

**DOES PLANT DIVERSITY CONTROL ANIMAL DIVERSITY?
AN EXPERIMENTAL APPROACH.**

A Thesis

Presented to

The Faculty of the School of Marine Science
The College of William and Mary in Virginia

In Partial Fulfillment

Of the Requirements for the Degree of
Master of Science

by

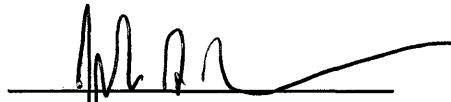
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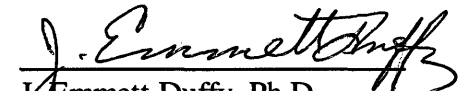
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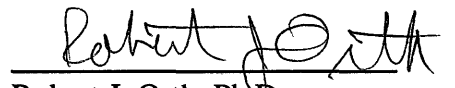
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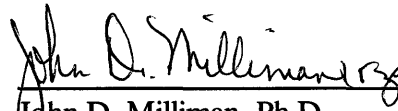

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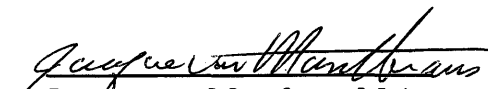

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ABSTRACT

Plant diversity reportedly promotes animal diversity, but there were no experimental tests of the relationship. Faunal diversity may decrease with diminishing plant diversity, potentially compromising ecosystem function. I manipulated plant species diversity and composition and measured animal diversity in a temperate seagrass bed in two experiments during June 1997. Although there was a weak positive relationship between animal species richness and plant diversity (Simpson's index) ($r^2 = 0.08$, $p = 0.035$), most animal diversity indices were more strongly related to the relative biomass of macroalgae within plant diversity treatments. Animal diversity and evenness were negatively correlated with the proportion of macroalgae within treatments ($r^2 = 0.24$, $p < 0.001$; $r^2 = 0.45$; $p < 0.001$, respectively). Animal density, evenness, and diversity were significantly different among treatments grouped by morphological similarity. Hence, epifaunal diversity was more a function of the species composition and structural characteristics (seaweeds versus seagrasses) of plant communities than of plant diversity.

To assess potential resource specialization, I collected epifauna occupying seagrasses and drift algae on nine dates between August 1996 and August 1997 at the same site. Three crustacean species, the amphipods *Cymadusa compta* and *Gammarus mucronatus*, and the isopod *Erichsonella attenuata*, comprised 77% of total epifauna sampled. There were no

clear patterns of host-plant specificity, although the relative abundances of taxa often differed among plant species.

Epifauna responded more strongly to specific plant species and structural attributes than to plant diversity *per se* in the experimental treatments and in undisturbed field situations, supporting the idiosyncratic hypothesis of community responses to diversity. Faunal responses to changes in diversity can be positive, negative, or indeterminate, and depend strongly upon species composition.

DOES PLANT DIVERSITY CONTROL ANIMAL DIVERSITY?

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INTRODUCTION

Biodiversity's functional relevance to ecosystem processes, including nutrient cycling and geochemical processes (Tilman et al. 1996, 1997, Hooper and Vitousek 1997, McGrady-Steed et al. 1997, Hooper 1998), primary productivity (Naeem et al. 1994, 1995, 1996, Tilman et al. 1996, 1997, Hooper and Vitousek 1997, Hooper 1998, Symstad et al. 1998), and drought and grazing resistance (Tilman and Downing 1994, McNaughton 1994, respectively), has only very recently been examined rigorously. For the most part, experimental evidence suggests that biodiversity is correlated with ecosystem productivity, stability, and sustainability (see Johnson et al. 1996 for a review).

The degree to which biodiversity *per se* causally affects ecosystem performance, however, is controversial. Huston (1997) recently critiqued some of the most compelling evidence and concluded that many diversity effects are due to experimental artifacts. Briefly, some 'diversity' relationships are detected simply because "the number of species is often correlated with variation in other biological or physical factors that can have a stronger effect on the experimental response than the putative primary treatment" (Huston 1997). One manner of controlling for these 'hidden treatments,' therefore, is to have replicates that differ in species composition at each level of species diversity. Further, if replicates consist of subsets of species grouped by functional similarity, one can compare the relative influence of species composition versus species diversity.

Some species, such as plants and corals, are absolutely critical to ecosystem function because their presence defines the ecosystem (e.g. boreal forest, coral reef). Perhaps their most fundamental ecosystem function is the preservation of numerous other species due to direct and indirect provision of habitat and resources (Lawton 1994). Specifically, resource heterogeneity can promote species diversity because organisms coexist through differential substrate utilization (MacArthur and MacArthur 1961, Kohn 1967, Abele 1974). Animal diversity, for example, is often correlated with plant diversity (Ricklefs 1990, Huston 1994). Increased diversity of 'structural species' such as plants increase habitat and resource heterogeneity, potentially allowing animals within a habitat ('interstitial species') to coexist (Huston 1994). The net effect is hypothesized to be enhanced animal diversity. Positive correlations between vegetational diversity (species and/or structural diversity) and animal diversity have been observed in many taxa, including birds (MacArthur 1958, MacArthur and MacArthur 1961, Willson 1974), lizards (Pianka 1966, 1967), small mammals (Rosenzweig and Winakur 1969, Kotler and Brown 1988), insects (Murdoch et al. 1972, Southwood et al. 1979, Strong and Levin 1979, Stinson and Brown 1983), fish (Tonn and Magnuson 1982), and marine invertebrates (Heck and Wetstone 1977).

Many positive correlations between animal diversity and plant diversity also can be attributed to variations in plant structural morphology, which commonly covaries with plant species richness (Murdoch et al. 1972, Strong and Levin 1979, Stinson and Brown 1983). Plants with distinct morphological characteristics, therefore, represent potential 'hidden treatments' when comparing animal diversity within plant assemblages differing in species

composition or species diversity. Comparisons between plant diversity gradients with the same range of diversity, but different species compositions defined by disparate structural morphology, should reveal the relative influences of species diversity and species composition on animal diversity.

Submerged aquatic plants are important autogenic ecosystem engineers, i.e., species whose existence changes the environment so drastically that without them, physical conditions would differ and many other species would disappear (Lawton 1994). For example, kelps (Jackson and Winant 1983), freshwater macrophytes (Carpenter and Lodge 1986, and references therein), and marine seagrasses (Fonseca et al. 1982, Fonseca and Calahan 1992) modulate current speed, decreasing erosion (Ward et al. 1984, Fonseca and Fisher 1986) and enhancing infaunal diversity (Orth 1977). Submersed plant canopy provides substrate and refugia for many species (Stevenson 1988, Orth 1992, and references therein), and faunal density and diversity is much greater in seagrass and algal beds than in adjacent unvegetated areas (Kikuchi 1974, Heck and Orth 1980, Gore et al. 1981, Sogard and Able 1991).

Seagrass beds are located in shallow and coastal areas (den Hartog 1970, Kuo et al. 1996) and are typified by rooted vascular plants. Drift and attached macroalgae, however, are also common within grassbeds (Penhale 1977, Cowper 1978, Schneider and Mann 1991a). Phytal epifauna living within the canopy, commonly dominated by amphipods, isopods, and gastropods, differ in relative abundance among plant species in seagrass beds (Lewis 1984, Stoner and Lewis 1985, Lewis 1987, Virnstein and Howard 1987a,b, Edgar and Robertson 1992). Mechanistic hypotheses for epifaunal distribution patterns among marine plants have

been examined (e.g. predation: Nelson 1979, 1981, Coen et al. 1981, Leber 1985, Hay et al. 1989, 1990, Duffy and Hay 1991b, 1994; competition: Nagle 1968, Coen et al. 1981, Edgar 1983c; habitat preference: Stoner 1980, Edgar 1983a,b,c, Bell and Westoby 1986, Hall and Bell 1988, Schneider and Mann 1991b, Edgar and Robertson 1992), yet the role of plant species richness in structuring seagrass epifaunal communities has not been rigorously considered. In fact, the direct influence of plant diversity on animal diversity has never been experimentally tested within any ecosystem.

To test whether plant diversity regulates animal diversity, I manipulated plant species richness and species composition (based on structural morphology) within a temperate seagrass bed, providing an experimental test of the influences of plant species diversity and composition on animal diversity. I also collected individual plant species within a seagrass bed and documented epifaunal species composition on nine sampling dates spanning one year to determine potential host-plant specialization.

METHODS

Study site and organisms

I studied a seagrass bed adjacent to the Goodwin Islands (37° 12'N 76° 23'W) located at the mouth of the York River in the Chesapeake Bay, Virginia, USA (Figure 1). Depth at mean low water is approximately 60 cm. Temperature and salinity typically range from 4 to 30°C and 15 to 20 psu, respectively. Sediments at the site average 85% sand and 13% silt/clay (Moore 1996).

The study area includes a seagrass and algal assemblage (Table 1) dominated by eelgrass, *Zostera marina* L., although widgeongrass, *Ruppia maritima* L., becomes abundant from July to August during the annual period of *Zostera* defoliation (Moore 1996). Drift algae were more abundant during the fall and winter, although ephemeral pockets of drift algae were not uncommon throughout the year. The most common drift algae encountered were the coarsely-branched red alga *Gracilaria verrucosa* Huds. and the foliose green alga *Ulva lactuca* L.. The coarsely-branched red alga *Aghardhiella tenera* J. Agard. and the finely-branched red alga *Ceramium rubrum* Huds. were collected infrequently.

The motile epifaunal community within Chesapeake Bay seagrass beds is relatively depauperate. Fewer than ten species of amphipods, isopods, and small gastropods typically comprise >85% of motile epifauna (Marsh 1973). Additionally, a few species of shrimps, crabs, and fishes can be found within seagrass beds of the region (Orth and Heck 1980, Heck and Orth 1980).

Figure 1. Site map.

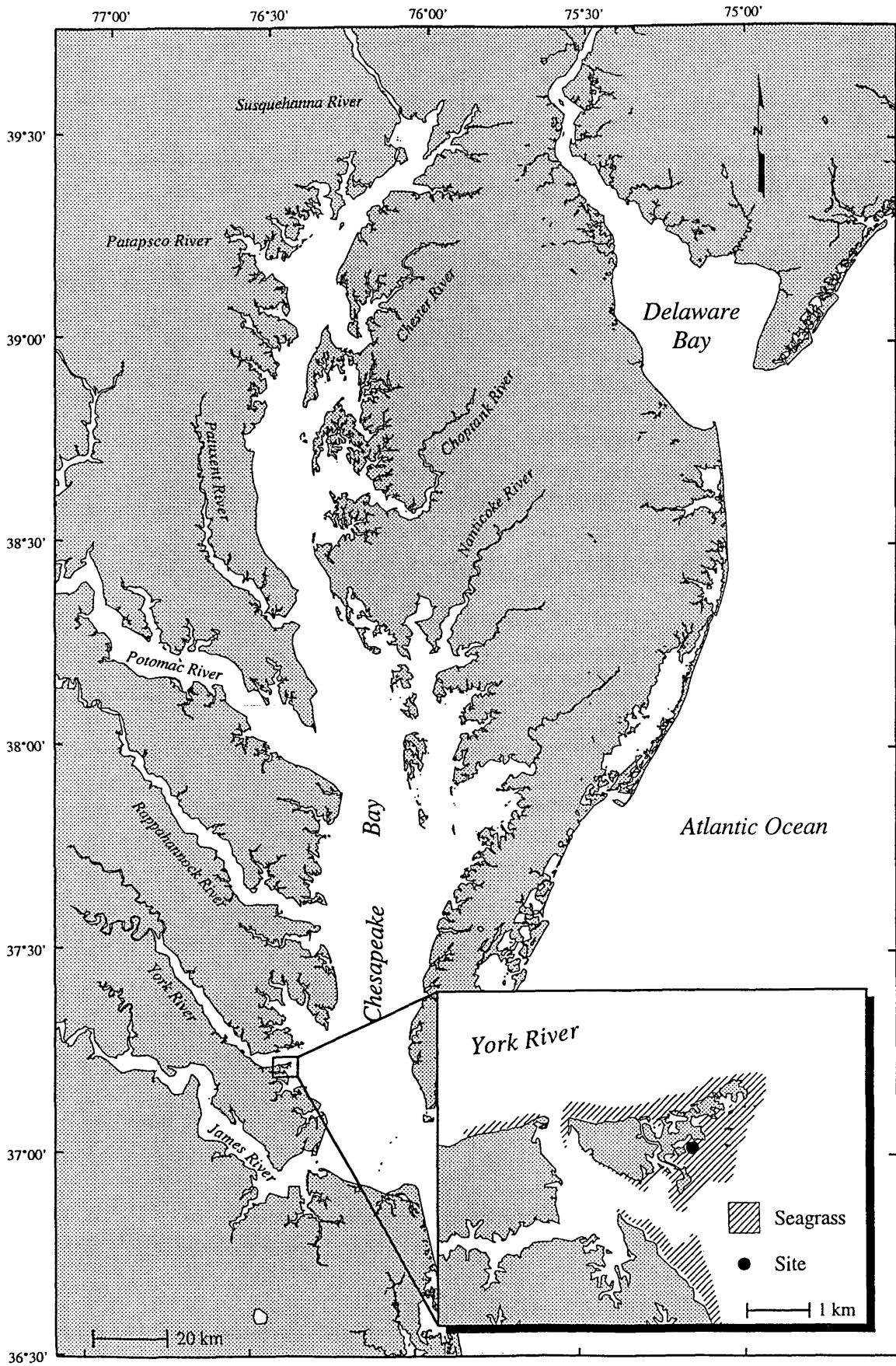








Table 1. Morphological classifications and frequency of observation (number of times sampled per number of collection dates) for seagrasses and drift algae collected during this study.

*indicates plants used within plant diversity experiments.

