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Simulated eelgrass *Zostera marina* structural complexity: effects of shoot length, shoot density, and surface area on the epifaunal community of San Diego Bay, California, USA

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ABSTRACT: In marine ecology, a long-standing issue has been determining which components of habitat structure predominantly influence ecological processes structuring communities. In seagrasses, faunal abundance and species diversity commonly are positively correlated with structural complexity (often quantified as shoot biomass or leaf surface area). These measures of complexity often covary with other attributes of seagrass structure, including shoot length and shoot density, which independently may influence ecological processes. We used artificial seagrass units (ASUs) to determine the relative influences of shoot length, shoot density, and surface area on epifaunal community structure in San Diego Bay, California, USA. Our first experiment tested how habitat attributes and exposure time influenced epifaunal density, diversity, and recruitment. In a second experiment we determined the interactive effects of habitat treatment and site on epifaunal density, diversity, biomass and community composition. In Expt 1, exposure time had a stronger effect on community measures than habitat treatment. When habitat treatment had an effect, surface area accounted for more of the variability in the epifaunal community than did shoot length and shoot density, but patterns of epifaunal density and recruitment were species-specific. In Expt 2, site explained proportionally more of the variation in epifaunal density and diversity than did eelgrass habitat characteristics. In >50% of the tests, surface area accounted for more variability in epifaunal density and diversity than did shoot length or shoot density, but responses to habitat treatments again were species-specific. Our results demonstrate that the effects of habitat characteristics are highly variable with site and exposure time, and that variability in epifaunal density and diversity in seagrass habitat cannot always be ascribed to simple species–area relationships.

KEY WORDS: ASU · Colonization · Community composition · Habitat structure · Seagrass · Species diversity

INTRODUCTION

A major goal of marine ecology is to determine how habitat structure may influence processes that shape faunal communities. In marine habitats such as seagrasses, coral and oyster reefs, and kelp forests, aspects of habitat structure at fine scales (i.e. structural complexity) and at landscape scales influence larval settlement (Eckman 1987) as well as post-settlement processes such as predation (Heck & Thoman 1981, Heck & Crowder 1991), competition (Coen et al. 1981, Edgar 1990), and emigration (Moksnes 2002) that also drive patterns of habitat colonization and faunal community structure. A framework for quantifying habitat structure developed by McCoy & Bell (1991) states that structure consists of 2 components: complexity (varia-

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tion attributable to the absolute abundance of individual structural components), and heterogeneity (variation attributable to the relative abundance of different structural components), and that measures of habitat structure as well as the effects of structure on ecological processes are scale dependent (see also Beck 1998, 2000). Despite this framework, inconsistencies among studies in the way in which habitat structure is defined and measured have limited our understanding of the relative importance of structure in ecological processes.

Seagrasses form a structurally complex marine habitat with high primary and secondary production in shallow water marine and estuarine environments (Hemminga & Duarte 2000). Seagrass shoots, roots and rhizomes provide extensive habitats for many economically important species, including crabs (Hovel & Lipcius 2001), shrimps (Coen et al. 1981), bivalves (Peterson 1986, Irlandi 1994), lobsters (Short et al. 2001) and fishes (Rooker et al. 1998, Hughes et al. 2002, Harris et al. 2004), as well as a diverse assemblage of macroinvertebrates that often serve as prey for these species. Faunal abundance, diversity, and survival typically are higher in seagrass than in surrounding unvegetated habitat (Orth 1992, Heck et al. 1995, Fonseca et al. 1998, Lee et al. 2001), and within seagrass patches, the abundance and diversity of mobile invertebrates and fishes often are correlated with increases in structural complexity (e.g. shoot density, surface area, or biomass per unit area: Heck & Orth 1980, Orth 1992, Hovel & Lipcius 2001). Areas of high structural complexity may enhance the refuge value of seagrass beds, particularly for vulnerable juvenile stages (e.g. decapod crustaceans: Heck & Thoman 1981, Heck & Wilson 1987, Hovel & Lipcius 2001; juvenile hard clams *Mercenaria mercenaria*: Irlandi 1994) and may offer greater living space or food for epifauna. Additionally, larvae, postlarvae and juveniles often actively select areas of high structural complexity (Bell & Westoby 1986).

Structural complexity in seagrass habitat has been quantified in a number of ways. Seagrass shoot biomass per unit area has frequently been used as a measure of habitat complexity, and often is correlated with various aspects of the associated epifaunal community including total epifaunal abundance, species richness, and species diversity (e.g. Heck & Wetstone 1977, Stoner 1980, Attrill et al. 2000, Pelicice et al. 2005). However, biomass covaries with many attributes of seagrass bed structure, including surface area, shoot length, and shoot density, all of which may independently influence ecological processes (e.g. predator–prey encounter rates) and therefore population dynamics and community composition. The confounding of shoot biomass with these other aspects of habitat structure has made it difficult to determine if positive correlations between structural complexity and faunal abundance and diversity are the result of a greater amount of habitat available, or from independent effects of shoot density and shoot length on ecological processes. In seagrass *Zostera marina* habitats in Great Britain, patterns of epifaunal community composition were best explained by the amount of seagrass present (=biomass per unit area) rather than by a derived index of structural complexity that incorporated shoot density, epiphyte biomass, and the number of leaves per shoot, suggesting that increased species diversity in structurally complex seagrass patches may be ascribed to simple species–area relationships (Attrill et al. 2000). In contrast, elements of structural complexity (e.g. shoot density) of seagrass habitat in Virginia, USA (Parker et al. 2001) and in Port Phillip Bay, Australia (Jenkins et al. 2002), had stronger influences on epifaunal abundance than did plant surface area.

Eelgrass *Zostera marina* L. is one of over 50 species of marine angiosperms comprising seagrasses (den Hartog 1977). *Z. marina* dominates shallow soft-sediment habitats in Southern California and is widespread throughout San Diego Bay at depths of <1 to ca. 5 m. Many commercially and recreationally important species utilize these beds as nurseries or foraging grounds, including the spiny lobster *Panulirus interruptus*, barred sand bass *Paralabrax nebulifer* and spotted sand bass *Paralabrax maculatofasciatus*. Eelgrass habitat structure and epifaunal community composition vary markedly among sites in San Diego Bay. Mean eelgrass shoot length decreases, and mean shoot density increases with distance from the bay mouth, and fish and invertebrate species richness generally is higher near the bay mouth than at mid-bay and back-bay sites (authors' unpubl. data). We used San Diego Bay as a model system to study the interactive effects of site and simulated eelgrass habitat structure on epifaunal community structure. Specifically, our goal was to determine the relative influences of habitat amount (=shoot surface area), shoot length and shoot density on the abundance, diversity, community composition, and biomass of *Z. marina* epifauna.

MATERIALS AND METHODS

Study site. Our experiments were conducted in San Diego Bay (32° 44′ N, 117° 10′ W), a seasonal hypersaline, low-inflow estuary in Southern California, USA (Largier et al. 1997). The bay is ca. 25 km long and is commonly divided into 4 eco-regions (US Department of the Navy, Southwest Division [USDoN, SWDIV], San Diego Bay Integrated Natural Resources Management Plan, and San Diego Unified Port District Public Draft,

September 1999; prepared by Tierra Data Systems, Escondido, CA), representing different environmental conditions, including current velocity, water residence time, temperature, salinity, and depth (Largier et al. 1997, Chadwick & Largier 1999). The northern eco-region (Expts 1 and 2) includes the bay mouth and is characterized by short water residence time, strong tidally driven currents, and low fluctuations in seasonal water temperatures and salinity (ca. 13 to 19°C and 33 to 35 psu). The southern eco-region, ca. 20 km from the bay mouth, has long water residence times, weaker currents, and higher fluctuations in seasonal water temperature and salinity (ca. 13 to 24°C and 32 to 37 psu). The 2 central eco-regions (north central and south central; Expt 2) have conditions intermediate to the northern and southern eco-regions.

General experimental design. To test how simulated eelgrass habitat structure influences epifaunal communities, we used artificial seagrass units (ASUs) to simulate eelgrass patches and to precisely control shoot surface area, shoot length, and shoot density in a design similar to that used by Jenkins et al. (2002). We chose these 2 variables (shoot length and shoot density) because they varied considerably among sites in a 2 yr survey of eelgrass habitat characteristics in San Diego Bay. Variability in other structural characteristics was less pronounced among our sampling sites. Using ASUs also allowed us to standardize patch size and the number of leaves per shoot among treatment combinations, thereby limiting the effect of additional confounding variables. ASUs are rapidly colonized by epifauna in San Diego Bay (Healey & Hovel 2004) and elsewhere (e.g. Virnstein & Curran 1986, Bologna & Heck 1999, Boström & Bonsdorff 2000). In addition, epifaunal densities, species diversity, and species composition are comparable between ASUs and naturally occurring eelgrass beds in San Diego Bay, and all species found in naturally occurring eelgrass were found in ASUs (Healey & Hovel 2004, authors' unpubl. data).

