certain seasons) appear to be the dominant grazers in this system. Our field sampling showed that, even over a limited time period approximately coincident with the experiment and among four closely situated sites, there was substantial temporal and spatial variation in both the absolute and relative abundances of grazer species (Fig. 8; Parker et al., *in press*), as appears typical of seagrass epifauna (Edgar 1990b, Thom et al. 1995). During their July peak, abundances of *Erichsonella*, *Idotea*, and *Cymadusa* varied among the four sites by factors of >5, >20, and >50 respectively. As the isopods in particular had large per capita impacts on epiphytes, such variation in abundance of individual grazer species is likely

TABLE 3. Results of stepwise (forward) multiple regressions testing the relative influence of individual grazer species vs. grazer species richness on epiphyte (chlorophyll *a*) and eelgrass biomass.

| Variable entered | Partial Model | | | |
|---|---------------|-------|-------|---------------|
| | r^2 | r^2 | F | P |
| Final epiphyte biomass (chl. <i>a</i>) | | | | |
| Regressions using grazer abundance ($N = 42$) | | | | |
| <i>Idotea</i> abundance | 0.176 | 0.176 | 8.58 | 0.0056 |
| Grazer species richness | 0.031 | 0.208 | 1.54 | 0.22 |
| <i>Erichsonella</i> abundance | 0.006 | 0.214 | 0.29 | 0.59 |
| <i>Gammarus</i> abundance | 0.003 | 0.217 | 0.15 | 0.70 |
| Regressions using grazer biomass ($N = 42$) | | | | |
| <i>Idotea</i> biomass | 0.192 | 0.192 | 9.54 | 0.0037 |
| <i>Erichsonella</i> biomass | 0.035 | 0.228 | 1.78 | 0.19 |
| Grazer species richness | 0.029 | 0.257 | 1.48 | 0.23 |
| <i>Gammarus</i> biomass | 0.010 | 0.267 | 0.50 | 0.48 |
| Final eelgrass biomass | | | | |
| Regressions using grazer abundance ($N = 48$) | | | | |
| <i>Erichsonella</i> abundance | 0.134 | 0.134 | 7.12 | 0.010 |
| <i>Idotea</i> abundance | 0.027 | 0.161 | 1.47 | 0.23 |
| <i>Gammarus</i> abundance | 0.011 | 0.173 | 0.60 | 0.44 |
| Grazer species richness | 0.007 | 0.179 | 0.34 | 0.56 |
| Regressions using grazer biomass ($N = 48$) | | | | |
| <i>Erichsonella</i> biomass | 0.204 | 0.204 | 11.76 | 0.0013 |
| <i>Gammarus</i> biomass | 0.045 | 0.249 | 2.70 | 0.11 |
| <i>Idotea</i> biomass | 0.022 | 0.271 | 1.36 | 0.25 |
| Grazer species richness | 0.006 | 0.277 | 0.33 | 0.57 |

Notes: Separate regressions used grazer abundance and grazer biomass as the independent variables. All analyses controlled for block effects by using the deviation from the block mean as the response variable. Variables are listed in the order in which they entered the model. *P* values ≤ 0.05 are in bold. *N* = number of mesocosms.

TABLE 4. Total epifauna collected from Allen's Island and Goodwin Island (Lower York River, Virginia, USA) on each of the three sampling dates in 1998. Percentage of the total number collected on that date is in parentheses.