Frequency no./dates	Species	Morphology	Abbreviations & Schematic
<u>Seagrasses</u>			
9/9	<i>Zostera marina</i> *	Flat, strap-like leaves. 'Unbranched'	Z 
3/9	<i>Ruppia maritima</i> *	Linear, thread-like leaves. 'Unbranched'	R 
<u>Drift Algae</u>			
Chlorophyta (green algae)			
3/9	<i>Ulva lactuca</i> *	Foliose, broad blades. 'Intermediate'	U 
Rhodophyta (red algae)			
6/9	<i>Gracilaria verrucosa</i> *	Coarsely-branched, cylindrical blades. 'Branched'	G 
2/9	<i>Agardhiella tenera</i>	Coarsely-branched, cylindrical blades. 'Branched'	A 
2/9	<i>Ceramium rubrum</i> *	Finely-branched, filamentous blades. 'Branched'	C 

Sampling of phytal epifauna on seagrasses and drift algae

Epifaunal abundance patterns on individual plant species in the field were determined by collecting epifauna and macrophytes simultaneously with a lidded core tube (0.40 m long, 0.03 m² area) on nine dates from August 1996 to August 1997 (N = 6 per plant species on most dates). The tube was placed gently over monospecific algal clumps or seagrass patches and inserted into the sediment. A rubber stopper was inserted into the lid, enclosing the resident epifauna, macrophyte, and approximately 5.0 to 10.0 cm of sediment. The core was removed and the contents were sieved through 1.0 mm mesh, placed into a plastic bag, and frozen until sorting. Depth and time were recorded at each sample location and standardized to depth at mean low water using the observed daily tidal curve (MLW = 0.61 m; N = 6 dates). One-way analysis of variance (ANOVA) for each of the first 6 sample dates indicated that plant species were not distributed at different depths within this study area, so depth was not recorded thereafter.

The aboveground biomass of each macrophyte, and of epiphytic algae, were determined separately in the laboratory after drying at 60°C for a minimum of 48 hours. Motile epifauna, including amphipods, isopods, gastropods, and shrimps, were enumerated and identified to species. Because detritus and leaf litter could not be discerned from buried material using this method, it was not weighed. Although care was taken to collect only the plant species being sampled, in some cases small amounts of non-target plants were included within the core tube. The average biomass of the target species in each sample was 84.1 % ±

19.2 % (1 S.D.), N = 139. Animal abundances were standardized to total dry plant biomass within each sample to compare animal density both within and between plant species.

Experimental manipulations of plant diversity

I manipulated plant species richness in the field and measured animal colonization after six days to test whether plant diversity influences animal diversity. Marine phytal epifauna often respond strongly to plant morphology (Dean and Connell 1987, Hacker and Steneck 1990, Schneider and Mann 1991b), so I created assemblages within species richness levels by grouping plants with similar morphology. Treatments with contrasting structural morphology, therefore, differed in species composition. The experimental design tested the effect of increasing plant species richness and differing species composition on animal diversity (Table 2).

I subjectively categorized plant morphology according to relative degree of branching (Table 1). For instance, *Gracilaria* and *Ceramium* are highly branched red algae, and were included within the gradient labeled 'branched plants'. *Zostera* and *Ruppia* were not branched in the vegetative stage used in these experiments and are considered 'unbranched plants'. Because *Ulva*, a foliose green alga, does not fit into either classification, it was tested alone and within both gradients at the 3- and 5- species treatment levels. Treatments containing both plant architectures or *Ulva* alone were considered intermediate in morphology. *Zostera*, the dominant submerged aquatic plant in the study area, was used as the low diversity treatment (1-species treatment) for the 'unbranched morphology' gradient. The branching red alga

Table 2. Design for plant diversity manipulation experiments. Unbranched treatments contained mostly seagrasses; branched treatments contained primarily branching algae. Treatments designated as intermediate either contain a combination of branched and unbranched plants, or are neither branched nor unbranched (*Ulva*). Treatment abbreviations in parentheses.

Species Composition	Plant Species Richness			
	1	2	3	5
Unbranched Plants	<i>Zostera</i> (Z)	<i>Zostera+</i> <i>Ruppia</i> (ZR)	<i>Zostera+</i> <i>Ruppia+</i> <i>Ulva</i> (ZRU)	
Intermediate	<i>Ulva</i> (U)	<i>Zostera+</i> <i>Gracilaria</i> (ZG)		<i>Zostera+</i> <i>Ruppia +</i> <i>Ulva+</i> <i>Gracilaria+</i> <i>Ceramium</i> (ZRUGC)
Branched Plants	<i>Gracilaria</i> (G)	<i>Gracilaria+</i> <i>Ceramium</i> (GC)	<i>Gracilaria+</i> <i>Ceramium+</i> <i>Ulva</i> (GCU)	

Gracilaria was used within each level of the branched gradient because it was the most commonly observed plant with branching morphology. Each gradient was then completed by adding plants in order of their estimated field abundances at this site (Table 1).

Two experiments were conducted (June 10-16 and June 17-23, 1997; N = 3 each date) during a period of naturally low (1 species, *Zostera*) plant diversity. I created plant diversity gradients by transplanting cores of the two seagrasses, *Zostera* and *Ruppia*, and anchoring drift algae (*Ulva*, *Gracilaria*, and *Ceramium*) within treatment plots. Treatments were created within randomly selected nonvegetated areas of the same seagrass bed in which the survey was conducted. Each replicate consisted of plants placed within a circular patch (0.139 m² area) that was identified with a labeled stake and buoy placed at the offshore edge. Seagrass cores were collected from immediately outside of the treatment plot with a core tube (0.023 m² area) and placed into the bare area. *Ruppia* was not abundant immediately within the study area at the time and was collected from a nearby (~25 m) inshore area. Seagrasses were gently shaken and scraped to remove animals. Because drift algae were not naturally abundant in the York River at the time, I collected algae from a nearby river (James River, <24 hours before use) and defaunated them with a liquid insecticide solution (approximately 5% Sevin, active ingredient: Carbaryl) <2 hours before use. The insecticide solution does not affect algal growth or survival (Carpenter 1986, J.E. Duffy, unpublished data). Drift algae were placed into plots with stout aluminum wire anchors driven into the sediment. I provided equal plant biomass (wet weight) both among treatments and between plant species within treatments when feasible.

I collected the treatments after six days based on previous studies indicating asymptotes in animal species richness and abundance after approximately one week (Stoner and Lewis 1985, Virnstein and Curran 1986), and rapid turnover (approximately 30 - 40% daily) of phytal epifauna (Howard 1985, Edgar 1992, Taylor 1998). A weighted PVC cylinder (82 cm tall, 0.139 m² area) which extended above the sea surface was placed around the treatments. Plants were removed by hand and sieved (1.0 mm mesh) before being placed into a plastic bag. The interior of the cylinder was then dip-netted (0.35 mm mesh) for five 30 second intervals. Two vinyl screens (each 1.0 mm mesh) were placed under the cylinder, and the entire apparatus was lifted above water level, sieving the entire interior. Seagrasses, drift, and epiphytic macroalgae were sorted to species and dried (minimum 48 hours) at 60°C. Fauna (excluding sessile animals and annelids) were enumerated and sorted to species. Faunal abundances were standardized to total dry plant biomass within each plot to compare treatments with different biomass.

Statistical Analyses

On dates when plant species richness in the field was high (5 species, August and September 1996, and January 1997), differences among plant species in total epifaunal density, and in the density of the three most common fauna, were analyzed with one-way ANOVAs (using Type III sums of squares for unbalanced sample sizes, Sokal and Rohlf 1995). Protected multiple comparisons were conducted with Student-Newman-Keuls tests modified by the Kramer procedure for unequal sample sizes and Ryan's stepwise procedure to control

the error rate (Day and Quinn 1989). On dates when only two plant species were collected, data were analyzed with t-tests. Where necessary, data were transformed ($\log x+1$, or $\log 100x+1$) to remove heteroscedasticity following Cochran's test. In cases of unequal sample size, I used the most conservative degrees of freedom to determine the critical value of C.

Plant diversity within experimental treatments was estimated with the Simpson index, $1/\lambda$, using the proportional biomass of each plant species. The Simpson index is a recommended diversity measure because it is relatively unbiased by sample size (Lande 1996). Animal diversity was estimated with simple species richness and the Simpson index (equation 5c in Lande 1996); evenness was estimated with E_{var} because of its sensitivity to both minor and abundant species (Smith and Wilson 1996). This feature is desirable when there are numerous rare but few dominant species.

To test the general influence of plant diversity across all plant species compositions, regressions were fitted between the dependent variables epifaunal density, species richness, Simpson diversity, and evenness, and the independent variable plant diversity, within each plot. Data from both experiments were pooled because trends of epifaunal community responses to plant diversity did not differ significantly between experiments, (analysis of covariance (ANCOVA) for effect of date on epifaunal density, species richness, evenness, and diversity; plant diversity was the covariate). Regressions were also fitted between epifaunal density and diversity indices and the proportion of macroalgae within each plot due to *post hoc* observations of its apparent influence on epifauna. Backwards elimination multiple regressions tested the relative influences of total dry plant biomass, relative algal abundance, and plant

diversity on epifaunal density and diversity within each plot. Independent variables were converted to standardized normal z-scores if their measurement units and magnitudes differed (Sokal and Rohlf 1995). Multiple regressions also tested effects of species-specific dry plant biomass on species-specific animal densities within treatment plots.

Simple linear regressions of epifaunal density and diversity indices against plant diversity within the two separate gradients (branched and unbranched plants) tested the effect of plant diversity unconfounded by plant species composition. The high diversity treatments (5-species, intermediate architecture) were included in both gradients. Additionally, ANCOVA tested effects of species composition (branched versus unbranched plants) on animal diversity while holding plant species diversity (the covariate) constant. ANCOVA factors were species composition (branched, unbranched, and intermediate), date of the experiment (June 10-16, June 17-23), and interaction. The covariate was plant species diversity (calculated with the Simpson index as above). Data were transformed (\sqrt{x}) following Cochran's tests if heteroscedasticity was detected.

RESULTS

Survey of phytal epifauna on seagrasses and drift algae

A total of 12,457 individuals representing 35 species was collected from six different plant species during the survey of phytal epifauna (Tables 1, 3). While *Zostera* persisted throughout the year, other plant species in my study area were ephemeral, leading to some sampling periods when one or more of those species were absent and could not be sampled. Drift algae were more common in fall and winter but relatively rare during other seasons. *Gracilaria* was the most common alga sampled and was present on all but three sampling dates.

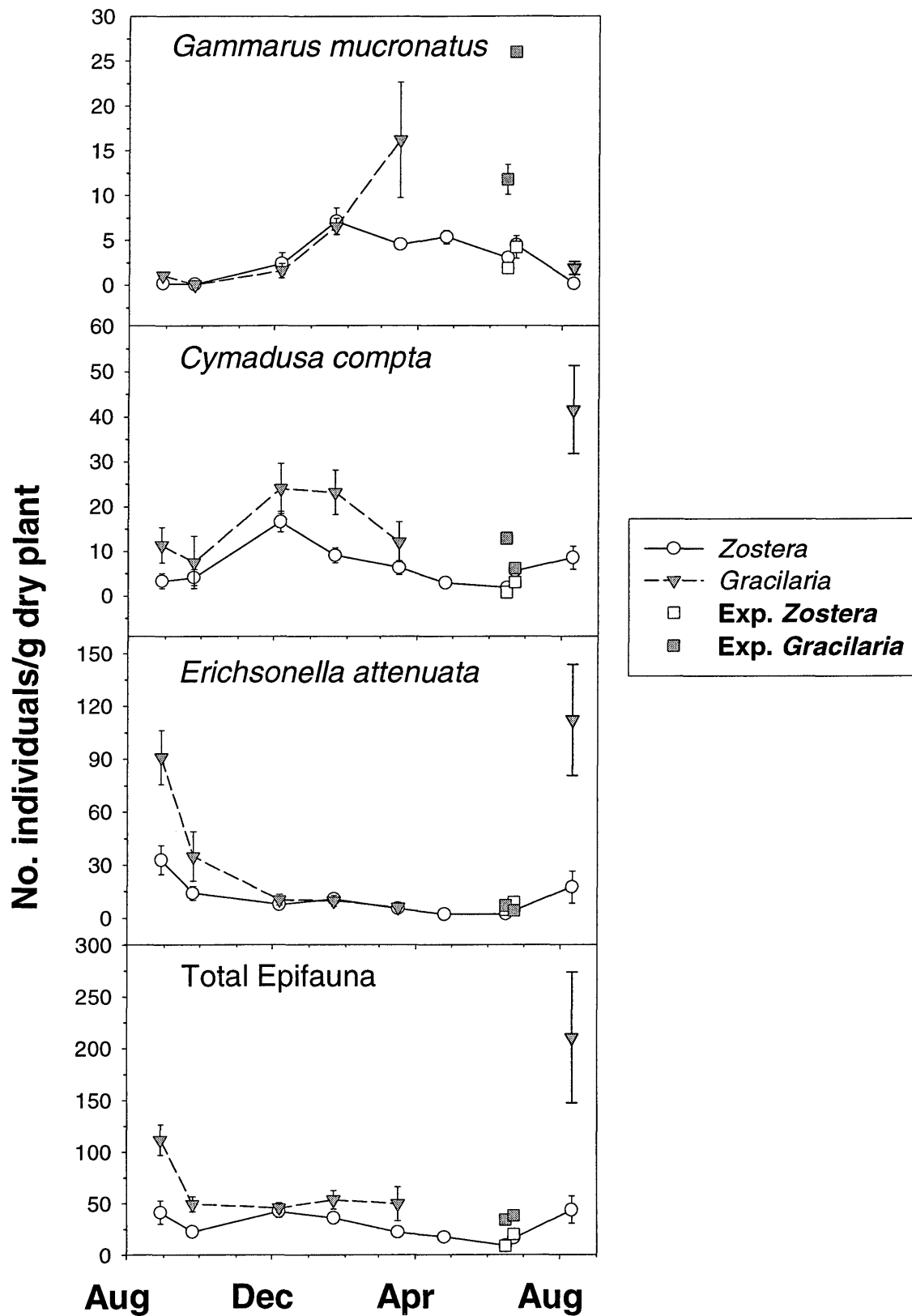
Three epifaunal species, the isopod *Erichsonella attenuata* Harger and the amphipods *Cymadusa compta* Smith and *Gammarus mucronatus* Say, constituted 75% of the total animal community, with one species, *Erichsonella*, accounting for over 43% of the total fauna collected (Table 3). *Erichsonella* peaked in abundance during late summer and fall, *Cymadusa* peaked in the fall/winter, and *Gammarus* was most abundant during late spring/early summer (Figure 2). Seasonal abundance peaks of these three epifaunal species are exaggerated on *Gracilaria* when compared to densities on *Zostera*.