Each 0.25 m^2 ASU consisted of simulated shoots (4.75 mm wide green polypropylene ribbon) tied to a 50 cm × 50 cm square of black Vexar® mesh (mesh size = 1 cm × 1 cm) lined on the bottom with 1 mm mesh window screening. Shoots were folded in two to form 2 simulated blades per shoot. We used a 2 × 2 fully crossed factorial design consisting of 2 levels of shoot length (short [S] = 20 cm and tall [T] = 80 cm) and 2 levels of shoot density (low [L] = 150 shoots m^{-2} and high [H] = 600 shoots m^{-2}). Shoot length and shoot density values were chosen (1) to represent the extremes for naturally occurring eelgrass beds in San Diego Bay, and (2) to achieve a 4-fold difference between the low and high values for each variable. This resulted in a 16-fold difference in surface area between the short shoot-low density (SL) and the tall shoot-high density (TH) plots and a 4-fold difference between the SL plots and the short shoot-high density (SH) and tall shoot-low density (TL) treatments (surface area ratios SL:SH:TL:TH = 1:4:4:16 = Low:Medium:Medium:High). This design allowed us to create 2 mid-level surface area treatments (SH and TL) which have equivalent total surface area but different structural configurations, thereby allowing us to separate surface area from structural attributes (length and height). We could then determine if epifaunal colonization varied primarily with shoot length (regardless of shoot density), shoot density (regardless of shoot length), or shoot surface area (regardless of either shoot length or density; Jenkins et al. 2002).

At the start of each experiment (see below), ASUs were tagged for individual identification and anchored with rebar stakes to featureless sediment (=no above-ground structure) no less than 5 m from existing eelgrass beds. Upon completion of each experiment, divers retrieved ASUs by rapidly placing a 500 µm mesh bag over each ASU, placing their hand under the unit, pushing the ASU up and into the bag, and sealing the bag using a drawstring. The bottom mesh lining of the ASU prevented the capture of infaunal species that may have already been present in the underlying sediment. The process of either deploying or retrieving the ASUs took approximately 1 h at each site. Once collected, the ASUs were brought back to the dock and epifauna were rinsed into a 1 mm sieve. Samples were then placed into plastic bags and frozen. In the laboratory, thawed samples were sorted to identify all organisms to the lowest possible taxonomic level, usually species. Species residing in the top few centimeters of sediment above the ASU were collected and recorded, including most bivalves. All polychaetes and Asian mussels *Musculista senhousia* were excluded from the samples, as both of these taxa resided in the sediment prior to ASU deployment and may have been inadvertently collected. Sorted epifauna were placed in a drying oven at 60°C for 48 h to obtain dry weights for crustaceans (primarily amphipods, isopods, and shrimp) and fishes. Of the major taxonomic groups collected from the ASUs (crustaceans, gastropods, and bivalves), the crustacean species (isopods, amphipods, crabs, and shrimps) were selected to represent those organisms most likely to be consumed by higher-order predators (e.g. fishes) that use eelgrass habitat for refuge and foraging (Warfe & Barmuta 2004).

Expt 1. The goal of Expt 1 was to determine how simulated eelgrass structural complexity and exposure time influence epifaunal colonization (i.e. all new individuals in ASUs) and recruitment (i.e. recently settled larvae or juveniles in ASUs). We deployed SL, SH, TL and TH ASUs (n = 12 each) on a shallow (1.5 to 2.6 m at MLLW, mean lower low water) sandy shoal adjacent

to an extensive eelgrass bed at Shelter Island (32° 43′ N, 117° 13′ W) in the northern eco-region of San Diego Bay. ASUs were deployed for each of 3 exposure times: 2, 4, or 6 wk. By varying exposure time, we could also determine the maximum length of time that ASUs could be deployed before fouling might influence the results and apply this knowledge to Expt 2. In San Diego Bay, 1 m^2 ASUs were extensively colonized by epifauna within 1 wk (Healey & Hovel 2004). We conducted 2 trials of this experiment (Trial 1: 31 March to 12 May 2004; Trial 2: 22 June to 4 August 2004) to account for potential differences in colonization rates among seasons. Prior to Trial 1, 6 permanent 35 m transects were established parallel to the eelgrass bed. ASUs were placed 5 m apart in random order within each block and transects were placed no less than 5 m apart (Fig. 1). Each transect consisted of 2 blocks, and each block consisted of 1 replicate of each of the 4 treatment combinations (N = 4 ASUs/block × 4 blocks/deployment time × 3 deployment times = 48 ASUs). At each exposure time, 4 blocks (not of the same transect) of ASUs were collected (4 ASUs/block × 4 blocks/deployment time = 16 ASUs).

We used separate 2-way fixed factor analyses of variance (ANOVAs) to test how (1) total epifaunal density, (2) species richness, and (3) Simpson's index of diversity (D_s) varied among the 4 simulated eelgrass habitat treatments and deployment time. We considered the effect of blocks on dependent variables in initial analyses, but did not include the blocks in our final analyses because effects were minimal and their inclusion reduced statistical power. Two-way ANOVAs also were used to test how the densities of the 3 most abundant taxa collected in this experiment varied with habitat treatment and deployment time. For all 2-way ANOVAs, we used techniques described in Graham & Edwards (2001) to calculate the proportion of the total variance (=magnitude of effect, ω^2) accounted for by each factor and by the error term when $p < 0.1$. This additional piece of information, akin to the coefficient of determination in regression analysis, typically is not considered for ANOVAs but provided us with an additional way to evaluate the strength of treatment effects on total epifaunal density, species richness, and D_s. For all statistical analyses, data for each trial were analyzed separately. D_s was chosen as a measure of species diversity because it represents the probability that 2 randomly chosen individuals in a sample are of different species (Hurlbert 1971). Results were qualitatively similar using the Shannon Index (H'). Cochran's test was used to test for heterogeneous variances, and we transformed data where necessary ($\log(x+1)$) to meet the assumptions of ANOVA in these and all subsequent tests. Rather than using an arbitrary alpha value of $p < 0.05$ to determine which trends were significant, we used resulting p-values, effect sizes, ω^2 terms and error bars to suggest which tests provided strong vs. weak evidence for effects of simulated eelgrass treatments on epifauna. This approach acknowledges the generally high levels of variability inherent in subtidal systems but still allows for rigorous hypothesis testing (Dayton et al. 1999).

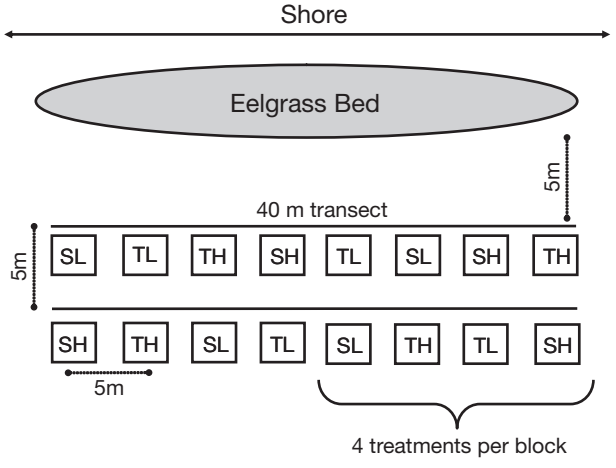

Fig. 1. Experimental layout for one site in San Diego Bay (not to scale). Each block (represented by the bracket) contained 1 replicate of each habitat treatment in random order. Not all transects are shown. SL: short shoots, low density; SH: short shoots, high density; TL: tall shoots, low density; TH: tall shoots, high density

Two-way ANOVAs were followed with *a priori* contrasts and Tukey least significant difference (LSD) post-hoc multiple comparisons to further test how total epifaunal density, species richness, D_s, and species' densities varied with habitat treatment and deployment time. We first evaluated the habitat treatment × time interaction term, and pooled data over treatments and deployment times when $p > 0.25$ (Underwood 1997). When a significant effect of deployment time was found, we used LSD multiple comparisons to test for trends in dependent variables, since no *a priori* hypotheses regarding this independent variable were made. When we found a significant effect of habitat treatment, we determined which means differed using sequential *a priori* contrasts (Underwood 1997, Jenkins et al. 2002, Gotelli & Ellison 2004). We first tested for a difference between the 2 equal surface area treatments (SH and TL). If no strong evidence for a difference was detected ($p > 0.1$), suggesting that simulated shoot surface area (but not shoot length or density) significantly influences the dependent variable, a second contrast was used to test whether the means for the different surface area treatments differed (e.g. SL < SH = TL < TH). If in the first contrast strong evidence for a difference in means for the SH and TL treatments was detected ($p < 0.1$), suggesting that shoot length, shoot density, or both of these factors were important, we

contrasted means for shoot length (SL = TL ≠ SH = TH) and shoot density (SL = TL ≠ SH = TH). This set of 2 contrasts also was run when a visual inspection of the means and variances for the SH and TL treatments suggested that differences could not be detected due to low statistical power. The first set of contrasts (testing for a surface area effect) are orthogonal, but the second set (testing for shoot length and shoot density effects) are not. However, any problem of non-independence among p-values resulting from non-orthogonality should be outweighed by the benefit of keeping the number of comparisons among means low (Underwood 1997, Jenkins et al. 2002, Quinn & Keough 2002).

Finally, we used 1-way ANOVAs to determine how recruitment of several species (see 'Results; Expt 1' below) varied among habitat treatments in Trial 2, in which large increases in newly settled juveniles were evident from one trial to the next. We refer to these events as recruitment based on the dramatic increases in abundance (ca. 30-fold) of very small individuals from one trial to the next. These tests of recruitment were conducted in weeks with peak abundances, which varied according to species.