| Taxon† | Epifaunal totals | | | |
|--|------------------|-----------|----------|-------------|
| | April | May | July | Grand total |
| <i>Gammarus mucronatus</i> (G) | 491 (61) | 1961 (87) | 361 (41) | 2813 (72) |
| <i>Caprella penantis</i> (G) ^{1,2} | 135 (17) | 103 (5) | 0 (0) | 238 (6) |
| <i>Cymadusa compta</i> (G) ^{3,4} | 6 (0.8) | 13 (0.6) | 201 (23) | 220 (6) |
| <i>Erichsonella attenuata</i> (G) | 10 (1) | 47 (2) | 115 (13) | 172 (4) |
| <i>Idotea baltica</i> (G) | 6 (0.8) | 20 (0.9) | 61 (7) | 87 (2) |
| <i>Edotea triloba</i> | 15 (2) | 28 (1) | 39 (4) | 82 (2) |
| <i>Bittium varium</i> (G) ⁵ | 29 (4) | 35 (2) | 15 (2) | 79 (2) |
| <i>Crangon septemspinosus</i> | 18 (2) | 5 (0.2) | 7 (0.8) | 30 (0.8) |
| Mysid | 13 (2) | 1 (0.04) | 0 (0) | 14 (0.4) |
| <i>Ampelisca abdita</i> | 2 (0.2) | 1 (0.04) | 10 (1) | 13 (0.3) |
| <i>Palaemonetes vulgaris</i> (G) ⁶ | 2 (0.2) | 4 (0.2) | 6 (0.7) | 12 (0.3) |
| <i>Palaemonetes intermedius</i> (G) ⁶ | 7 (0.9) | 1 (0.04) | 3 (0.3) | 11 (0.3) |
| Juvenile caprellids (G) ^{1,2} | 9 (1) | 2 (0.1) | 0 (0) | 11 (0.3) |
| Unidentified larvae | 11 (1) | 0 (0) | 0 (0) | 11 (0.3) |
| <i>Elasmopus levis</i> | 2 (0.2) | 5 (0.2) | 2 (0.2) | 9 (0.2) |
| Unidentified amphipods | 2 (0.2) | 4 (0.2) | 0 (0) | 6 (0.2) |
| <i>Mitrella lunata</i> | 0 (0) | 5 (0.2) | 1 (0.1) | 6 (0.2) |
| <i>Paracaprella tenuis</i> | 4 (0.5) | 0 (0) | 0 (0) | 4 (0.1) |
| <i>Palaemonetes pugio</i> (G) ⁶ | 3 (0.4) | 1 (0.04) | 0 (0) | 4 (0.1) |
| <i>Microprotopus raineyi</i> | 0 (0) | 0 (0) | 3 (0.3) | 3 (0.1) |
| <i>Hydrobia</i> sp. | 1 (0.1) | 0 (0) | 1 (0.1) | 2 (0.05) |
| <i>Corophium acherusicum</i> | 0 (0) | 1 (0.04) | 0 (0) | 1 (0.03) |
| <i>Palaemonetes</i> sp. | 0 (0) | 0 (0) | 1 (0.1) | 1 (0.03) |
| <i>Caprella equilibra</i> (G) ^{1,2} | 1 (0.1) | 0 (0) | 0 (0) | 1 (0.03) |
| <i>Leptochelia</i> sp. | 1 (0.1) | 0 (0) | 0 (0) | 1 (0.03) |
| All epifaunal taxa | 801 | 2248 | 879 | 3928 |

† G = grazer, based on evidence for that species or congeners referenced in the numbered superscript citations: ¹ Brawley and Fei 1987; ² Duffy 1990; ³ Zimmerman et al. 1979; ⁴ Duffy and Harvilicz, *in press*; ⁵ van Montfrans et al. 1982; ⁶ Morgan 1980.

to have important consequences for grazing impact that are not reflected in estimates of aggregate grazer abundance. For example, the potential grazing impact estimated at three of our four field sites was greatest in July despite the fact that total grazer abundances at those sites were only about half the values measured in May (Fig. 9); this result is driven primarily by increased abundance of *Erichsonella*, with its high per capita grazing rate, in July (Fig. 8). Therefore, grazer species composition may be at least as important as total grazer abundance in affecting plant populations.

Similarly, other studies have shown that species-level characteristics of marine grazers can confound patterns estimated from hypothesized functional groups. Paine (1992) found that, in a rocky intertidal community, two of the eight invertebrate grazer species he studied strongly reduced recruitment of the dominant brown seaweed, whereas the other six species had negligible effects. Using mesocosm experiments in a seaweed-dominated hard-substratum community, Duffy and Hay (2000) found that algal abundance and community structure differed markedly between treatments with and without amphipods, despite similar abundances of gastropods, isopods, and total mesograzers. Duffy (1990) similarly showed that co-occurring amphipod species differed in the sign of their effects on biomass of the host macroalga (see also Duffy and

Harvilicz, *in press*). In the pelagic realm, a detailed study of copepod dynamics revealed that production calculated from demographics of individual species differed considerably in magnitude and seasonal timing compared with estimates based on size structure or total biomass of the zooplankton (Davis 1987). In our experiment, secondary production varied by an order of magnitude among the three species (Fig. 4) despite all three being peracarid crustaceans of roughly similar body size. While it clearly will be impossible to study every species in every system, these considerations nevertheless underscore that assignments of species to functional groups or guilds should be based as much as possible on empirical knowledge of their functional characteristics, rather than simply on taxonomic relationships or similarity in body size.

Intense interest in the ecosystem consequences of declining diversity has stimulated a wave of experimental studies searching for general relationships between species richness and processes such as productivity and nutrient dynamics. The vast majority of these studies have targeted terrestrial (mostly grassland) plant communities, with several notable exceptions from aquatic microbial communities. While a few studies have also included animals in their design (Naem et al. 1994, Mikola and Setälä 1999, Jonsson and Malmqvist 2000), the role of animal diversity in eco-