Generally, when algal species were present, and the abundance of individual epifaunal species was high, species abundances were higher on seaweeds relative to seagrasses (Table 4), despite the apparent preponderance of seagrasses within the entire plant community. None of the numerically dominant epifaunal species had distributions restricted to a specific plant

Table 3. Total abundances of all species collected during the survey and experimental portions of this study. * denotes organisms commonly described as epifauna.

Species found during survey	#	% of total	Species found during experiments	#	% of total
<i>Erichsonella attenuata*</i>	5344	42.90%	<i>Gammarus mucronatus*</i>	5827	52.77%
<i>Cymadusa compta*</i>	3195	25.65%	<i>Cymadusa compta*</i>	2260	20.47%
<i>Gammarus mucronatus*</i>	1088	8.73%	<i>Erichsonella attenuata*</i>	2123	19.23%
<i>Edotea triloba</i>	971	7.79%	<i>Edotea triloba</i>	425	3.85%
<i>Elasmopus levis*</i>	622	4.99%	<i>Crangon septemspinosa</i>	147	1.33%
<i>Bittium varium*</i>	356	2.86%	<i>Elasmopus levis*</i>	61	<1%
<i>Ampithoe longimana*</i>	173	1.39%	<i>Palaemonetes pugio*</i>	52	<1%
<i>Ampelisca abdita</i>	143	1.15%	Unidentified Ampeliscids	25	<1%
<i>Palaemonetes pugio*</i>	111	<1%	<i>Bittium varium*</i>	24	<1%
<i>Callinectes sapidus</i>	91	<1%	<i>Callinectes sapidus</i>	18	<1%
<i>Caprella penantis*</i>	64	<1%	<i>Menidia menidia</i>	14	<1%
<i>Hydrobia</i> sp.	50	<1%	<i>Nassarius obsoletus</i>	10	<1%
<i>Listriella clymenellae</i>	48	<1%	<i>Palaemonetes vulgaris*</i>	9	<1%
<i>Crangon septemspinosa</i>	34	<1%	<i>Nassarius vibex</i>	8	<1%
<i>Palaemonetes vulgaris*</i>	31	<1%	<i>Caprella penantis*</i>	8	<1%
Unidentified Ampeliscids	31	<1%	<i>Idotea baltica*</i>	7	<1%
<i>Nassarius vibex</i>	28	<1%	<i>Hydrobia</i> sp.	7	<1%
Unidentified Xanthids	19	<1%	<i>Mitrella lunata*</i>	5	<1%
<i>Paracaprella tenuis*</i>	16	<1%	Unidentified Tanaid	3	<1%
<i>Gobiesoma bosc</i>	13	<1%	<i>Palaemonetes intermedius*</i>	2	<1%
<i>Palaemonetes intermedius*</i>	5	<1%	Unidentified Gastropod	2	<1%
Unidentified Tanaid	4	<1%	<i>Gobiesoma bosc</i>	1	<1%
<i>Nassarius obsoletus</i>	3	<1%	<i>Eurypaneopus depressus</i>	1	<1%
<i>Listriella plumulosis</i>	2	<1%	<i>Paracaprella tenuis*</i>	1	<1%
Unidentified Gastropod	2	<1%	<i>Symphurus plagiusa</i>	1	<1%
<i>Anguilla rostra</i>	2	<1%	<u><i>Ampithoe longimana*</i></u>	<u>1</u>	<u><1%</u>
<i>Dulichchiella appendiculata*</i>	2	<1%	Total	11,042	
<i>Lucania parva</i>	2	<1%			
Unidentified Atyid	1	<1%			
Unidentified Corophiid	1	<1%			
<i>Microprotopus raneyi</i>	1	<1%			
<i>Urosalpinx cinerea</i>	1	<1%			
<i>Mitrella lunata*</i>	1	<1%			
<i>Sympleustes glaber</i>	1	<1%			
<u><i>Idotea baltica*</i></u>	<u>1</u>	<u><1%</u>			
Total	12,457				

Figure 2. Mean abundance (± 1 SE) of the three most common epifaunal species and total epifauna occupying *Zostera marina* and *Gracilaria verrucosa* at Goodwin Islands on nine sampling periods from August 1996 to August 1997. Densities on plants deployed during diversity experiments in June 1997 (Exp. *Zostera* and *Gracilaria*) are shown for comparison.



species, but there were several instances of differences in the abundances of individual taxa among plant species (Table 4, Figure 3). On dates when plant species diversity was high (5 species), there was only one date (September) when total animal densities differed significantly among plant species (Table 4). Although multiple comparisons (SNK tests) failed to reveal distinct differences in species-specific densities among specific plant species in several instances, there are significantly higher densities on drift algae relative to seagrasses. This is especially apparent for the amphipod *Cymadusa*, as its density was significantly higher on algae on all three dates, and again much higher on *Gracilaria* in August 97, although there are only data for two plant species.

Experimental manipulations of plant diversity

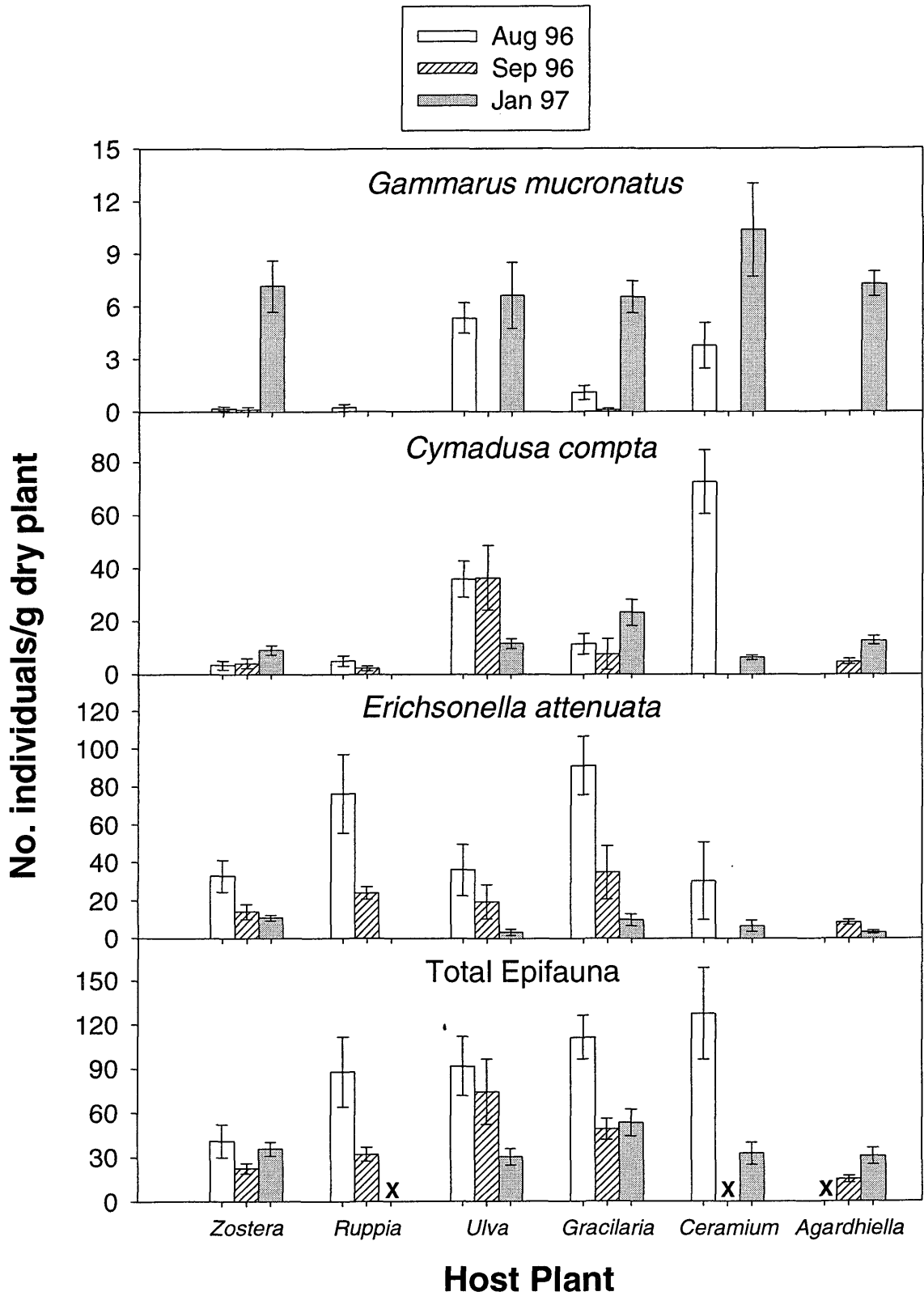
A total of 11,042 individuals representing 26 species was collected during the two experiments in June 1997 (Table 3). The collection was dominated by the amphipod *Gammarus*, which comprised over 50% of the total animals collected. Overall, animal abundance and plant biomass were positively correlated ($r^2 = 0.52$; $p < 0.001$).

The experimental treatments adequately recreated plant diversity gradients; nominal and observed diversity in each treatment were positively correlated: species richness $r^2 = 0.36$; $p < 0.001$; diversity $r^2 = 0.71$; $p < 0.001$. Although there were significant differences in plant biomass among treatments (2-way ANOVA, Treatment: $p < 0.001$, Date: $p = 0.035$, Treatment*Date: $p = 0.021$), plant biomass was not significantly related to plant diversity ($r^2 = 0.00$; $p = 0.99$).

Table 4. One-way ANOVAs testing differences in epifaunal density (no./g dry plant) among plant species collected during field survey. ANOVAs were performed using type III sums of squares for unbalanced data and were only performed for dates when more than one plant species was collected. †, ‡ data analyzed following transformation ($\log x+1$; and $\log 100x+1$, respectively) to remove heteroscedasticity (Cochran's test). SNK tests were performed with the Kramer modification for unequal sample sizes and Ryan's stepwise procedure to control the experiment-wise error rate, with treatments ranked in ascending order. Underlined treatments are not significantly different from each other. Bold indicates statistical significance at $p < 0.05$. N = sample size. See Table 2 for plant abbreviations. "-" = not applicable.

Date	Aug. 29, 96	Sept. 25, 96	Dec. 7, 96	Jan. 22, 97	Mar. 17, 97	Apr. 25, 97	Aug. 11, 97
Plants	Z R U G C	Z R U G A	Z G	Z U G C A	Z G	Z R	Z G
N	6 7 6 6 5	6 6 6 3 3	6 5	6 4 5 5 3	6 6	6 6	6 6
	F P	F P	F P	F P	F P	F P	F P
Total Density	2.31 0.086	14.03‡ <0.001	0.17 0.689	1.96 0.144	2.72 0.130	11.27 0.007	5.97 0.035
SNK	-	<u>A Z R U G</u>	-	-	-	R Z	Z G
<i>Gammarus</i>	6.63‡ 0.001	0.68 0.615	0.29 0.604	0.61† 0.664	3.28 0.100	7.34 0.022	5.48 0.041
SNK	<u>R Z G C U</u>	-	-	-	-	R Z	Z G
<i>Cymadusa</i>	16.78† <0.001	6.79† 0.001	1.76 0.218	7.00† 0.001	1.52 0.246	0.11 0.745	13.77† 0.004
SNK	<u>Z R G U C</u>	<u>R Z A G U</u>	-	<u>C Z U A G</u>	-	-	Z G
<i>Erichsonella</i>	2.91 0.042	1.48 0.248	0.40 0.545	2.18 0.113	0.04 0.852	0.12 0.737	8.33 0.016
SNK	<u>C Z U R G</u>	-	-	-	-	-	Z G

Figure 3. Mean abundance (± 1 SE) of the three most common epifaunal species and total epifauna occupying each plant species at Goodwin Islands on dates when plant species richness was high (5 species). X: plant not observed. Sample sizes and statistical results testing differences in density among plant species shown in Table 4.



There were few significant effects of plant diversity on epifaunal diversity. Animal density and plant diversity ($r^2 = 0.04$, $p = 0.146$), animal diversity and plant diversity ($r^2 = 0.06$; $p = 0.075$), and animal evenness and plant diversity ($r^2 = 0.03$; $p = 0.204$) (Figure 4), were not significantly related. However, there was a weak significant positive correlation between animal species richness and plant diversity ($r^2 = 0.08$; $p = 0.035$).

Regressions of epifaunal diversity within plant diversity gradients with disparate structural morphologies indicate differences in the effect of plant species diversity on epifaunal diversity with changes in plant species composition. There were no relationships between any of the animal community variables (density, species richness, evenness, and diversity) and plant diversity within the branched gradient, which includes branching red algae at each species level and both plant architectures at the 5-species level, (Table 5, Figure 4). In contrast, within the unbranched gradient, which has branching red algae only within the 5-species treatment, there was a significant positive relationship between epifaunal density and plant diversity ($r^2 = 0.22$, $p = 0.021$), and a negative relationship between animal evenness and plant diversity ($r^2 = 0.28$, $p = 0.008$; Table 5, Figure 4).