Expt 2. To determine the interactive effect of simulated eelgrass structural complexity and site on epifaunal community composition, we deployed 6 replicate ASUs of each treatment combination at each of 2 sites in San Diego Bay on 11 May 2004 (Trial 1) and 3 August 2004 (Trial 2) (N = 4 ASUs/block × 6 blocks/site × 2 sites = 48 ASUs). The 2 sites were located in different eco-regions, with Shelter Island (32° 43′ N, 117° 13′ W) in the northern eco-region and Coronado (32° 41′ N, 117° 9′ W) in the southern central eco-region, just south of the Coronado Bay Bridge. At Shelter Island, ASUs were placed on the same sandy shoal as in Expt 1, whereas ASUs at Coronado were placed on unvegetated soft sediment parallel to the deepest edge (3 m at MLLW) of the existing eelgrass bed. At each site, ASUs were placed in random order on 5 m centers along three 35 m transects established parallel to the existing eelgrass bed (Fig. 1). All ASUs were deployed for 4 wk. This length of time was chosen because epiphytic growth was minimal and because results of Expt 1 indicated that epifaunal community structure generally did not differ between the 4 and 6 wk exposure times (see 'Results; Expt 1' below). ASUs were recovered and samples were processed in the laboratory as described above for Expt 1.

We used 2-way, fixed factor ANOVAs to test how (1) total epifaunal density, (2) species richness, (3) D_s, (4) crustacean biomass, and (5) fish biomass varied among the 2 sites and the 4 simulated eelgrass treatments. The relative importance (ω^2) of individual factors was calculated as described above. Due to the strong relative contribution of site and the repeated interaction of site and habitat treatment detected by the 2-way ANOVAs, 1-way ANOVAs investigating the effect of habitat treatment were run separately for each site. *A priori* contrasts (as described in 'Expt 1' above) were used to determine which means differed when $p < 0.1$ in the ANOVAs. Data were analyzed separately for each trial.

We employed multivariate analyses to analyze community composition using the PRIMER software package (Plymouth Marine Laboratory; Clarke & Warwick 1994). Non-metric multidimensional scaling (nMDS) ordinations of all replicates were plotted based on Bray-Curtis similarities, which were calculated on non-transformed abundance data. One-way analysis of similarities (ANOSIM; Clarke & Warwick 1994) were used to test for differences among ASU treatments.

RESULTS

Expt 1

Due to rough weather conditions 2 SL ASUs and 1 SH ASU were lost during Week 4 of Trial 1. Over the course of the 2 trials, we collected a total of 24 524 individuals representing 62 species, including 14 bivalve, 7 crab, 7 fish, 18 gastropod, 6 shrimp and 10 other species (Table 1). For both trials, Gammaridae spp. and *Caprella californica* were the two most abundant taxa, together composing 52 and 33% of the cumulative total in Trials 1 and 2, respectively.

During both trials, total epifaunal density varied by both habitat treatment and deployment time, but there was no interactive effect of these 2 factors (Table 2). In both trials, habitat treatment generally had a larger influence on total epifaunal density than did deployment time (Table 2). In Trial 1, total epifaunal density was significantly higher in Week 2 than in Weeks 4 and 6. In contrast, in Trial 2, total epifaunal density was significantly higher in Weeks 4 and 6 than in Week 2. Effects of habitat treatment also differed between the 2 trials. There was a significant positive effect of simulated shoot surface area on total epifaunal density in Trial 1, whereas in Trial 2 both shoot length and shoot density had a significant positive effect on total epifaunal density (Table 3, Fig. 2).

For both trials, habitat treatment did not significantly influence species richness and D_s, but both species richness and D_s were significantly higher in Weeks 4 and 6 than in Week 2 (Table 2, Fig. 2). For both variables, differences among deployment times were relatively slight.

The most abundant taxa in Expt 1 were *Caprella californica* (amphipod), Gammaridae spp. (amphipod), *Hippolyte californiensis* (small grass shrimp) and *Alia*

carinata (small gastropod) (Table 1). Responses to habitat treatment and deployment time varied among these species. Although *H. californiensis* appeared to respond to habitat attributes at Shelter Island, the data did not meet the assumptions of ANOVA even after transformation. During Trial 1, *C. californica* density was significantly higher in Week 6 than in Weeks 2 and 4, and there was a significant influence of surface area on *C. californica* density (Habitat treatment [HT]: $F_{3,33} = 3.5$, $p = 0.03$, $\omega^2 = 4.5$; Deployment time [DT]: $F_{2,33} = 8.1$, $p < 0.001$, $\omega^2 = 8.6$; HT × DT: $F_{6,33} = 0.9$, $p = 0.5$; Table 3). In Trial 2, there was a significant interactive effect of habitat treatment and deployment time on *C. californica* density (HT: $F_{3,33} = 3.2$, $p = 0.04$, $\omega^2 = 4.1$; DT: $F_{2,33} = 2.2$, $p = 0.12$; HT × DT: $F_{6,33} = 2.245$, $p = 0.06$, $\omega^2 = 4.65$; Table 3). For Gammaridae spp., in Trial 1 density was significantly higher in Week 2 than in Weeks 4 and 6, and there was no significant effect of habitat treatment (HT: $F_{3,33} = 1.8$, $p = 0.16$; DT: $F_{2,33} = 3.3$, $p = 0.05$, $\omega^2 = 3.11$; HT × DT: $F_{6,33} = 0.18$, $p = 0.98$; Table 3). In Trial 2, there was a significant interactive effect of habitat treatment and deployment time on Gammaridae spp. (HT: $F_{3,33} = 4.9$, $p < 0.001$, $\omega^2 = 7.27$; DT: $F_{2,33} = 0.06$, $p = 0.95$; HT × DT: $F_{6,33} = 2.25$, $p = 0.06$, $\omega^2 = 4.66$; Table 3). *A. carinata* density was positively influenced by shoot surface area in both Trials 1 and 2 (HT: $F_{3,33} = 38.3$, $p < 0.001$, $\omega^2 = 43.19$; DT: $F_{2,33} = 0.72$, $p = 0.492$; HT × DT: $F_{6,33} = 1.64$, $p = 0.17$; Table 3). In Trial 2, *A. carinata* density was significantly higher in Week 6 than in Weeks 2 and 4 (HT: $F_{3,33} = 3.4$, $p = 0.03$, $\omega^2 = 4.66$; DT: $F_{2,33} = 3.12$, $p = 0.06$, $\omega^2 = 2.71$; HT × DT: $F_{6,33} = 1.1$, $p = 0.382$).

Table 1. Number of individuals captured for species composing 99% of the total catch for Expt 1 at Shelter Island. Taxonomic class of each species is given as follows: A, amphipod; B, bivalve; D, decapod; E, echinoderm; G, gastropod; I, isopod; V, vertebrate. Common name is given where possible

Taxon	Common name	Class	Total	% total
Caprella californica	Skeleton shrimp	A	5029	20.51
Gammaridae spp.	Amphipod	A	4557	18.58
Hippolyte californiensis	California grass shrimp	D	2498	10.19
Alia carinata	Carinate dovesnail	G	1859	7.58
Pyromaia tuberculata	American spider crab	D	1825	7.44
Bulla gouldiana	California bubble snail	G	1462	5.96
Argopecten aequisulcatus	Speckled scallop	B	1443	5.88
Laevicardium substriatum	Pacific egg cockle	B	1007	4.11
Pandalus sp.	Shrimp	D	963	3.93
Serolis carinata	Isopod	I	738	3.01
Paracerceis sculpta	Isopod	I	633	2.58
Lyonsia californica	California lyonsia	B	447	1.82
Musculista senhousia	Asian mussel	B	295	1.20
Crangon sp.	Shrimp	D	263	1.07
Macoma nasuta	Bent-nosed macoma	B	249	1.02
Tagelus californianus	California jackknife	B	239	0.97
Pagurus sp.	Hermit crab	D	100	0.41
Nassarius mendicus	Lean basket-whelk	G	89	0.36
Nassarius perpinguis	Fat dog whelk	G	80	0.33
Heterostichus rostratus	Giant kelpfish	V	76	0.31
Heptacarpus pictus	Transparent shrimp	D	57	0.23
Lophopanopeus bellus bellus	Black-clawed crab	D	50	0.20
Mactra californica	California surf clam	B	41	0.17
Crepidula norrisiarum	Shelf limpet	G	41	0.17
Conus californicus	California cone snail	G	39	0.16
Cancer sp.	Crab	D	39	0.16
Paranthura elegans	Isopod	I	37	0.15
Dendraster excentricus	Eccentric sand dollar	E	34	0.14
Nassarius tegula	Western mud nassa	G	34	0.14
Tellina sp.	Bivalve	B	32	0.13
Gobidae sp.	Goby	V	32	0.13
Solen rosaceus	Rosy jackknife	B	32	0.13
Lacuna unifasciata	One-band lacuna	G	28	0.11
			24348	**99.29**

Table 2. Results of 2-way ANOVAs testing the effects of habitat treatment and deployment time on total epifaunal density (TED), species richness, and Simpson's index of diversity (D_s) for both trials of Expt 1. ω^2: proportion of the variance accounted for by each variable. p-values < 0.1 are in bold. –: variance not calculated, since p-value > 0.1