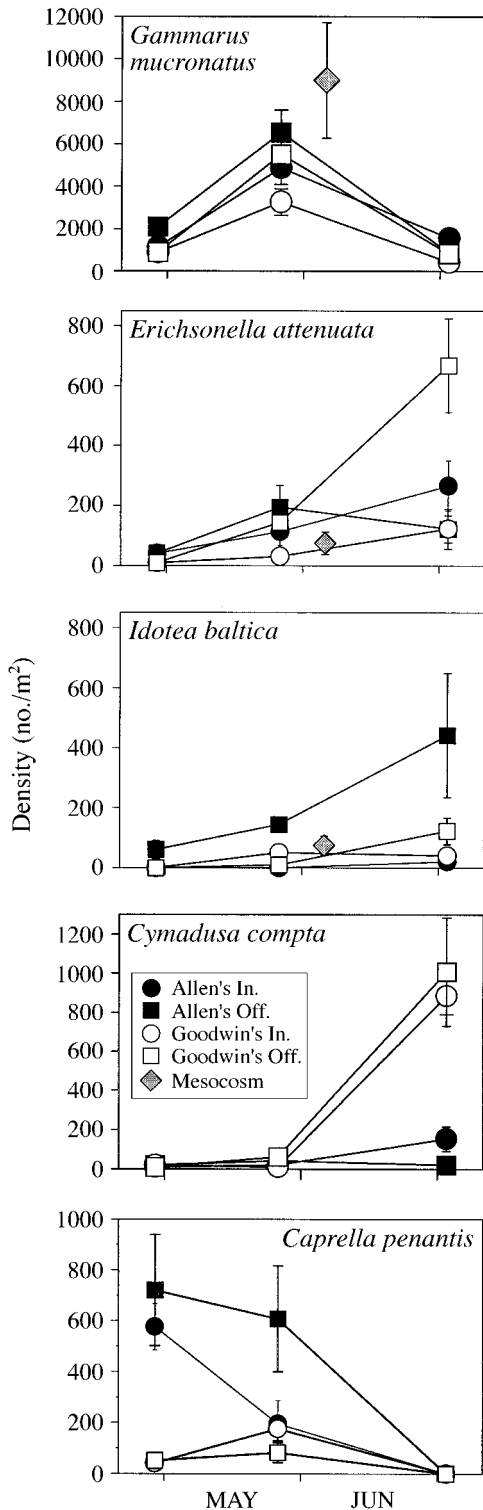


FIG. 8. Densities ($\bar{X} \pm 1$ SE) of the five numerically dominant grazer species at in- and offshore margins of two eel-grass beds at Allen's and Goodwin Islands in the lower York River estuary (Virginia, USA) during late spring-early summer 1988. For comparison, mean densities of the three grazer species in the mesocosm experiment (three-species treatment) are also shown on the date when the experiment terminated. $N = 9$ replicate samples for each symbol.

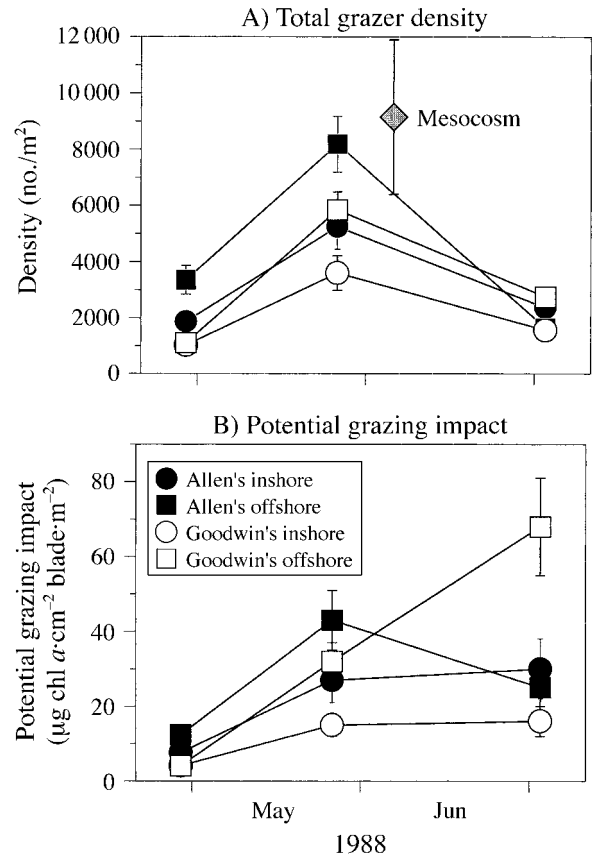


FIG. 9. Total density of grazers (A) and estimated potential grazing impact (B) at four sites in the lower York River estuary. Data are $\bar{X} \pm 1$ SE. Potential grazing impacts were calculated as the product of grazer density (A) and per capita effects (Fig. 6), summed over all grazer species. Total grazer density at the end of the mesocosm experiment (three-species treatment) is shown for comparison. See *Methods: Field survey of grazer assemblages . . .* for location specifics.

system processes remains largely unexplored (Schläpfer and Schmid 1999). We found that, as in many plant assemblages (e.g., Hooper and Vitousek 1997), even generalist grazer species differed considerably in their impact on ecosystem processes. Understanding whether and how ecosystem functional processes are sensitive to changes in species richness higher in the food web remains an important challenge for ecology.

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