Plant species composition had a larger influence on animal diversity than did plant species diversity. After controlling for plant species diversity as the covariate, epifaunal density was higher and evenness lower in treatments containing branched plants (Figure 5a, Table 6). Treatments containing both plant morphologies or *Ulva* alone had intermediate values. The effect of species composition was highly significant ($p < 0.001$) for both variables, but the covariate, plant species diversity, was only significant for animal density ($p = 0.027$). Animal

Figure 4. Correlations between epifaunal density, species richness, evenness (E_{var}), and Simpson diversity against plant Simpson diversity and the proportion of algal biomass within experimentally established plant diversity gradients. Regression statistics and solid regression line for all data are shown only when statistically significant, $p < 0.05$. Dashed and dotted regression lines (shown even if non-significant) are for unbranched and branched plant diversity gradients, respectively. Regression statistics for branched and unbranched plant comparisons are in Table 5. See Table 2 for treatment abbreviations.

Epifaunal

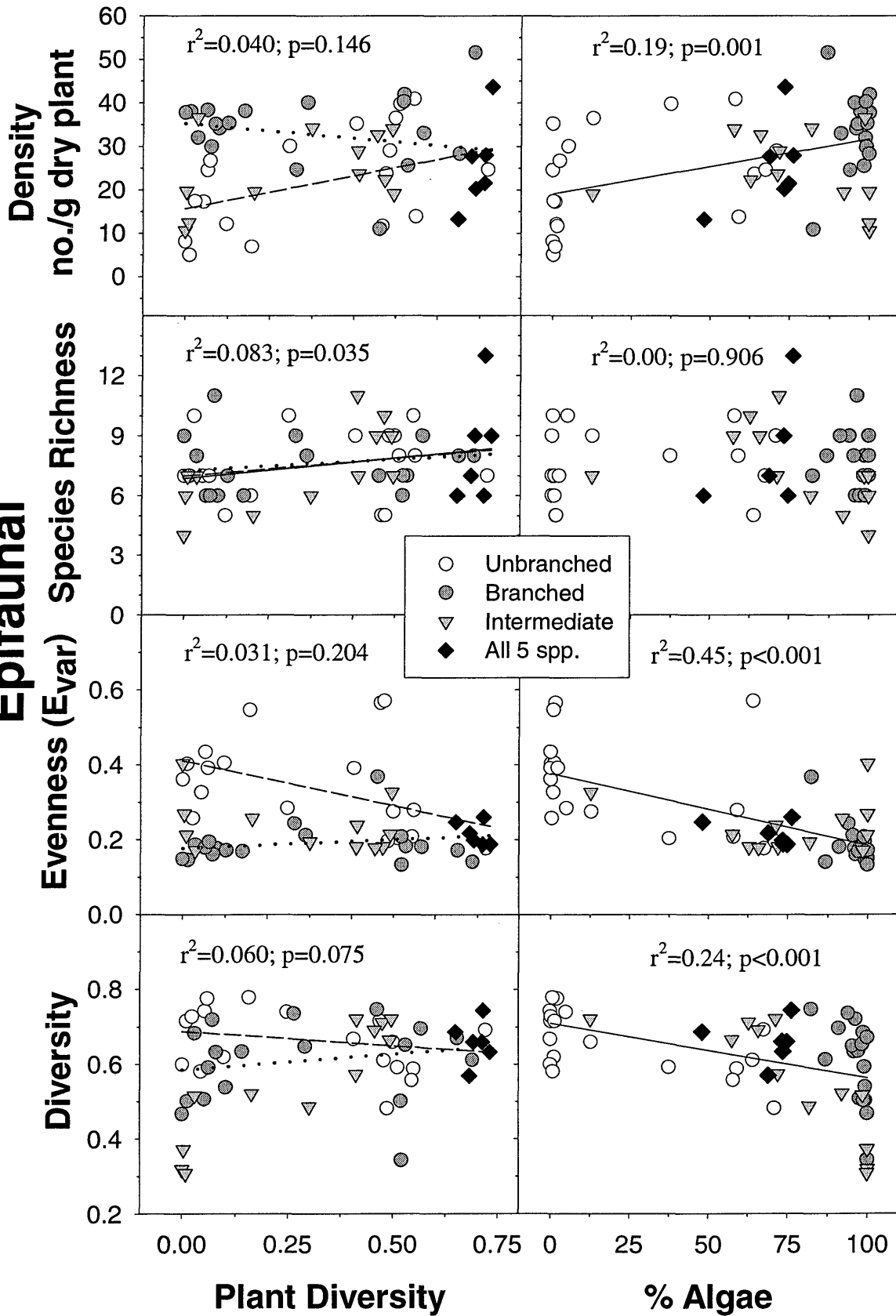


Table 5. Simple linear regressions testing effects of plant diversity on animal density, species richness, evenness, and Simpson diversity for the two separate experimental diversity gradients differing in species composition. Note presence of both plant morphologies (branched and unbranched) within 5-species treatment, *ZRUGC*. Bold indicates statistical significance at $p < 0.05$. See Table 2 for treatment abbreviations.

Plant Species Composition	EPIFAUNAL DENSITY		SPECIES RICHNESS		EVENNESS		SPECIES DIVERSITY	
	Coefficient	p	Coefficient	p	Coefficient	p	Coefficient	p
Intercept	15.7	<0.001	7.01	<0.001	0.412	0.000	0.690	<0.001
Unbranched Plant Diversity (Z, ZR, ZRU, ZRUGC)	19.0	0.021	1.76	0.251	-0.241	0.008	-0.0773	0.194
Intercept	35.3	<0.001	7.29	<0.001	0.178	<0.001	0.586	<0.001
Branched Plant Diversity (G, GC, GCU, ZRUGC)	-8.37	0.245	1.09	0.413	0.0457	0.214	0.084	0.261

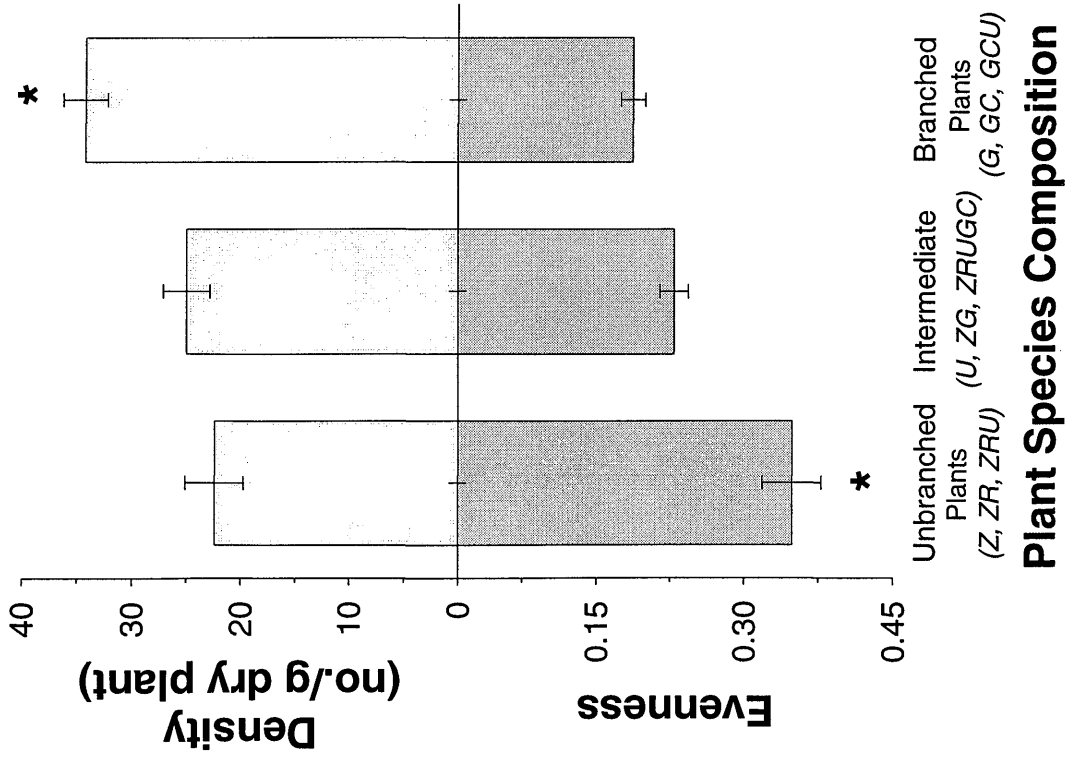
species richness did not differ with species composition; animal species diversity differed with species composition, but there were significant interactions (as well as untransformable heteroscedasticity) (Figure 5b, Table 6). Increased animal density and lower evenness within branched treatments were due to the dominance of amphipods within branched plant treatments (Figure 6).

In addition to the influences of plant species diversity and composition, there were obvious influences of the relative abundance of macroalgae (regardless of structural morphology) within the experimentally established plant communities. There was a positive correlation between epifaunal density and the proportion of seaweed within plots ($r^2 = 0.19$; $p = 0.001$), and negative correlations between epifaunal diversity and % algae ($r^2 = 0.24$; $p < 0.001$) and epifaunal evenness and % algae ($r^2 = 0.45$; $p < 0.001$) (Figure 4).

Results of backwards elimination multiple regressions, which evaluate each independent variable while holding the others statistically constant, differ from those of the univariate regressions. When epifaunal abundance (not density), richness, evenness, and diversity were regressed against each plant community factor (biomass, % algae, and diversity), plant biomass and % algae still affected animal abundance, but plant diversity had significant positive influences on both animal species richness (as in the univariate regression) and diversity (Table 7). Animal diversity was not related to plant diversity in the univariate regression (Figure 4, Table 5). Also, as in the univariate regressions, % algae had a negative impact on animal evenness and diversity. This is somewhat complicated because plant biomass and % algae are collinear ($r^2 = 0.36$; $p < 0.001$), but other results indicate that specific algal abundance had a

Figure 5. A. Mean epifaunal density, evenness, and B. species richness, and Simpson diversity (± 1 SE) for different plant species compositions in experiments. Data pooled from both dates (N = 3 each date) after time-treatment interactions were non-significant for density, evenness, and species richness. Results of ANCOVA with plant Simpson diversity as the covariate shown in Table 6. * indicates a mean significantly different from the others (SNK tests performed with Ryan's procedure). See Table 2 for treatment combinations.

A



B

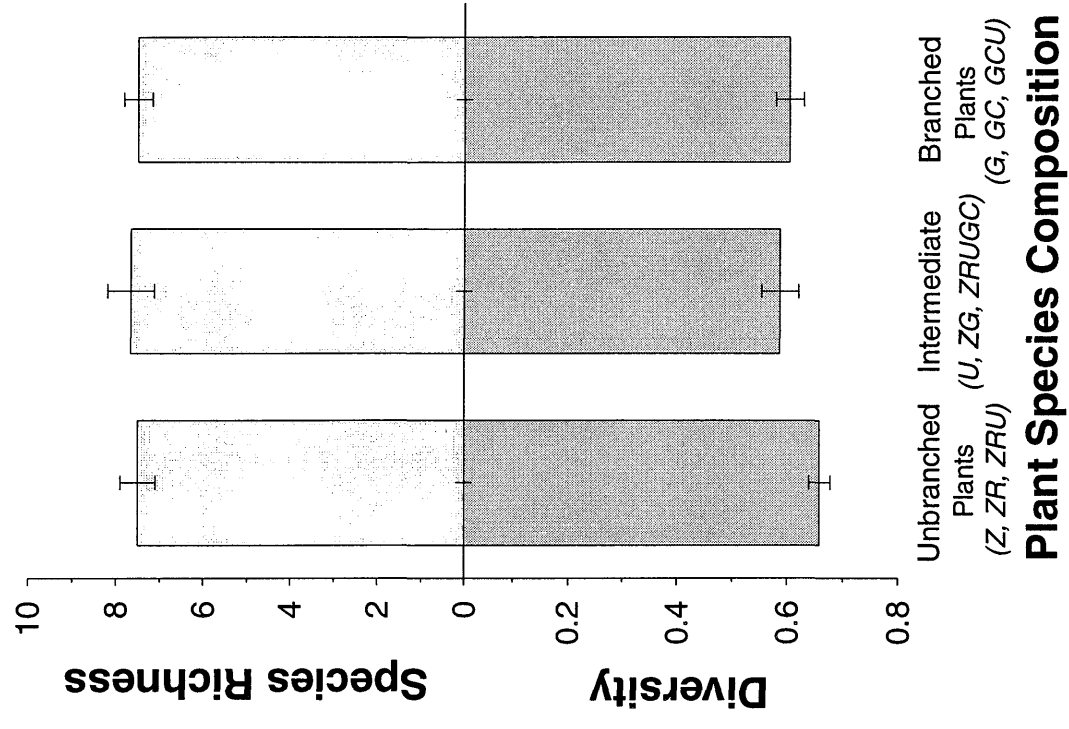
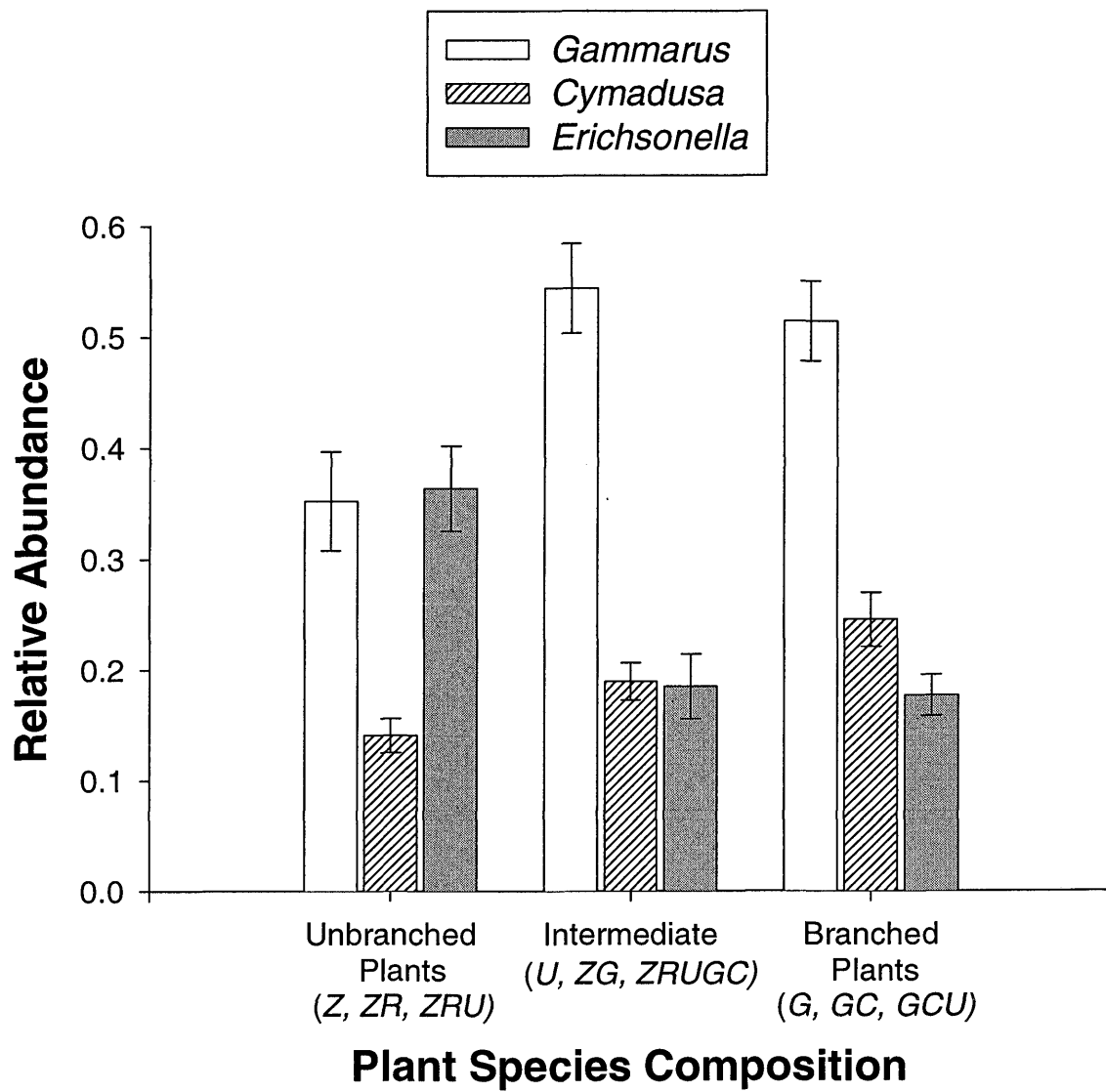