	TED					Species richness					D_s				
	df	MS	*F*	p	ω^2	df	MS	*F*	p	ω^2	df	MS	*F*	p	ω^2
Trial 1															
Habitat treatment (HT)	3	57449	6.777	**<0.001**	**10.63**	3	3.67	0.467	0.707	–	3	0.013	1.494	0.234	–
Deployment time (DT)	2	27704	3.268	**0.051**	**2.78**	2	49.43	6.288	**0.005**	**7.06**	2	0.081	9.472	**0.001**	**9.79**
HT × DT	6	4495.3	0.53	0.781	–	6	3.628	0.462	0.832	–	6	0.012	1.387	0.249	–
Residual	33	8476.9			88.32	33	7.861			96.17	33	0.009			88.17
Trial 2															
Habitat treatment (HT)	3	203661	15.87	**<0.001**	**22.96**	3	4.556	0.511	0.677	–	3	0.005	2.016	0.129	–
Deployment time (DT)	2	60449	4.71	**0.015**	**3.82**	2	97.56	10.94	**<0.001**	**12.3**	2	0.015	6.084	**0.005**	**7.9**
HT × DT	6	9027.2	0.703	0.649	–	6	7.535	0.845	0.544	–	6	0.003	1.276	0.293	–
Residual	36	12835			74.14	36	8.917			87.1	36	0.002			87.54

Table 3. Results of *a priori* contrasts for all response variables with a p-value < 0.1 (shown in bold) in 1-way ANOVAs on habitat treatment in Expt 1 at Shelter Island. Yes: strong evidence for an effect of shoot surface area (SA), shoot density, or shoot length. TED: total epifaunal density; DNT: did not test; SL: short shoots, low density; SH: short shoots, high density; TL: tall shoots, low density; TH: tall shoots, high density. Full species names as in Table 1

Trial	Dependent variable	SA				Shoot density		Shoot length		SA?	Density?	Length?
		SH ≠ TL		SL < SH = TL < TH		SL = TL ≠ SH = TH		SL = SH ≠ TL = TH				
		F	p	*F*	p	*F*	p	*F*	p			
1	TED	0.05	0.82	7.02	**0.02**	9.97	DNT	8.02	DNT	Yes	–	–
2	TED	3.72	**0.08**	10.34	DNT	32.01	**0.00**	8.59	**0.01**	–	Yes	Yes
1	*C. californica*	0.14	0.71	3.79	**0.08**	2.28	DNT	4.17	DNT	Yes	–	–
1	*A. carinata*	1.13	0.31	49.41	**0.00**	37.45	DNT	58.16	DNT	Yes	–	–
2	*A. carinata*	0.00	0.95	4.79	**0.05**	3.53	DNT	3.88	DNT	Yes	–	–
2. Week 4	*L. substriatum*	5.28	0.11	2.14	DNT	0.42	0.56	15.20	**0.03**	–	–	Yes
2. Week 2	*B. gouldiana*	2.26	0.23	8.02	DNT	10.86	**0.05**	1.37	0.33	–	Yes	–
2. Week 4	*B. gouldiana*	0.24	0.66	6.91	**0.08**	4.97	DNT	2.38	DNT	Yes	–	–
2. Week 6	*A. aequisculcatus*	1.15	0.36	5.13	DNT	2.29	0.23	9.17	**0.06**	–	–	Yes

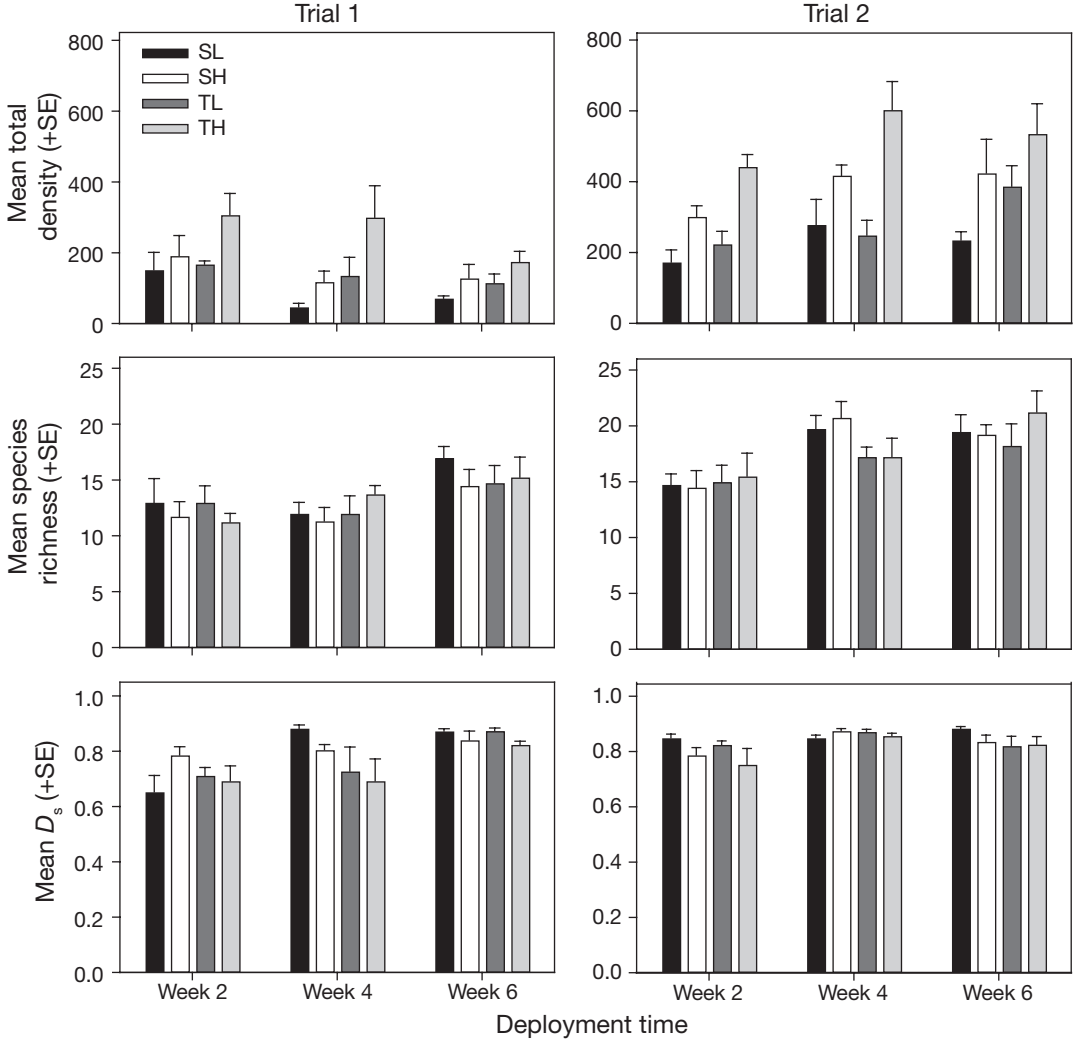

Fig. 2. Mean epifaunal density, species richness, and Simpson's index of diversity (D_s) in artificial seagrass units (ASUs) for Expt 1. Error bars are +SE. Abbreviations as in Fig. 1

During both trials, various species had large recruitment pulses and/or settlement events, including the clam *Laevicardium substriatum*, the cloudy bubble snail *Bulla gouldiana*, and the speckled scallop *Argopecten aequisulcatus* (Fig. 3). *L. substriatum* had a dramatic peak in recruitment in Week 4 of Trial 2, and *L. substriatum* recruitment was significantly higher in the short shoot treatments than in the tall shoot treatments ($F_{3,12}$ = 5.3, p = 0.02; Table 3). *B. gouldiana* had an almost 200% increase in mean density from Trial 1 to Trial 2. Peak recruitment occurred during Week 2 of Trial 2, with a significantly greater number of individuals occurring in high shoot density treatments than in the 2 low shoot density treatments ($F_{3,12}$ = 5.3, p = 0.02; Fig. 3, Table 3). In Week 4, however, *B. gouldiana* recruitment increased significantly with surface area ($F_{3,12}$ = 3.6, p = 0.04). *A. aequisulcatus* recruitment peaked in Week 6 of Trial 2, and recruitment was significantly higher in tall shoot treatments than in the 2 short shoot treatments ($F_{3,12}$ = 4.36, p = 0.027; Fig. 3, Table 3).