Figure 6. Mean relative abundance (± 1 SE) of the three most common epifaunal species within experimental treatments. Data pooled from both dates (N = 3 each date). See Table 2 for treatment abbreviations.



greater impact on epifaunal density and diversity than seagrass biomass. Specifically, there were significant effects of algal biomass on epifaunal density, species richness, evenness, and diversity, but no significant variation was attributed to seagrass biomass (Table 7).

Additionally, species-specific responses show *Gammarus* and *Cymadusa* responded positively to *Ulva* and *Gracilaria*, and *Ulva*, *Gracilaria*, and *Ceramium*, respectively.

Density of the isopod *Erichsonella* was significantly related to the biomass of all plant species except the foliose alga *Ulva* (Table 7, Figure 7).

Because multiple regression results of epifaunal diversity against plant diversity were statistically significant, and simple regression results were not, I performed residual analysis to separate the confounding effects of plant diversity and macroalgal abundance on epifaunal diversity. Specifically, I withdrew residuals from the regression between epifaunal diversity and % algae, and fitted a regression between the residuals and plant diversity. I then withdrew the residuals from a regression between epifaunal diversity and plant diversity, and regressed them against % algae. Results were consistent with simple regressions for the entire data set and for the two different species compositions. Epifaunal diversity and plant diversity were weakly correlated after removing the confounding effect of % algae, whereas epifaunal diversity was more strongly correlated with % algae after accounting for changes in plant diversity (Figure 8).

Table 7. Backwards elimination multiple regression analyses for plant diversity manipulations. A) animal community responses to standardized normal plant community parameters, B) animal community responses to specific plant species biomasses, and C) species-specific animal responses to specific plant biomasses within treatment plots. Bold indicates statistical significance at $p < 0.05$. “-“ indicates variable removed during backwards elimination. All regressions significant at $p < 0.05$.

A Factors	EPIFAUNAL ABUNDANCE		SPECIES RICHNESS		EVENNESS		SPECIES DIVERSITY	
	Coefficient	p	Coefficient	p	Coefficient	p	Coefficient	p
Intercept	213	<0.0001	7.66	<0.0001	0.255	<0.0001	0.617	<0.0001
Plant Biomass	66.3	<0.0001	-	-	-	-	-0.0303	0.069
% Algae	34.8	0.006	-	-	-0.0728	<0.0001	-0.0397	0.019
Plant Diversity	-	-	0.490	0.035	-	-	0.0307	0.023
B								
Intercept	-2.53	0.940	7.88	<0.0001	0.346	<0.0001	0.716	<0.0001
<i>Zostera</i>	11.8	0.062	-	-	-	-	-	-
<i>Ruppia</i>	86.8	0.066	-	-	-	-	-	-
<i>Ulva</i>	23.2	<0.0001	-0.162	0.057	-0.0113	0.010	-0.0394	<0.0001
<i>Gracilaria</i>	37.0	<0.0001	-	-	-0.0224	<0.0001	-0.00332	<0.0001
<i>Ceramium</i>	46.3	0.012	-	-	-	-	-	-

Table 7, Continued.

C	GAMMARUS		CYMADUSA		ERICHSONELLA	
	Coefficient	p	Coefficient	p	Coefficient	p
Intercept	13.4	0.316	9.64	0.082	8.01	0.122
<i>Zostera</i>	-	-	-	-	4.46	<0.0001
<i>Ruppia</i>	-	-	-	-	25.2	0.015
<i>Ulva</i>	17.2	<0.0001	2.38	0.046	-	-
<i>Gracilaria</i>	19.7	<0.0001	7.84	<0.0001	4.69	<0.0001
<i>Ceramium</i>	-	-	15.8	0.008	18.6	<0.0001

Figure 7. Mean abundance (± 1 SE) of the three most common epifauna and of total epifauna within experimental treatments. Vertical lines separate treatments with different numbers of plant species. Data pooled from both dates (N = 3 each date). See Table 2 for treatment abbreviations.

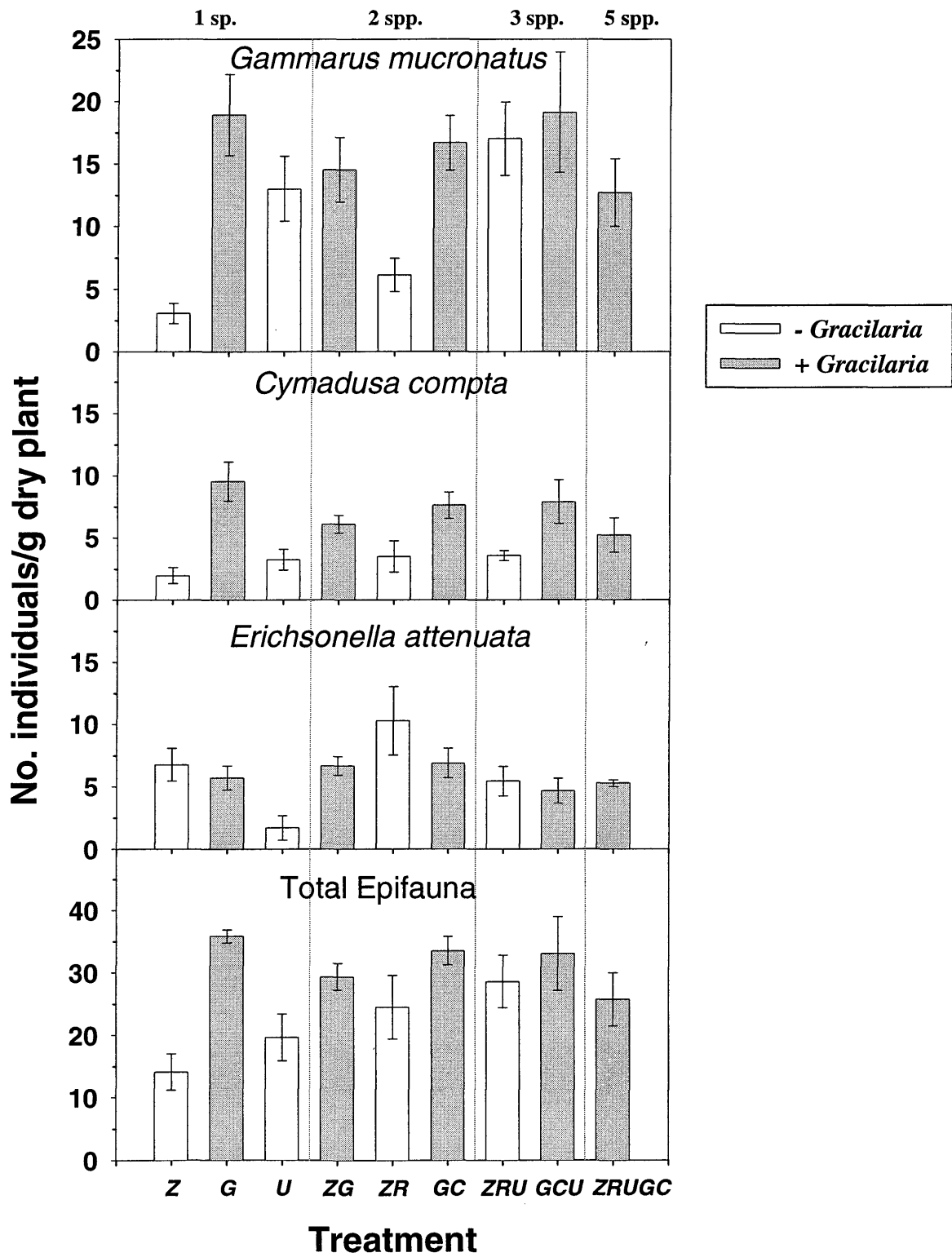
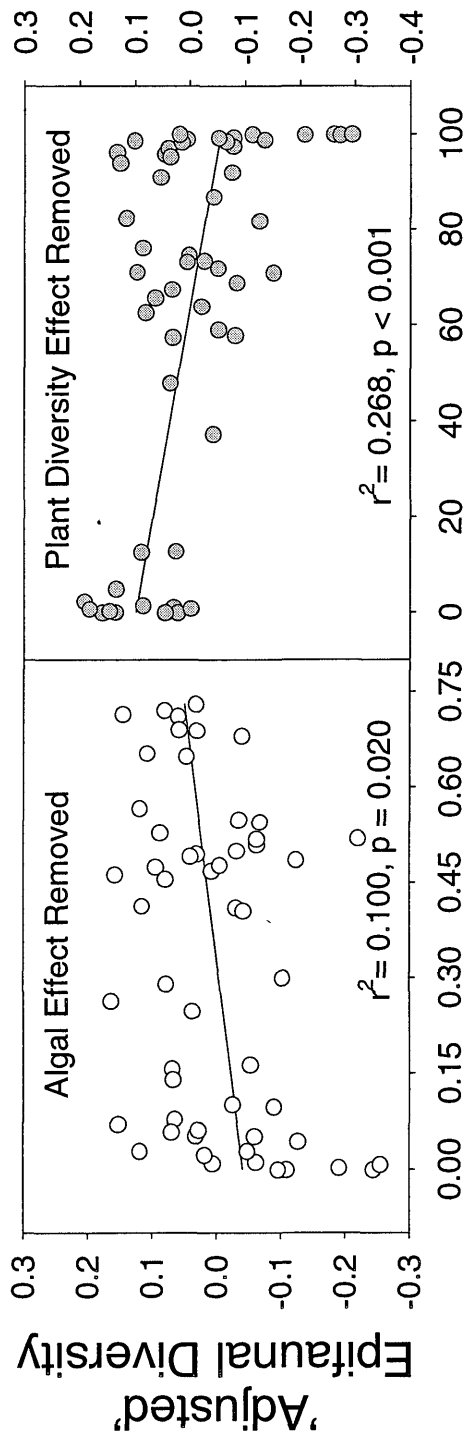


Figure 8. Regressions of epifaunal diversity against plant diversity and relative algal abundance within each plot after the confounding influences of the other were removed through residual analysis. See text for details.



Plant Diversity

% Algae

DISCUSSION

Plant and animal diversity are often positively correlated (MacArthur 1958, MacArthur and MacArthur 1961, Pianka 1966, 1967, Rosenzweig and Winakur 1969, Murdoch et al. 1972, Tonn and Magnuson 1982, among others), but there were no experimental tests of the relationship. Faunal diversity may decrease with diminishing plant diversity, potentially compromising ecosystem function. I tested the effect of plant diversity on animal diversity in a temperate seagrass bed. I found highly significant effects of plant species composition (seaweeds versus seagrasses), but relatively weak effects of plant diversity, on animal diversity. In a concurrent field survey, animal community structure differed among plant species in a seagrass bed, but there were no host-plant specialists. Animals responded to specific plant species and plant structural attributes in the experimental treatments and in undisturbed field situations, supporting the conclusion that communities can respond idiosyncratically to changes in species diversity.

Biodiversity and ecosystem function

There are several hypotheses about the effect of biodiversity on ecosystem function (Lawton 1994, Johnson et al. 1996). In the redundant species hypothesis, some minimal number of species is critical but beyond that species perform basically redundant tasks (Walker 1992). The rivet hypothesis proposes that all species make at least some contribution to ecosystem processes (Ehrlich and Ehrlich 1981). The idiosyncratic hypothesis states that

species composition affects ecosystem processes more than diversity alone (Lawton 1994, Naeem et al. 1995). Consequently, the first two hypotheses predict a generally positive relationship between diversity and ecosystem function, whereas the idiosyncratic hypothesis predicts positive, negative, or indeterminate effects varying with species composition.

Results of the plant diversity manipulations in this study support the idiosyncratic hypothesis: the effects of changing species composition (seagrass versus seaweed) on epifaunal density and diversity were greater than those of changing plant diversity. In support of diversity effects, there were weak but significant positive correlations between animal species richness and plant diversity across all plant species compositions ($r^2 = 0.083$, $p = 0.035$, Figure 4), and between animal diversity and plant diversity after removing the confounding influence of algal biomass ($r^2 = 0.100$, $p = 0.020$, Figure 8). In most cases, however, animal density and diversity were more strongly affected by the relative abundance of macroalgae within the experimentally established plant communities (Figure 4, Figure 8).

Plant species composition in the experiments (primarily branching seaweeds versus unbranched seagrasses) overshadowed influences of species diversity on epifaunal communities. Although treatment combinations were created with the intent of contrasting plant structural morphology, they probably contrasted species assemblages with a high or low proportion of macroalgae. The unbranched plant groups are almost entirely composed of seagrasses; macroalgae was included only in the 3-species treatment, *ZRU* (Table 2). The branched plant treatments included only macroalgae, and the intermediate treatments (except *Ulva* alone) contained a mixture of both. Epifaunal densities were higher and evenness was

lower in plant communities with a higher relative abundance of seaweed (Figure 5), similar to simple and multiple regression results (Figure 4, Tables 6 and 7). Thus, the comparison of branched versus unbranched plant architectures probably was masked by the influence of macroalgal abundance on epifauna. Although plant biomass and the proportional abundance of macroalgae were collinear, species-specific multiple regressions provide further supporting evidence that seaweed relative abundance had a greater impact than seagrass biomass on epifaunal diversity. Specifically, total animal density, evenness, diversity, and densities of two of the three most common epifauna were significantly related only to algal biomass, and not to the biomass of the two seagrass species (Table 7).

Similar to other studies (Hooper 1998, Symstad et al. 1998), the creation of plant diversity gradients with different species compositions resulted in different responses to plant diversity. Specifically, the inclusion of seaweeds within the highest richness levels (*ZRU* and *ZRUGC*, Table 2) likely caused significant correlations between epifaunal density and evenness and plant diversity within the unbranched (primarily seagrass) plant diversity gradient (Table 5, Figure 4). In contrast, there were no significant relationships between epifaunal diversity indices and plant diversity in the branched plant diversity gradient (Table 5, Figure 4), likely because plant species with large effects (seaweeds) were included within each treatment level. The relative abundance of macroalgae within species diversity levels, therefore, can be considered a hidden treatment (Huston 1997), i.e., a biological factor with disproportionate effects on epifaunal density and diversity relative to the primary experimental factor, plant species diversity.

Animal diversity versus plant diversity

It is unclear if the weak relationships between epifaunal species richness and diversity against plant diversity are biologically meaningful. The positive correlation between epifaunal species richness and plant diversity was due to the average addition of only a single species over the entire range of observed plant diversity. The correlation between animal diversity and plant diversity was only obtained after statistical removal of the conflicting, negative impact of algal biomass. There was no evidence of guild expansion or addition in high plant species diversity treatments that might indicate increased resource availability (e.g. Willson 1974).

In many previous studies, animal diversity was more closely related to habitat complexity, which includes substrate diversity (Abele 1974, Kohn 1967, O'Connor 1991) and vegetational structural diversity (MacArthur and MacArthur 1961, Pianka 1966, 1967, Murdoch et al. 1972, Bell and Coen 1982, Stinson and Brown 1983), than to plant species richness. As discussed, though, it was probably the proportional abundance of macroalgae, and not the intended comparisons of plant morphology, that affected epifaunal diversity in this study. This effect is similar to those observed by Willson (1974) and Strong and Levin (1979), where the addition of trees to a vegetational series had disproportionate effects (relative to understory species) on avian and insect species diversity, respectively. Contrary to those studies, however, the disproportionate effects of a particular plant type in this study primarily affected animal abundance rather than species richness. Significant increases in the density of *Gammarus*, and decreases in the density of *Erichsonella*, on treatments containing seaweeds

caused a decline in epifaunal evenness in the unbranched and intermediate plant species compositions (Figures 5 and 6).

Weak species diversity effects could be due to natural consequences of this particular system or to experimental artifacts. Communities with abundant functional types or guilds and more habitat specialists than generalists, such as terrestrial grasslands, are predicted to respond positively to increases in resource heterogeneity (Huston 1994). In contrast, although marine epifauna are commonly very abundant on drift algae (Gore et al. 1981, Stoner 1985, Fredette and Diaz 1986, Lewis 1987, Virnstein and Howard 1987b, Holmquist 1997), they are generally not host-plant specialists (Lubchenco and Gaines 1981, Hay et al. 1988a, b, Hay and Fenical 1988, this study). Also, the vast majority of epifauna (>95% of total) collected were mesograzers (sensu Brawley 1992), functionally similar herbivores which graze upon macrophytes and/or their microalgal coating. Additionally, the relatively short experimental duration might have excluded taxa with longer dispersal times. For example, if the most abundant organism on experimental treatments, *Gammarus*, is particularly adept at colonizing seaweeds, then changes in epifaunal structure should occur during succession (e.g. Dean and Connell 1987), a process which could not be determined in the time frame examined here.

Grassbed faunal structure

The distribution of epifauna within seagrass beds has potentially important consequences for community structure and function. Epifauna are important prey for juvenile fishes and decapod crustaceans (Kikuchi 1974, Adams 1976, Leber 1985, Edgar and Shaw 1995), and

can enhance seagrass growth by grazing light-inhibiting periphyton from seagrass blade surfaces (Orth and van Montfrans 1984, van Montfrans et al. 1984, Neckles et al. 1993, Jernakoff et al. 1996). This study and others (Gore et al. 1981, Stoner 1985, Lewis 1987, Virnstein and Howard 1987b, Mann and Schneider 1991a, Holmquist 1997) have shown that epifaunal densities are generally higher on drift algae than on seagrasses. This pattern can have several significant consequences. If predation mortality differs with varying plant structural complexity (Nelson 1979, Leber 1985), then increased plant structural diversity may lower predation rates on epifaunal prey and diminish trophic transfer, or shift the competitive balance among predators with different feeding modes (Orth et al. 1984, Heck and Orth 1984, Heck and Crowder 1991, Orth 1992). Furthermore, consistently higher densities of total or specific epifauna on drift algae could decrease the grazing of periphyton from seagrass blade surfaces. Alternatively, the refuge (or other) value of algae could result in higher per-area grazer densities, thus increasing periphyton grazing. Unfortunately, although mesograzers can have species-specific effects on algal growth and survival (Duffy 1990), and their effects vary with species composition and environmental conditions (Neckles et al. 1993), knowledge of their functional ecology is limited (Bell 1991, Duffy and Hay 1991a, Brawley 1992).

Epifauna responded idiosyncratically to specific plant species in the experiment and field collections. For instance, density of *Cymadusa* was highest on three different macroalgae (*Ceramium*, *Ulva*, and *Gracilaria*) on three different dates in field conditions (Table 4), but was consistently higher on experimental treatments containing *Gracilaria* than those lacking this alga (Figure 7). Similarly, in fall collections the abundance of the isopod *Erichsonella* was very

high on the same plant (*Gracilaria*) that the amphipod *Gammarus* dominated in the June field experiment. Also, the abundance of *Erichsonella* was markedly lower on *Ulva* than on other plants in the experiment (Figure 7), presumably because it can not grasp its foliose surface.

Total epifaunal distributions among plants in the field sampling and experiment were similar; densities of particular taxa were often higher on seaweeds than on seagrasses, but there were no clearly interpretable patterns of plant-animal specificity (Table 4, Figure 7). Host-plant use in terrestrial insects can be a function of host population stability (Courtney and Chew 1987); the ephemerality of drift algae (Cowper 1978, Bell et al. 1995) may prevent evolutionary selection for true host-specificity among seagrass epifauna. In phytophagous insects, host-specificity appears favored because insects inhabit and feed directly on their hosts (Ehrlich and Raven 1964). In contrast, marine phytal epifauna which feed directly upon their host appear to be the exception, rather than the rule (but see Griffiths 1979, Hay et al. 1989, 1990, Tegner and Dayton 1987, Duffy 1990, Chess 1993). Host-plant specificity in this system, therefore, may be constrained by the duration and intensity of the interaction between plants and animals.

Habitat preference has the strongest evidence among mechanistic hypotheses for differential host-plant use among phytal epifauna. Amphipods discriminate between seagrass species differing in morphology (Stoner 1980), and macrofauna actively select dense stands of seagrass in both the presence and absence of predators (Bell and Westoby 1986). Plants with disparate morphologies provided equal refuge from predation for epifauna (Schneider and Mann 1991b), indicating predation alone could not explain distribution patterns. Complex habitats of drift algae and seagrasses provided differential refuge value for specific prey, however, so the

effect of predation and refuge can be species-specific (Leber 1985). Amphipods often partition habitat by selecting seaweeds with architectural features (e.g. frond spacing) closely matching their body size (Hacker and Steneck 1990, Edgar 1983a,c), which may in part explain the dense epifaunal communities occupying the seaweeds encountered in this study. Each of the seaweeds collected is either highly branched (*Agardhiella*, *Gracilaria*, and *Ceramium*), or highly convoluted (*Ulva*), attributes to which thigmotactic amphipods respond very strongly (Olyslager and Williams 1993). Preference for specific plant attributes may be due to species-specific biological traits, including differential crypsis or tenacity (which may explain the low densities of *Erichsonella* on the foliose alga *Ulva* in this study; Hacker and Steneck 1990), but predation pressure alone generally does not explain epifaunal distributions among plant species. Predation, however, may be the ultimate, evolutionary cause for habitat preference (Bell and Westoby 1986).

Preferred habitats, however, may be preempted by exploitative competition among functionally similar mesograzers. Although epifauna partition habitat and have similar diets (Kitting 1984), competition has rarely been considered a proximal cause for distribution patterns, primarily because resources previously have not been considered to limit populations (e.g. Fredette et al. 1990). In contrast, a series of recent papers present evidence that epifauna are constrained by food limitations (Edgar 1990a,b, 1991, Edgar and Aoki 1993), which implies that competition between species with similar resource requirements should exist (Huston 1994). Seasonal and monthly shifts in the dominance structure of species occupying plants (Table 4) in this study hint that possible temporal and spatial partitioning of resources occurred. For

instance, peak abundances of the three most common epifauna were complementary; each animal had its maximal abundance when others were less abundant (Figure 2). Fauna which were most abundant in the background *Zostera* community had even higher specific densities on *Gracilaria* (Figure 2). Epifaunal relative abundances also differed significantly among plant species on several dates (Table 4), indicating spatial partitioning of habitat. Changes in abundances of individual taxa among plant species also differed between dates, indicating an interaction between host-plant use and time.

It is unlikely that epifauna gain protection from predation by associating with chemically defended plants in this study area. Herbivorous fishes are not common in Chesapeake Bay (Orth and Heck 1980), and *Gracilaria*, which commonly had very high epifaunal densities (Figure 2), is not chemically defended (Holmlund et al. 1990). Although some species of the green algal genus *Ulva* reportedly have toxic exudates and lower ambient oxygen concentrations when found in dense mats (Johnson and Welsh 1985), *Ulva* species are not known to be chemically defended from herbivorous fishes (Hay et al. 1988b).

In conclusion, idiosyncratic epifaunal responses to specific plants, and to plant species composition, were much stronger than overall responses to plant species diversity. Positive correlations between epifaunal species richness and diversity and plant diversity could not be attributed to a specific biological effect and were relatively weak. In contrast to terrestrial ecosystems, the apparent absence of host-plant specialists and paucity of functional types or guilds might explain why plant species diversity had weak effects on animal diversity in this temperate seagrass bed. If species composition affects ecosystem processes more than species

richness alone, rudimentary knowledge of the number of species within a community clearly is not enough information to predict the outcome of current species loss on ecosystem performance (Wilson 1988).

APPENDIX I - Data: Survey of phytal epifauna on seagrasses and drift algae

Mean and standard error for specific and total dry plant biomass (g), and specific and total animal density (No. individuals/g dry plant) for each plant species collected on each date of the field survey of phytal epifauna on seagrasses and drift algae.

Appendix I, Table 1. Mean and standard error for specific and total dry plant biomass (g), and specific and total animal density (No. individuals/g dry plant) for each plant species collected on August 29, 1996. Sample size in parentheses.