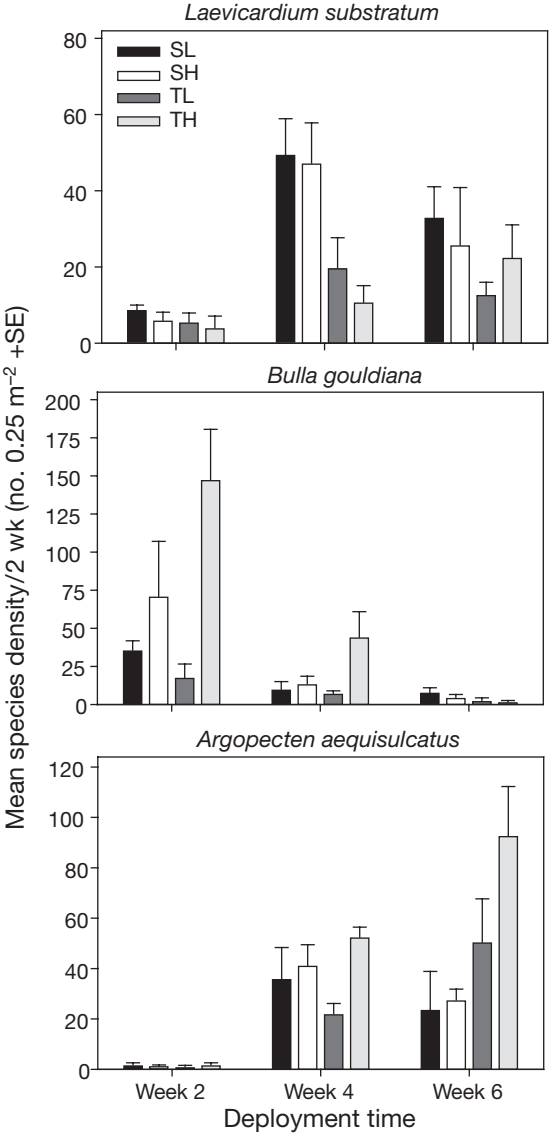

Fig. 3. Densities of *Laevicardium substriatum*, *Bulla gouldiana*, and *Argopecten aequisulcatus* in Trial 2 of Expt 1. Error bars are +SE. Abbreviations as in Fig. 1

Expt 2

At Coronado, we collected a total of 3803 individuals over 2 trials comprising 30 different species (Table 4). The taxa included 6 bivalve, 2 crab, 5 fish, 6 gastropod, 5 shrimp, and 6 other species types. Three species comprised nearly 70% of the total abundance at Coronado, including the isopod *Paracercius sculpta*, the bivalve *Tellina* sp., and the spider crab *Pyromaia tuberculata*. At Shelter Island, we collected a total of 13 093 individuals over 2 trials comprising 48 species (Table 4). The taxa included 9 bivalve, 7 crab, 5 fish, 11 gastropod, 5 shrimp, and 11 other species types. The 3 most abundant species at Shelter Island, the isopod *Caprella californica*, the grass shrimp *Hippolyte californiensis*, and the spider crab *P. tuberculata* comprised 60% of the total number of individuals collected there. Of the species found at Shelter Island during Expt 2, 23 were not found at Coronado, and 6 species found at Coronado were not found at Shelter Island (Table 4).

In both trials, total epifaunal density was significantly higher at Shelter Island than at Coronado, and site explained almost 3 times as much of the variance in total epifaunal density as did habitat treatment (Table 5). In Trial 1 at Coronado, total epifaunal density was significantly higher in tall shoot treatments than in the short shoot treatments, whereas in Trial 2 the only difference among means that could be detected was between the TH and SL treatments (Table 6). At Shelter Island, total epifaunal density increased with shoot density during Trial 1 and with surface area during Trial 2 (Table 6, Fig. 4). As with total epifaunal density, species richness also showed strong responses to both habitat treatment and site, and site explained a greater proportion of the variance in species richness than did habitat treatment. At Coronado, species richness had a response to habitat in Trial 1, but not Trial 2. Although a response to habitat was detected in the 1-way ANOVA, we were unable to detect which attribute of the habitat was influencing this pattern using *a priori* contrasts. At Shelter Island, species richness did not differ among habitat treatments in Trial 1, but did in Trial 2, where it was higher in short shoot length than in the tall shoot length treatments (Table 6, Fig. 4). There was a signif-

Table 4. Number of individuals captured for species comprising 99% of the total catch for Expt 2. Taxonomic class of each species is given as in Table 1. Common name is given where possible

Taxon	Common name	Class	Total	% total
Coronado				
Paracerceis sculpta	Isopod	I	1353	40.09
Tellina sp.	Bivalve	B	509	15.08
Pyromaia tuberculata	American spider crab	D	389	11.53
Gammaridae spp.	Amphipod	A	343	10.16
Hippolyte californiensis	California grass shrimp	D	161	4.77
Pandalus sp.	Shrimp	D	148	4.39
Alia carinata	Carinate dovesnail	G	123	3.64
Caprella californica	Skeleton shrimp	A	74	2.19
Bulla gouldiana	California bubble snail	G	54	1.60
Crepidula norrisiarum	Shelf limpet	G	24	0.71
Alpheus californiensis	California snapping shrimp	D	22	0.65
Argopecten aequisulcatus	Speckled scallop	B	21	0.62
Serolis carinata	Isopod	I	19	0.56
Heterostichus rostratus	Giant kelpfish	D	18	0.53
Ostrea lurida	Olympia oyster	B	16	0.47
Lophopanopeus bellus bellus	Black-clawed crab	D	15	0.44
Gobidae sp.	Goby	V	13	0.39
Laevicardium substriatum	Pacific egg cockle	B	13	0.39
Heptacarpus pictus	Transparent shrimp	D	12	0.36
Nassarius tegula	Western mud nassa	G	10	0.30
			3337	**98.87**
Shelter Island				
Caprella californica	Skeleton shrimp	A	3024	23.10
Hippolyte californiensis	California grass shrimp	D	2502	19.11
Pyromaia tuberculata	American spider crab	D	2309	17.64
Gammaridae spp.	Amphipod	A	1603	12.24
Alia carinata	Carinate dovesnail	G	674	5.15
Pandalus sp.	Shrimp	D	471	3.60
Laevicardium substriatum	Pacific egg cockle	B	409	3.12
Paracerceis sculpta	Isopod	I	312	2.38
Argopecten aequisulcatus	Speckled scallop	B	309	2.36
Serolis carinata	Isopod	I	230	1.76
Bulla gouldiana	California bubble snail	G	132	1.01
Paranthura elegans	Isopod	I	117	0.89
Tagelus californianus	California jackknife	B	117	0.89
Macoma nasuta	Bent-nosed macoma	B	102	0.78
Lophopanopeus bellus bellus	Black-clawed crab	D	97	0.74
Crangon sp.	Shrimp	D	74	0.57
Portunus xantusii xantusii	Xantus' swimming crab	D	69	0.53
Leptopecten latiauratus	Kelp scallop	B	64	0.49
Hypsoblennius gentilis	Bay blenny	V	63	0.48
Lyonsia californica	California lyonsia	B	56	0.43
Paralabrax clathratus	Kelp bass	V	45	0.34
Cancer sp.	Crab	D	43	0.33
Tellina sp.	Bivalve	B	37	0.28
Heterostichus rostratus	Giant kelpfish	V	32	0.24
Nassarius mendicus	Lean basket-whelk	G	31	0.24
Crepidula norrisiarum	Shelf limpet	G	24	0.18
			12 946	**98.88**

icant interactive effect of habitat treatment and site on D_s in Trial 1, whereas in Trial 2, D_s varied only between sites.

At Coronado, D_s was significantly higher in the intermediate shoot surface area treatment than in low and high surface area treatments in Trial 1, but no response to habitat treatment was detected in Trial 2 (Fig. 4). A response to habitat treatments was detected for both trials at Shelter Island. *A priori* contrasts suggested that D_s varied with surface area in Trial 1, but we could not determine a specific pattern (Table 6). In Trial 2 at Shelter Island, D_s decreased with increasing surface area (Table 6, Fig. 4).

Non-metric MDS stress levels for each trial at each site were below 0.07 for all 3-dimensional output, indicating good ordination with a low likelihood of misinterpretation (Clarke & Warwick 1994). At Coronado during Trial 1, community assemblages for each treatment combination were statistically different from each other, except when comparing the SL and SH treatments (Table 7, Fig. 5). During Trial 2, 4 of the 6 comparisons were statistically different, with no difference detected between the SH and TL plots or the TL and TH plots. At Shelter Island, community assemblages differed among all treatments during Trial 1, and in Trial 2, 5 out of the 6 pairwise comparisons were statistically different (Table 7, Fig. 5). No difference was detected between the equal surface area treatments during Trial 2 at Shelter Island (SH and TL).

For crustacean biomass, there was a significant interactive effect of habitat treatment and site in Trial 1, with the habitat treatment × site term accounting for ca. 18% of the variance (Table 8). In Trial 2 both habitat treatment and site independently influenced crustacean biomass, and habitat treatment accounted for more of the variance in biomass than did site. For both trials, the error term accounted for ca. 70% of the variance in crustacean biomass. Due to the strong effect of site, we conducted separate tests for effects of habitat treatments for each site. In Trial 1 at Coronado, surface area had a positive effect on crustacean biomass, whereas in Trial 2 at Coronado, crustacean biomass was ca. 4 times higher in high shoot density plots than in low shoot density plots, but the effect of shoot density was not significant due to high within-treatment variance

Table 5. Results of 2-way ANOVAs testing the effects of habitat treatment and site on total epifaunal density (TED), species richness, and Simpson's index of diversity (D_s) in Expt 2. ω^2: proportion of the variance accounted for by each variable. p-values < 0.1 are in bold