	Zostera (6)		Ruppia (7)		Ulva (6)		Gracilaria (6)		Ceramium (5)		Polysiphonia (2)	
	Mean	SEM	Mean	SEM	Mean	SEM	Mean	SEM	Mean	SEM	Mean	SEM
<i>Zostera marina</i>	2.941	0.478	0.101	0.029	0.000	0.000	0.059	0.020	0.017	0.000	0.051	0.018
<i>Ruppia maritima</i>	0.277	0.093	1.414	0.246	0.094	0.030	0.067	0.000	0.045	0.004	0.000	0.000
<i>Ulva lactuca</i>	0.039	0.002	0.104	0.054	1.303	0.295	1.605	0.410	0.153	0.107	0.063	0.016
<i>Gracilaria verrucosa</i>	0.078	0.049	0.053	0.028	0.038	0.021	0.002	0.030	0.532	0.000	0.302	0.203
<i>Ceramium rubrum</i>	0.000		0.000		0.000		0.059	0.030	0.000	0.000	0.000	0.000
<i>Polysiphonia denudata</i>	0.000		0.020		0.034	0.008	0.008	0.006	0.004	0.001	0.000	0.000
<i>Enteromorpha intestinalis</i>	0.002	0.000	0.004	0.001	0.003	0.000	0.008	0.006	0.604	0.142	0.415	0.236
Total Plant Biomass (g)	3.297	0.452	1.543	0.255	1.432	0.305	1.712	0.400	0.604	0.142	0.415	0.236
<i>Gammarus mucronatus</i>	0.203	0.101	0.239	0.179	5.341	0.866	1.094	0.396	3.771	1.318	7.891	3.282
<i>Cymadusa compta</i>	3.340	1.616	4.937	1.937	35.908	6.804	11.357	3.948	72.329	11.955	69.476	30.370
<i>Erichsonella attenuata</i>	32.893	8.230	76.420	20.782	36.172	13.509	91.128	15.392	30.333	20.453	155.300	56.990
<i>Edotea triloba</i>	1.609	1.077	3.258	1.054	1.824	0.512	2.562	1.408	2.656	1.548	12.220	4.540
<i>Eiasmopus levis</i>	1.774	0.563	0.076	0.076	7.504	2.675	0.156	0.156	1.560	0.958	40.917	29.744
<i>Ampithoe longimana</i>	0.521	0.235	0.561	0.413	1.347	0.435	0.538	0.317	4.478	1.203	21.505	21.505
<i>Bittium varium</i>	0.506	0.164	0.977	0.801	3.674	1.026	3.335	1.723	2.461	1.014	3.561	2.025
<i>Hydobia</i> sp.	0.035	0.035	0.241	0.162	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
<i>Mitrella lunata</i>	0.035	0.035	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
<i>Ampelisca abdita</i>	0.103	0.103	0.471	0.405	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
<i>Caprella penantis</i>	0.000	0.000	0.486	0.405	0.072	0.072	1.155	0.494	7.274	3.962	13.825	13.825
<i>Paracaprella tenuis</i>	0.000	0.000	0.000	0.000	0.000	0.000	0.138	0.138	2.893	1.170	0.768	0.768
<i>Callinectes sapidus</i>	0.040	0.040	0.081	0.081	0.190	0.122	0.156	0.156	0.000	0.000	0.000	0.000
<i>Listriella clymenellae</i>	0.000	0.000	0.287	0.154	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
Total Animal Density	41.058	11.227	88.035	23.832	92.031	20.244	111.619	14.863	127.756	31.131	325.464	29.375

Appendix 1, Table 2. Mean and standard error for specific and total dry plant biomass (g), and specific and total animal density (No. individuals/g dry plant) for each plant species collected on September 25, 1996. Sample size in parentheses.

September 25, 1996	Zostera (6)		Ruppia (6)		Ulva (6)		Gracilaria(3)		Agardhiella(3)	
	Mean	SEM	Mean	SEM	Mean	SEM	Mean	SEM	Mean	SEM
<i>Zostera marina</i>	2.171	0.291	0.068		0.042		0.000		0.000	
<i>Ruppia maritima</i>	0.194	0.081	1.682	0.355	0.055	0.026	0.171	0.082	0.095	0.054
<i>Ulva lactuca</i>	0.000		0.000		0.495	0.076	0.043	0.006	0.000	
<i>Gracilaria verrucosa</i>	0.006	0.002	0.005	0.002	0.023	0.004	1.975	0.842	0.087	
<i>Ceramium rubrum</i>	0.000		0.000		0.000		0.000		0.000	
<i>Agardhiella tenera</i>	0.000		0.000		0.075		0.276	0.220	0.832	0.398
<i>Enteromorpha intestinalis</i>	0.000		0.000		0.000		0.000		0.000	
<i>Champia parvula</i>	0.000		0.000		0.000		0.013		0.000	
Encrusting sponge	0.045	0.017	0.066		0.240		0.000		0.078	
Total Plant Biomass (g)	2.357	0.325	1.706	0.356	0.599	0.093	2.305	0.671	0.982	0.425
<i>Gammarus mucronatus</i>	0.137	0.137	0.000	0.000	0.000	0.000	0.092	0.092	0.000	0.000
<i>Cymadusa compta</i>	4.116	1.804	2.159	0.864	36.278	12.153	7.506	5.848	4.708	1.081
<i>Erichsonella attenuata</i>	14.083	3.917	24.019	3.235	19.511	8.997	34.845	13.995	8.498	1.427
<i>Edotea triloba</i>	0.408	0.408	0.215	0.215	1.966	1.079	0.312	0.192	0.000	0.000
<i>Crangon septemspinosa</i>	0.000	0.000	0.557	0.390	0.447	0.447	0.092	0.092	0.183	0.183
<i>Elasmopus levis</i>	0.564	0.235	0.000	0.000	11.284	7.650	1.764	1.764	0.954	0.954
<i>Amphioe longimana</i>	0.214	0.137	0.057	0.057	0.728	0.460	0.000	0.000	0.367	0.367
<i>Palaemonetes pugio</i>	0.438	0.191	0.628	0.220	0.398	0.398	1.477	0.742	0.000	0.000
<i>Palaemonetes vulgaris</i>	0.527	0.157	0.116	0.116	0.649	0.413	0.189	0.189	0.000	0.000
<i>Palaemonetes intermedius</i>	0.000	0.000	0.148	0.098	0.000	0.000	0.000	0.000	0.000	0.000
<i>Bittium varium</i>	0.666	0.452	0.397	0.252	0.569	0.390	1.544	1.544	0.000	0.000
<i>Hydrobia</i> sp.	0.000	0.000	0.204	0.204	0.187	0.187	0.000	0.000	0.000	0.000
Unidentified Ampeliscid	0.479	0.199	2.261	1.394	0.000	0.000	0.000	0.000	0.000	0.000
<i>Caprella penantis</i>	0.000	0.000	0.000	0.000	0.000	0.000	0.221	0.221	0.000	0.000
<i>Paracaprella tenuis</i>	0.000	0.000	0.215	0.215	0.000	0.000	0.000	0.000	0.000	0.000
<i>Callinectes sapidus</i>	0.418	0.194	0.447	0.283	1.129	0.768	1.034	0.476	0.000	0.000
Unidentified Xanthid	0.113	0.074	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
Unidentified Gastropod	0.045	0.045	0.000	0.000	0.187	0.187	0.000	0.000	0.000	0.000
Unidentified Corophiid	0.045	0.045	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
<i>Listriella clymenellae</i>	0.241	0.241	0.592	0.235	1.149	0.803	0.000	0.000	0.000	0.000
<i>Microtopotus raneyi</i>	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.183	0.183
Total Animal Density	22.494	3.508	32.017	4.710	74.481	22.252	49.074	7.255	14.893	2.304

Appendix 1, Table 3. Mean and standard error for specific and total dry plant biomass (g), and specific and total animal density (No. individuals/g dry plant) for each plant species collected on December 7, 1996. Sample size in parentheses.

	Zostera (6)		Gracilaria(6)	
	Mean	SEM	Mean	SEM
<i>Zostera marina</i>	1.293	0.305	0.928	0.435
<i>Ruppia maritima</i>	0.242	0.073	0.614	0.138
<i>Gracilaria verrucosa</i>	0.124	0.078	1.530	0.546
<i>Polysiphonia denudata</i>	0.020	0.013	0.012	0.009
Total Plant Biomass (g)	1.680	0.278	3.084	0.888
<i>Gammarus mucronatus</i>	2.444	1.214	1.627	0.792
<i>Cymadusa compta</i>	16.598	2.287	24.047	5.558
<i>Erichsonella attenuata</i>	7.683	2.814	10.336	3.157
<i>Edotea triloba</i>	2.608	0.714	1.783	1.130
<i>Elasmopus levis</i>	1.894	0.593	1.407	1.124
<i>Amphioe longimana</i>	0.518	0.191	0.166	0.117
<i>Dulichella appendiculata</i>	0.000	0.000	0.047	0.047
<i>Palaemonetes pugio</i>	0.595	0.337	0.373	0.144
<i>Palaemonetes vulgaris</i>	0.134	0.134	0.081	0.050
<i>Bittium varium</i>	4.728	1.828	2.668	0.752
<i>Hydrobia</i> sp.	0.000	0.000	0.119	0.119
<i>Ampelisca abdita</i>	3.590	1.323	1.761	0.709
<i>Callinectes sapidus</i>	0.605	0.279	0.409	0.175
<i>Gobiosoma bosc</i>	0.097	0.097	0.047	0.047
<i>Luciana parva</i>	0.000	0.000	0.084	0.084
Unidentified Xanthid	0.000	0.000	0.034	0.034
<i>Nassarius vibex</i>	0.657	0.523	0.167	0.167
<i>Listriella clymenellae</i>	0.190	0.128	0.554	0.239
Total Animal Density	42.340	6.168	45.708	4.960

Appendix I, Table 4. Mean and standard error for specific and total dry plant biomass (g), and specific and total animal density (No. individuals/g dry plant) for each plant species collected on January 22, 1997. Sample size in parentheses.

	Zostera (6)		Gracilaria(5)		Ulva (4)		Agardhiella(3)		Cerarium(5)	
	Mean	SEM	Mean	SEM	Mean	SEM	Mean	SEM	Mean	SEM
<i>Zostera marina</i>	1.909	0.215	0.462	0.149	0.404	0.135	0.443	0.147	0.101	0.015
<i>Ruppia maritima</i>	0.193	0.053	0.177	0.046	0.141	0.030	0.227	0.141	0.350	0.184
<i>Ulva lactuca</i>	0.001	0.001	0.002	0.001	1.130	0.426	0.003	0.002	0.000	0.000
<i>Gracilaria verrucosa</i>	0.082	0.081	1.093	0.295	0.004	0.003	0.051	0.037	0.015	0.011
<i>Cerarium rubrum</i>	0.069	0.055	0.034	0.022	0.103	0.053	0.042	0.042	1.135	0.196
<i>Agardhiella tenera</i>	0.000	0.000	0.000	0.000	0.000	0.000	1.408	0.884	0.000	0.000
<i>Enteromorpha intestinalis</i>	0.002	0.001	0.000	0.000	0.001	0.001	0.000	0.000	0.000	0.000
<i>Polysiphonia denudata</i>	0.016	0.012	0.026	0.017	0.016	0.006	0.085	0.046	0.040	0.027
Total Plant Biomass (g)	2.272	0.217	1.793	0.415	1.799	0.403	2.258	0.762	1.640	0.351
<i>Gammarus mucronatus</i>	7.177	1.465	6.543	0.916	6.639	1.883	7.280	0.708	10.389	2.660
<i>Cymadusa compta</i>	9.092	1.700	23.178	4.917	11.570	1.881	12.606	1.655	6.242	0.942
<i>Erichsonella attenuata</i>	10.820	1.373	9.775	3.109	3.285	1.585	3.306	0.876	6.629	2.904
<i>Edotea triloba</i>	2.755	0.773	4.376	1.187	1.737	0.560	1.794	0.932	3.309	1.786
<i>Eiasmopus levis</i>	1.101	0.614	2.970	2.299	1.200	0.609	1.017	0.584	0.921	0.269
<i>Ampithoe longimana</i>	0.060	0.060	0.177	0.177	0.323	0.323	0.000	0.000	0.256	0.158
<i>Duilchiella appendiculata</i>	0.000	0.000	0.000	0.000	0.000	0.000	0.088	0.088	0.000	0.000
<i>Palaemonetes pugio</i>	0.736	0.181	0.287	0.188	0.766	0.392	1.076	0.626	0.256	0.158
<i>Palaemonetes intermedius</i>	0.082	0.082	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
<i>Bittium varium</i>	2.162	0.713	2.357	0.946	0.094	0.094	1.017	0.584	1.046	0.544
<i>Hydrobia</i> sp.	0.000	0.000	0.088	0.088	0.000	0.000	0.000	0.000	0.000	0.000
<i>Ampelisca abdita</i>	0.888	0.267	2.541	0.928	2.419	0.749	0.329	0.211	0.581	0.295
<i>Caprella penantis</i>	0.082	0.082	0.000	0.000	0.000	0.000	0.000	0.000	0.744	0.478
<i>Paracaprella tenuis</i>	0.060	0.060	0.067	0.067	0.000	0.000	0.000	0.000	0.000	0.000
<i>Callinectes sapidus</i>	0.254	0.126	0.289	0.198	0.986	0.556	0.383	0.193	0.549	0.343
<i>Gobiosoma bosc</i>	0.000	0.000	0.067	0.067	0.000	0.000	0.000	0.000	0.372	0.239
<i>Luciana parva</i>	0.000	0.000	0.000	0.000	0.000	0.000	0.088	0.088	0.000	0.000
Unidentified Xanthid	0.000	0.000	0.134	0.134	0.000	0.000	0.000	0.000	0.000	0.000
Unidentified Tanaid	0.125	0.125	0.298	0.298	0.000	0.000	0.000	0.000	0.000	0.000
<i>Nassarius vibex</i>	0.000	0.000	0.102	0.102	0.000	0.000	0.000	0.000	0.000	0.000
<i>Nassarius obsoletus</i>	0.072	0.072	0.000	0.000	0.094	0.094	0.000	0.000	0.000	0.000
<i>Listriella clymenellae</i>	0.269	0.189	0.169	0.107	0.570	0.271	1.533	1.403	1.004	0.921
<i>Listriella plumulosis</i>	0.000	0.000	0.000	0.000	0.476	0.308	0.000	0.000	0.000	0.000
<i>Sympleustes glaber</i>	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.141	0.141
Total Animal Density	35.736	4.722	53.418	9.193	30.159	5.556	30.519	5.588	32.439	7.595

Appendix I, Tables 7, 8, and 9. Mean and standard error for specific and total dry plant biomass (g), and specific and total animal density (No. individuals/g dry plant) for each plant species collected on June 16, June 23, and August 11, 1997. Sample size in parentheses.