	TED					Species richness					D_s				
	df	MS	*F*	p	ω^2	df	MS	*F*	p	ω^2	df	MS	*F*	p	ω^2
Trial 1															
Habitat treatment (HT)	3	29983	7.273	**0.001**	**10.98**	3	11.39	4.141	**0.012**	**4.07**	3	0.033	3.491	**0.024**	**6.48**
Site (S)	1	221283	53.67	**<0.001**	**30.74**	1	341.3	124.1	**<0.001**	**53.2**	1	0.007	0.722	0.401	–
HT × S	3	9458	2.294	**0.093**	**2.27**	3	5.5	2	0.129	–	3	0.023	2.406	**0.081**	**3.66**
Residual	40	4123			56.02	40	2.75			41.5	40	0.01			90.1
Trial 2															
Habitat treatment (HT)	3	90064	8.778	**<0.001**	**12.28**	3	10.19	3.327	**0.029**	**1.33**	3	0.025	1.727	0.177	–
Site (S)	1	706160	68.82	**<0.001**	**35.69**	1	1292	421.8	**<0.001**	**80**	1	0.537	37.3	**<0.001**	**27.7**
HT × S	3	20169	1.966	0.135	–	3	5.69	1.857	0.152	–	3	0.01	0.72	0.546	–
Residual	40	10261			50.51	40	3.07			18.2	40	0.014			71.2

Table 6. Results of *a priori* contrasts for all response variables with a p-value < 0.1 (shown in bold) in 1-way ANOVAs on habitat treatment in Expt 2. Yes: strong evidence for an effect of shoot surface area (SA), shoot density, or shoot length. COR: Coronado; SI: Shelter Island; SR: species richness; D_s: Simpson's index of diversity; CBD: could not be determined; B: biomass; other abbreviations as in Table 3

Trial	Site	Dependent variable	SA				Shoot density		Shoot length		SA?	Density?	Length?
			SH ≠ TL		SL < SH = TL < TH		SL = TL ≠ SH = TH		SL = SH ≠ TL = TH				
			F	p	*F*	p	*F*	p	*F*	p			
1	COR	TED	0.85	**0.40**	3.05	DNT	2.67	0.16	8.64	**0.03**	–	–	Yes
1	COR	SR	2.20	0.20	0.05	0.84	2.25	DNT	12.97	DNT	CBD	–	–
1	COR	D_s	2.03	0.21	7.84	**0.04**	4.59	DNT	0.02	DNT	Yes	–	–
1	SI	TED	4.62	**0.08**	0.59	DNT	14.62	**0.01**	0.62	0.47	–	Yes	–
1	SI	D_s	3.70	0.11	0.75	0.43	5.47	DNT	0.14	DNT	CBD	–	–
2	SI	TED	1.74	0.24	6.35	**0.05**	18.07	DNT	5.70	DNT	Yes	–	–
2	SI	SR	10.00	**0.03**	0.05	DNT	1 .54	0.27	10.43	**0.02**	–	–	Yes
2	SI	D_s	2.40	0.18	6.80	**0.05**	6.63	DNT	22.71	DNT	Yes	–	–
1	COR	Crustaceans (B)	0.02	0.90	17.60	**0.01**	4.63	DNT	4.18	DNT	Yes	–	–
1	COR	Fishes (B)	0.02	0.89	5.40	**0.07**	3.31	DNT	2.58	DNT	Yes	–	–
1	SI	Crustaceans (B)	1.95	0.22	9.25	**0.03**	0.78	DNT	0.15	DNT	Yes	–	–
1	SI	Fishes (B)	0.27	0.62	20.09	**<0.01**	13.49	DNT	8.62	DNT	Yes	–	–
2	SI	Crustaceans (B)	0.44	0.54	11.17	**0.02**	6.73	DNT	4.56	DNT	Yes	–	–
2	SI	Fishes (B)	0.34	0.58	17.51	**0.01**	15.38	DNT	9.59	DNT	Yes	–	–

(Fig. 6). At Shelter Island, there was a significant effect of surface area on crustacean biomass in both trials, but in Trial 1 biomass was highest in treatments with intermediate levels of surface area (SH and TL plots) and lowest in SL plots, and in Trial 2 biomass increased with increasing surface area (Table 6, Fig. 6).

There was a significant effect of habitat treatment, site, and habitat treatment × site on fish biomass in both trials, but in both trials habitat treatment explained more of the variance in fish biomass than did site and the interaction term. Approximately 60 to 70% of the variance in fish biomass was unexplained (Table 8). Fish biomass increased with surface area in both trials at both sites, except for Trial 2 at Coronado (Table 6, Fig. 6). In cases where surface area was significant, fish biomass was ca. 10 times higher in the TH plots than in all other treatments.

DISCUSSION

The addition of seagrass to relatively unstructured sediment substantially increases faunal abundance (Lee at al. 2001, Jenkins et al. 2002), species richness (Lee at al. 2001), and species diversity (Orth 1992). It is unclear, however, which features of seagrass habitat have the greatest influence on community structure. While numerous studies have investigated the effects of individual habitat characteristics such as shoot length and shoot density on fauna (e.g. Bell & Westoby 1986, Webster et al. 1998, Horinouchi & Sano 1999, Boström & Bonsdorff 2000, Jenkins et al. 2002, Warfe & Barmuta 2004), these attributes naturally covary and often vary with other habitat characteristics including available surface area, epiphyte growth, leaves per seagrass shoot, patch age and patch size. This natural

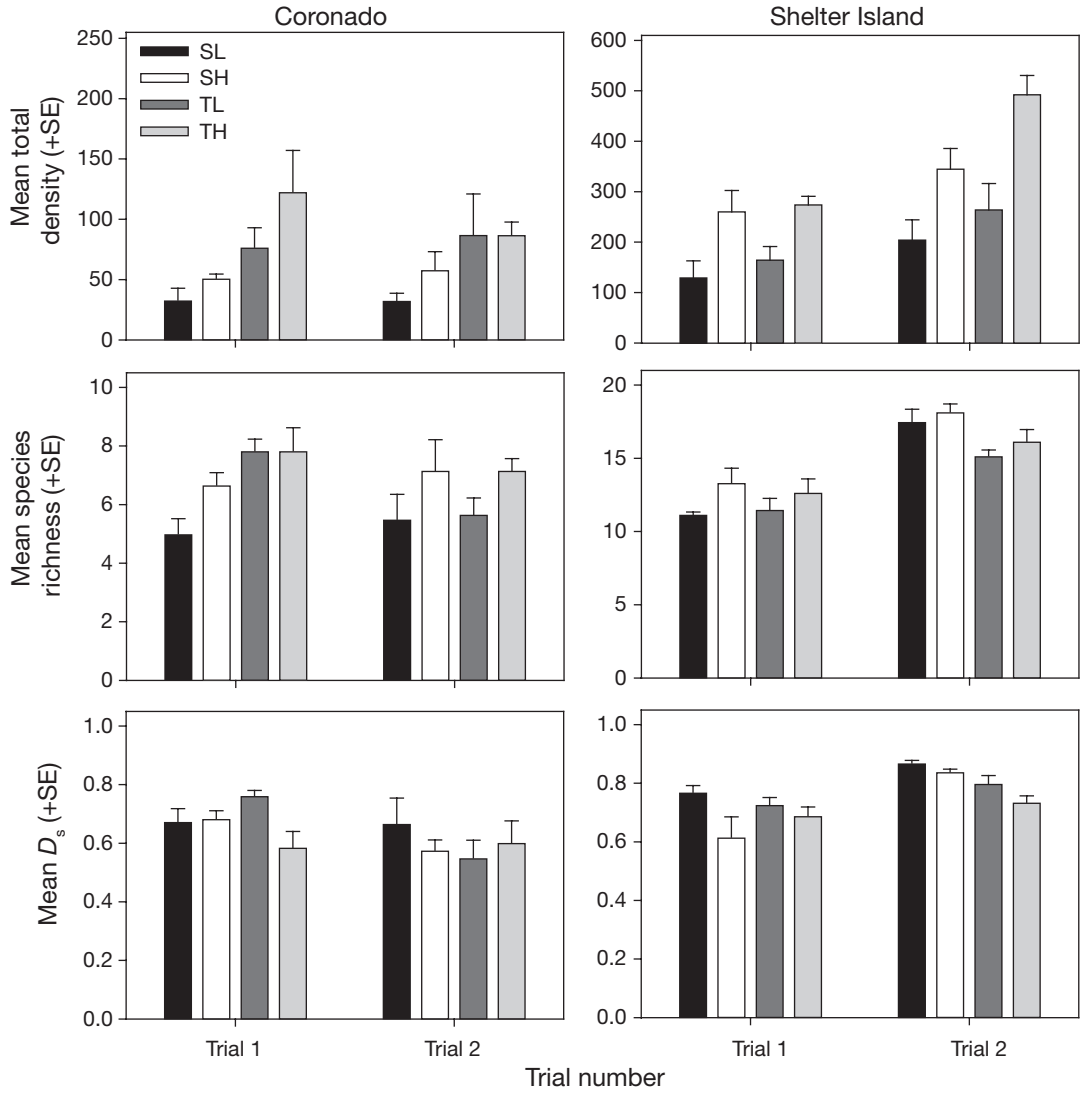

Fig. 4. Mean total epifaunal density, species richness, and Simpson's index of diversity (D_s) in ASUs for Expt 2. Error bars are +SE. Abbreviations as in Fig. 1

Table 7. Results of analysis of similarities (ANOSIM) on non-transformed abundance data testing for differences in community structure between treatments from each site during 2 trials of Expt 2. p-values < 0.1 are in bold. SL: short shoots, low density; SH: short shoots, high density; TL: tall shoots, low density; TH: tall shoots, high density

Pairwise comparisons	Trial 1		Trial 2	
	Coronado	Shelter Island	Coronado	Shelter Island
	p	p	p	p
SL vs. SH	0.145	**0.009**	**0.028**	**0.011**
SL vs. TL	**0.022**	**0.017**	**0.061**	**0.058**
SL vs. TH	**0.032**	**0.006**	**0.004**	**0.002**
SH vs.TL	**0.082**	**0.045**	0.584	0.747
SH vs. TH	**0.002**	**0.009**	**0.089**	**0.004**
TL vs. TH	**0.004**	**0.006**	0.379	**0.024**

covariation makes it difficult to determine which aspects of seagrass habitat structure may have the strongest influence on epifaunal abundance and community structure.