June 16, 1997		Zostera (6)		June 23, 1997		Zostera (6)		August 11, 1997		Zostera (6)		Gracilaria (6)	
		Mean	SEM			Mean	SEM			Mean	SEM	Mean	SEM
<i>Zostera marina</i>		5.268	0.870	<i>Zostera marina</i>		5.605	0.439	<i>Zostera marina</i>		1.237	0.394	0.032	0.023
<i>Ruppia maritima</i>		0.050	0.040	<i>Ruppia maritima</i>		0.028	0.015	Encrusting sponge	<i>Zostera</i>	7.398	3.256	0.073	0.073
<i>Ulva lactuca</i>		0.001	0.001	<i>Ulva lactuca</i>		0.000	0.000	<i>Ruppia maritima</i>		0.058	0.012	0.095	0.027
<i>Gracilaria verrucosa</i>		0.033	0.025	<i>Gracilaria verrucosa</i>		0.011	0.010	<i>Ulva lactuca</i>		0.000	0.000	0.001	0.001
<i>Ceramium rubrum</i>		0.000	0.000	<i>Ceramium rubrum</i>		0.001	0.001	<i>Gracilaria verrucosa</i>		0.036	0.026	1.054	0.343
Total Plant Biomass (g)		5.353	0.863	Total Plant Biomass (g)		5.644	0.435	<i>Agardhiella tenera</i>		0.012	0.009	0.014	0.007
<i>Gammarus mucronatus</i>		3.038	0.618	<i>Gammarus mucronatus</i>		4.518	0.477	Total Plant Biomass (g)		8.741	3.127	1.268	0.331
<i>Cymadusa compta</i>		1.843	0.297	<i>Cymadusa compta</i>		5.622	0.982	<i>Gammarus mucronatus</i>		0.211	0.064	1.941	0.737
<i>Erichsonella attenuata</i>		2.413	0.514	<i>Erichsonella attenuata</i>		4.370	0.471	<i>Cymadusa compta</i>		8.533	2.590	41.520	9.763
<i>Edotea triloba</i>		0.395	0.157	<i>Edotea triloba</i>		0.573	0.228	<i>Erichsonella attenuata</i>		17.563	9.083	112.390	31.576
<i>Crangon septemspinosa</i>		0.145	0.046	<i>Crangon septemspinosa</i>		0.196	0.081	<i>Edotea triloba</i>		9.427	2.680	31.589	17.364
<i>Elasmopus levis</i>		0.206	0.073	<i>Crangon septemspinosa</i>		0.146	0.058	<i>Crangon septemspinosa</i>		0.029	0.029	0.295	0.188
Unidentified Ampeliscid		0.086	0.042	Unidentified Ampeliscid		0.155	0.061	<i>Elasmopus levis</i>		4.142	1.032	2.048	1.222
<i>Callinectes sapidus</i>		0.119	0.059	<i>Callinectes sapidus</i>		0.120	0.040	<i>Ampithoe longimana</i>		1.608	0.449	1.987	1.279
<i>Palaemonetes pugio</i>		0.095	0.062	<i>Palaemonetes pugio</i>		0.112	0.052	<i>Palaemonetes pugio</i>		0.050	0.050	0.340	0.340
<i>Palaemonetes vulgaris</i>		0.018	0.018	<i>Palaemonetes vulgaris</i>		0.045	0.045	<i>Palaemonetes vulgaris</i>		0.209	0.124	0.000	0.000
<i>Bittium varium</i>		0.287	0.110	<i>Bittium varium</i>		0.053	0.034	<i>Palaemonetes intermedius</i>		0.129	0.129	0.000	0.000
<i>Nassarius vibex</i>		0.041	0.041	<i>Nassarius vibex</i>		0.114	0.037	<i>Bittium varium</i>		1.088	0.430	2.098	1.214
<i>Caprella penantis</i>		0.058	0.058	<i>Caprella penantis</i>		0.000	0.000	<i>Hydrobia sp.</i>		0.000	0.000	0.729	0.651
Total Animal Density		8.745	1.257	Total Animal Density		16.023	1.670	<i>Ampelisca abdita</i>		0.194	0.194	2.646	2.646
								<i>Caprella penantis</i>		0.000	0.000	0.086	0.086
								<i>Paracaprella tenuis</i>		0.000	0.000	1.569	1.296
								<i>Callinectes sapidus</i>		0.065	0.065	1.496	1.299
								<i>Gobiosoma bosc</i>		0.048	0.048	0.252	0.171
								Unidentified Xanthid		0.078	0.045	0.000	0.000
								<i>Nassarius vibex</i>		0.030	0.019	0.295	0.188
								<i>Nassarius obsoletus</i>		0.065	0.065	0.000	0.000
								<i>Idotea baltica</i>		0.000	0.000	0.165	0.165
								Total Animal Density		43.470	13.236	201.446	63.289

APPENDIX II - Data: Plant diversity manipulation experiments

Mean and standard error for specific and total dry plant biomass (g), plant Simpson diversity, specific and total animal density (No. individuals/g dry plant), animal species richness, Simpson diversity, and evenness for each treatment on each date of plant diversity manipulation experiments.

Treatment mean and standard error for dry plant biomass (g) and plant Simpson Diversity from plant diversity manipulation experiments.
 Treatment abbreviations are: Z:*Zostera marina*, R:*Ruppia maritima*, U:*Ulva lactuca*, G: *Gracilaria verrucosa*, C:*Ceramium rubrum*.

Treatment	16Jun97		23Jun97		16Jun97		23Jun97		16Jun97		23Jun97		16Jun97		23Jun97	
	Z	SEM	Z	SEM	G	SEM	U	SEM	U	SEM	ZG	SEM	ZG	SEM	ZR	SEM
<i>Zostera marina</i>	7.280	1.733	5.452	1.069	0.280	0.141	0.073	0.056	0.768	0.604	2.469	0.413	2.367	0.636	1.642	0.307
<i>Ruppia maritima</i>	0.076	0.055	0.080	0.011	0.031	0.027	0.019	0.009	0.243	0.182	0.033	0.018	0.025	0.006	0.634	0.025
<i>Ulva lactuca</i>	0.001	0.001	0.000	0.000	0.000	0.000	0.005	0.005	3.865	2.157	0.000	0.000	0.015	0.010	0.000	0.000
<i>Gracilaria verrucosa</i>	0.020	0.018	0.008	0.008	9.031	1.380	10.716	1.537	0.134	0.119	4.879	0.294	5.678	1.226	0.149	0.136
<i>Ceramium rubrum</i>	0.000	0.000	0.017	0.017	0.003	0.003	0.000	0.000	0.004	0.004	0.017	0.017	0.005	0.005	0.000	0.000
Other	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.003	0.003
Total Plant Biomass (g)	7.377	1.685	5.557	1.068	9.344	1.492	10.813	1.475	5.015	1.359	7.399	0.681	8.090	1.574	2.428	0.451
Simpson Diversity	0.036	0.031	0.040	0.009	0.060	0.016	0.021	0.016	0.230	0.139	0.448	0.018	0.401	0.056	0.458	0.027

Treatment	23Jun97		16Jun97		23Jun97		16Jun97		23Jun97		16Jun97		23Jun97		16Jun97		23Jun97	
	ZR	SEM	GC	SEM	GC	SEM	ZRU	SEM	ZRU	SEM	GCU	SEM	ZRUGC	SEM	ZRUGC	SEM	ZRUGC	SEM
<i>Zostera marina</i>	3.036	0.684	0.370	0.138	0.099	0.080	2.359	0.327	2.117	0.258	0.435	0.374	0.327	0.284	2.085	0.849	2.456	0.400
<i>Ruppia maritima</i>	0.235	0.111	0.118	0.059	0.026	0.017	0.254	0.079	0.628	0.152	0.039	0.022	0.039	0.031	0.295	0.061	0.438	0.152
<i>Ulva lactuca</i>	0.036	0.022	0.108	0.098	0.138	0.138	3.189	0.845	4.278	0.563	3.144	0.470	5.180	0.711	1.760	0.451	3.960	0.229
<i>Gracilaria verrucosa</i>	0.014	0.014	5.939	0.520	5.230	0.231	0.021	0.021	0.937	0.766	4.245	0.820	2.756	1.206	2.236	0.130	2.995	0.149
<i>Ceramium rubrum</i>	0.041	0.041	1.320	0.995	0.218	0.047	0.000	0.000	0.088	0.088	1.211	0.496	0.326	0.113	0.354	0.180	0.401	0.179
Other	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
Total Plant Biomass (g)	3.361	0.808	7.856	0.605	5.711	0.198	5.823	0.790	8.048	0.718	9.074	0.776	8.628	1.578	6.730	0.690	10.251	0.537
Simpson Diversity	0.155	0.055	0.324	0.127	0.152	0.071	0.512	0.021	0.584	0.070	0.624	0.048	0.501	0.019	0.692	0.021	0.701	0.016

(continued), Treatment mean and standard error for total plant biomass (g), specific animal density (no. individuals/g dry plant), total epifaunal density, species richness, Simpson Diversity, and evenness from plant diversity manipulation experiments.

Treatment abbreviations are: Z: *Zostera marina*, R: *Ruppia maritima*, U: *Ulva lactuca*, G: *Gracilaria verrucosa*, C: *Ceramium rubru*

Treatment	23Jun97		16Jun97		23Jun97		16Jun97		23Jun97		16Jun97		23Jun97					
	Mean	SEM	Mean	SEM	Mean	SEM	Mean	SEM	Mean	SEM	Mean	SEM	Mean	SEM				
Total Plant Biomass (g)	3.361	0.808	7.856	0.605	5.711	0.198	5.823	0.790	8.048	0.718	9.074	0.776	8.628	1.578	6.730	0.690	10.251	0.537
<i>Gammarus mucronatus</i>	5.325	2.195	13.068	2.868	20.318	1.591	15.124	4.327	18.915	4.580	16.827	5.584	21.415	8.893	8.556	2.452	16.851	3.657
<i>Cymadusa compta</i>	4.868	2.418	8.773	1.664	6.414	1.271	2.826	0.347	4.276	0.383	10.679	1.163	5.084	2.535	4.214	0.758	6.165	2.838
<i>Erichsonella attenuata</i>	6.457	1.968	8.139	1.729	5.608	1.583	5.160	2.330	5.705	1.226	6.567	1.210	2.743	0.150	5.744	0.050	4.805	0.379
<i>Edotea triloba</i>	3.243	1.795	0.523	0.102	1.925	1.240	1.685	0.842	1.363	0.366	0.408	0.124	1.449	0.482	0.972	0.517	1.228	0.167
<i>Crangon septemspinosa</i>	0.350	0.109	0.628	0.435	0.287	0.201	0.586	0.219	0.285	0.225	0.254	0.191	0.118	0.118	0.705	0.643	0.036	0.036
<i>Elasmopus levis</i>	0.000	0.000	0.110	0.110	0.000	0.000	0.063	0.063	0.453	0.228	0.068	0.034	0.095	0.052	0.050	0.050	0.832	0.832
Ampeliscids	0.358	0.180	0.000	0.000	0.057	0.057	0.069	0.069	0.126	0.011	0.070	0.070	0.000	0.000	0.060	0.060	0.100	0.056
<i>Callinectes sapidus</i>	0.000	0.000	0.000	0.000	0.000	0.000	0.063	0.063	0.091	0.046	0.088	0.088	0.000	0.000	0.060	0.060	0.062	0.031
<i>Palaemonetes pugio</i>	0.000	0.000	0.356	0.193	0.113	0.056	0.000	0.000	0.071	0.071	0.079	0.040	0.030	0.030	0.170	0.105	0.262	0.038
<i>Palaemonetes vulgaris</i>	0.000	0.000	0.074	0.074	0.225	0.225	0.000	0.000	0.049	0.049	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
<i>Palaemonetes intermedius</i>	0.000	0.000	0.000	0.000	0.063	0.063	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
<i>Bitium varium</i>	0.168	0.168	0.092	0.046	0.000	0.000	0.000	0.000	0.139	0.084	0.000	0.000	0.030	0.030	0.042	0.042	0.036	0.036
<i>Hydrobia</i> sp.	0.000	0.000	0.000	0.000	0.000	0.000	0.069	0.069	0.036	0.036	0.000	0.000	0.059	0.059	0.060	0.060	0.036	0.036
<i>Nassarius obsoletus</i>	0.000	0.000	0.090	0.090	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.120	0.120	0.000	0.000
<i>Nassarius vibex</i>	0.266	0.165	0.082	0.042	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.060	0.060	0.000	0.000
<i>Mitrella lunata</i>	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.030	0.030	0.000	0.000	0.000	0.000
<i>Idotea balthica</i>	0.000	0.000	0.000	0.000	0.119	0.060	0.069	0.069	0.000	0.000	0.110	0.058	0.000	0.000	0.000	0.000	0.000	0.000
<i>Caprella penantis</i>	0.000	0.000	0.000	0.000	0.000	0.000	0.063	0.063	0.000	0.000	0.000	0.000	0.000	0.000	0.060	0.060	0.000	0.000
<i>Ampithoe longimana</i>	0.084	0.084	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
Unidentified Tanaid	0.084	0.084	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
Unidentified Gastropod	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.060	0.060	0.000	0.000
<i>Symphurus plagiatus</i>	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
<i>Menidia menidia</i>	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
<i>Paracaprella tenuis</i>	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
<i>Gobiosoma bosc</i>	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
<i>Eurypanopeus depressus</i>	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
Mean Density	21.202	7.225	31.936	3.911	35.128	2.924	25.780	7.538	31.508	4.867	35.149	8.222	31.054	10.046	20.935	4.272	30.594	6.886
Mean Species Richness	7.667	1.202	8.000	1.000	7.000	0.577	7.000	1.000	8.667	0.882	7.667	0.333	6.667	0.333	8.333	2.333	8.333	0.667
Mean Simpson Diversity	0.766	0.012	0.689	0.029	0.593	0.031	0.598	0.007	0.577	0.061	0.646	0.017	0.531	0.118	0.697	0.025	0.622	0.027
Mean Evenness (E _{av})	0.408	0.076	0.198	0.023	0.193	0.012	0.351	0.112	0.194	0.009	0.166	0.012	0.236	0.069	0.232	0.022	0.202	0.009

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