In this study, we determined the relative importance of simulated shoot length, shoot density, and shoot surface area for the eelgrass epifaunal community in San Diego Bay using artificial seagrass to create simulated patches of equal age and size in which shoot length, shoot density, and shoot surface area varied independently. We found that (1) all habitat variables influenced the eelgrass epifaunal community, but shoot surface area influenced epifaunal density and diversity more often than did shoot length and shoot density; (2) effects of habitat

variables on epifaunal density and diversity often varied between trials within sites, as well as between sites in San Diego Bay; (3) habitat variables appeared to have stronger effects on epifaunal density and community composition than on species richness and species diversity; and (4) site often explained proportionally more of the variation in epifaunal density and diversity than did eelgrass habitat characteristics. Overall, our results indicate that eelgrass habitat characteristics such as shoot length and shoot density, in addition to habitat surface area, can influence epifaunal communities, but that the effects of habitat characteristics are highly variable with site and through time.

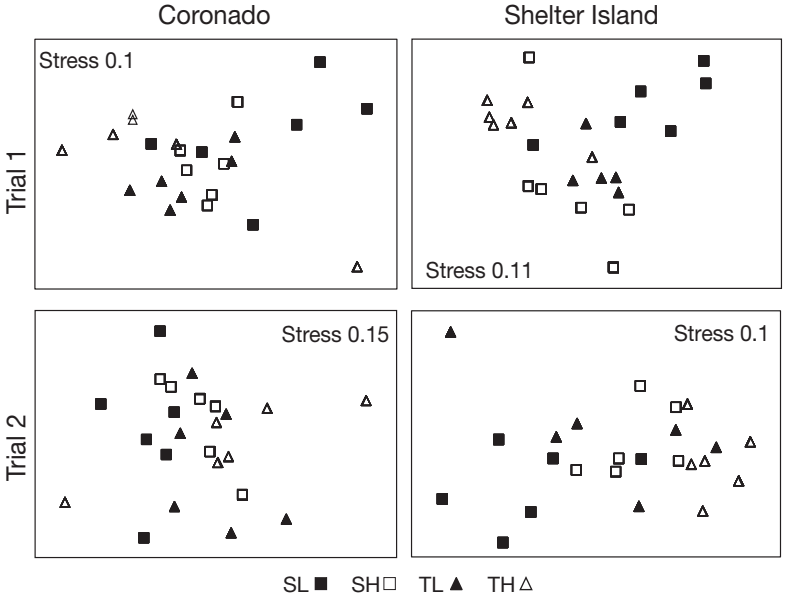

Fig. 5. Non-metric multidimensional scaling (nMDS) ordination based on non-transformed abundance data and Bray-Curtis similarities from Expt 2. Abbreviations as in Fig. 1

Effects of habitat structure on epifaunal density and diversity

In this study, we used a factorial experimental design and *a priori* contrasts to test whether epifaunal density, diversity, and community composition varied primarily with available surface area or with habitat characteristics that commonly covary with surface area (i.e. shoot length and shoot density). Though shoot surface area influenced the epifaunal community more often than did shoot length or density, in several cases epifauna clearly responded to shoot length, shoot density, or both of these variables, indicating that attributes of eelgrass habitat other than simply the amount of habitat present in an area can influence processes structuring epifaunal populations and communities.

Our results contrasted those of Attrill et al. (2000), who found that total epifaunal abundance and species richness had a positive relationship with seagrass biomass, but no relationship to a derived complexity index that incorporated shoot density, the number of leaves per shoot, epiphyte biomass and fractal dimension. From this result they suggested that positive relationships between seagrass habitat complexity and epifaunal diversity often may be simple species–area functions, and that epifaunal community structure is less likely linked with other habitat attributes (see also Stoner 1980). Other studies, however, indicate that seagrass faunal communities strongly respond to various aspects of seagrass habitat structure. In Australian seagrass beds, harpacticoid copepod abundance increased with shoot density but not with shoot length or surface area, whereas there were no effects of seagrass habitat

Table 8. Results of 2-way ANOVAs testing the effects of habitat treatment and site on crustacean and fish biomasses in Expt 2. ω^2: proportion of the variance accounted for by each variable. p-values < 0.1 are in bold

	Crustaceans					Fishes				
	df	MS	*F*	p	ω^2	df	MS	*F*	p	ω^2
Trial 1										
Habitat treatment (HT)	3	0.007	4.936	**0.005**	**8.68**	3	0.308	13.09	**<0.001**	**25.4**
Site (S)	1	0.034	2.2	0.146	–	1	0.106	4.509	**0.04**	**2.44**
HT × S	3	0.14	8.912	**<0.001**	**17.6**	3	0.065	2.75	**0.055**	**3.66**
Residual	40	0.016			72.8	40	0.024			68.6
Trial 2										
Habitat treatment (HT)	3	0.245	9.356	**<0.001**	**18**	3	0.141	11.27	**<0.001**	**18.5**
Site (S)	1	0.468	17.86	**<0.001**	**12.1**	1	0.204	16.24	**<0.001**	**9.19**
HT × S	3	0.045	1.723	0.178	–	3	0.098	7.787	**<0.001**	**12.3**
Residual	40	0.026			68.4	40	0.013			60.1

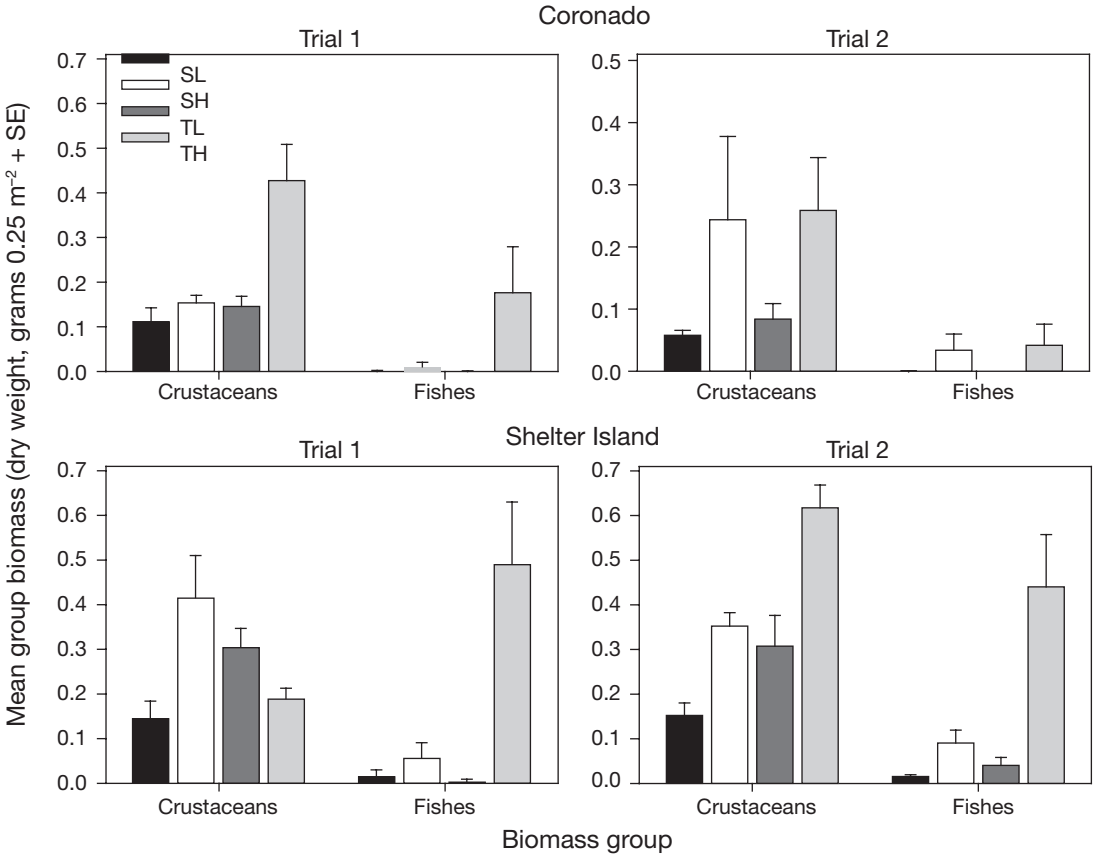

Fig. 6. Mean group biomass (+SE) for crustaceans and fishes from ASUs in Expt 2. Abbreviations as in Fig. 1

characteristics on species richness (Jenkins et al. 2002). In seagrass beds in Virginia, USA, Parker et al. (2001) experimentally manipulated plant species diversity and surface area and found that surface area had a stronger influence on the density of mobile epifauna than did plant species diversity. However, after controlling for surface area, epifauna exhibited a response to plant diversity which was positively correlated with increased structural complexity. Many amphipods in their study had increased abundances when the highly branched red alga *Gracilaria verrucosa* was present, further suggesting that multiple interactions between the epifaunal community and various habitat features are occurring (Parker et al. 2001).

Part of the variability among results may be due to the scaling of the study organisms used; meiofauna (which respond to shoot density but not to surface area; Jenkins et al. 2002) may perceive seagrass habitat differently than do macrofauna (which responded only to surface area in Attrill et al. 2000). However, in our study, macrofauna such as bivalves, shrimp, gastropods, and fishes responded to eelgrass shoot density and height as well as to surface area. Shoot length and density may therefore influence ecological processes that structure populations and communities. For macrofauna that are prey to higher-order predators, dense seagrass shoots may confer more refuge because predator movement and detection of prey may be restricted. Longer shoots may increase density or diversity by providing different microhabitats for species (e.g. gastropods and bivalves may inhabit the base of shoots, and mobile crustaceans may live in the shoot canopy). Seagrass shoot length and density also may influence water flow near the sediment interface (Gambi et al. 1990, Kutija & Hong 1996, Abdelrhman 2003), which in turn may influence larval settlement rates as well as patterns of sediment and detritus delivery and retention (Eckman 1983, Peterson 1986, Bologna & Heck 2002, Peterson et al. 2004). Although we did not quantify water flow in our ASUs, we observed large differences in sediment quality among habitat treatments in the field. After several weeks in San Diego Bay, the base of SL plots consisted largely of coarse sediment, whereas TH plots appeared to trap primarily fine sediments, which suggests that flow rates in the TH plots were lower than in SL plots.

Of the 3 community structure variables (total epifaunal density, species richness, and D_s) total epifaunal density exhibited the strongest response to eelgrass habitat structure. In both experiments, the relative

influence of shoot surface area, shoot density, and shoot length on epifaunal density varied between trials and sites. Although densities of 2 of the most abundant taxa, *Caprella californica* and *Alia carinata*, were linked most strongly to surface area, species recruitment varied with shoot length or shoot density in 3 out of 4 cases, and responses to structure among the recruiting species were dramatically different. As abundant species comprise a disproportionate amount of the total density, species-specific responses largely may account for the inconsistent pattern of total epifaunal density between trials and sites.

When differences in species richness and D_s were detected among treatments, the magnitude of the difference often was relatively small, typically representing an increase of ca. 1 species to a plot. Variability in D_s was more strongly linked to shoot surface area than to shoot length or density. However, D_s increased with shoot surface area at Coronado, and decreased with shoot surface area at Shelter Island. At Shelter Island, species richness was highest in the short shoot treatments, suggesting that D_s may have increased with decreasing surface area due to greater evenness within low surface area plots. Evenness may be higher in plots with lower amounts of habitat if species in those treatments are more transitory than in other treatments, or if plots with high habitat amount are dominated by one or a few abundant species.

In our study, deployment time (in Expt 1) and site (in Expt 2) often explained more of the variance in epifaunal community structure than did simulated eelgrass habitat treatments. In Expt 1, recruitment pulses for several species partially were responsible for the strong influence of deployment time on community structure. The clam *Laevicardium substriatum*, the cloudy bubble snail *Bulla gouldiana*, and the speckled scallop *Argopecten aequisulcatus* all exhibited obvious pulses of recruitment, as indicated by dramatic increases in density (Fig. 3), and ca. 5- to 8-fold decreases in mean body size among deployment times. Effects of eelgrass habitat structure on recruitment varied among the 3 species; *L. substriatum* recruitment was highest in short eelgrass shoots, *B. gouldiana* recruitment was highest in dense shoots, and *A. aequisulcatus* recruitment was highest in long eelgrass shoots. Patterns of recruitment among the 3 species likely were due to both pre- and post-settlement processes acting on larvae and juveniles. Though our experiments were not designed to test why recruitment may vary with habitat structure, recruitment may be maximal where shoots are long or dense if these plots buffer currents that deliver larvae, and if increased structure inhibits predator search and capture. Recruitment of near-surface dwelling bivalves such as *L. substriatum* may be highest in short shoot treatments if they prefer coarser sediment that existed at the base of these plots. Scallops, which attach themselves to seagrass shoots as juveniles, may have preferred long simulated shoots to maximize the range at which they can attach to shoots above the sediment.

In Expt 2, for many variables the ω^2 for site was either approximately equal to or sizably greater than that of habitat treatment. Generally higher epifaunal density and diversity in ASUs at Shelter Island (northern eco-region) than in ASUs at Coronado (central eco-region) may have been due to greater larval delivery at Shelter Island caused by stronger currents, or by a greater mix of bay and ocean water at Shelter Island than at Coronado. Similarly, in Australia the effects of artificial seagrass structural characteristics on copepod abundance were consistent among sites and through time, but results for taxonomic richness depended strongly on site (Jenkins et al. 2002). In a UK *Zostera marina* bed, infaunal macroinvertebrate diversity increased with shoot density and the number of leaves per shoot (Webster et al. 1998), but because habitat structure covaried with site it was difficult to determine if correlations between structure and diversity were due primarily to habitat structure or to site. While our use of ASUs restricted our study to small, simulated eelgrass beds, our design enabled us to distinguish between the effects of site and simulated structure on epifaunal density and diversity in San Diego Bay.

Community composition

Community composition varied strongly among habitat treatments, suggesting that species composing the epifaunal community differ with simulated eelgrass habitat structure (Fig. 5). For all trials and sites, community composition within SL and TH treatments differed dramatically, whereas composition differed between the 2 equal surface area plots (SH and TL) in Trial 1 but not in Trial 2. Shoot surface area, length and density therefore all may influence the types of species inhabiting eelgrass patches. Community composition also varied strongly between Shelter Island and Coronado (data not shown). In Expt 2, 23 of the 48 species collected at Shelter Island were not found at Coronado, and 6 of the 30 species found at Coronado were not found at Shelter Island.

Multivariate analyses that test (e.g.) for similarities and dissimilarities in species composition among treatments or sites often may reveal differences in the epifaunal community that are not seen when assessing species richness, density or diversity. For instance, community composition in the SL treatment generally was most dissimilar from other treatments (Table 7,

Fig. 5). The majority of the difference between treatments is a reflection of the dominant species responses. For example, spider crab *Pyromaia tuberculata* and isopod *Paracercius sculpta* abundances were repeatedly higher in the medium and high surface area plots while *Laevicardium substriatum* abundances were often higher in the low surface area plots. These species' habitat preferences contributed to the dissimilarity between the low surface area plots and the medium and high surface area plots. MDS was used by Webster et al. (1998) to investigate community differences between samples collected from areas in naturally occurring *Zostera marina* beds differing in shoot density. They found that low shoot density samples were not similar to medium and high density plots, but also found high dissimilarity among replicate low-density eelgrass patches. In a study similar to ours, Lee et al. (2001) tested for differences in the epifauna community among seagrass patches that differed in shoot density and shoot height. The only treatments considered statistically different using univariate tests of total faunal abundance were the TH plots vs. the control (no shoot) plots. However, principal component analysis (PCA) revealed strong grouping of plots within different habitat structure treatments.

Epifaunal biomass

Seagrass beds are considered vital habitat throughout the world due to their high primary and secondary production, and they therefore help form critical links between organisms occupying different trophic levels in coastal and estuarine waters. In our study, we used total biomass of motile, canopy-dwelling crustaceans (e.g. amphipods, isopods, and shrimp) as an estimate of the amount of food available for consumption by larger organisms utilizing seagrass beds as foraging grounds (e.g. fishes, lobsters, and crabs; Heck & Crowder 1991). Biomass of canopy-dwelling crustaceans clearly varied with shoot surface area and not with shoot length or shoot density. Crustacean biomass increased with surface area at Coronado and in Trial 2 at Shelter Island, but in Trial 1 at Shelter Island, crustacean biomass was highest at intermediate levels of shoot surface area. Motile invertebrates, which can utilize the entire canopy, may be selecting higher surface area plots due to the refuge provided by increased structure. In addition to providing protection from predation, the increased surface area may provide more food for these organisms, which often feed on microinvertebrates and epiphytes growing on the eelgrass blades.

We also measured the biomass of fishes found in our ASUs. Dominant fishes were the juvenile giant kelpfish *Heterostichus rostratus*, pipefish *Sygnathus* spp., and arrow gobies *Clevelandia ios*. Similar to canopy-dwelling crustaceans, fish biomass increased with shoot surface area (Fig. 6, Table 6). Fish may choose high surface area treatments because they likely are predators of canopy-dwelling crustaceans. Additionally, pipefish, gobies and juvenile kelpfish may select ASUs that provide refuge from larger fishes that forage in seagrass habitat. Fish biomass typically was dramatically higher in TH ASUs than in all other treatments, suggesting that a threshold amount of eelgrass habitat may be necessary before fish choose to inhabit a patch. We note, however, that our ASUs simulated small, isolated seagrass patches, and fish responses to structure may be different in larger, continuous seagrass habitat.

Implications

Seagrass habitats are productive, support a diverse suite of epifaunal and infaunal species, and function as a protective refuge and as foraging grounds for many commercially and recreationally important species. These and other ecosystem services have caused seagrasses to be considered 'essential fish habitat' under the Magnuson-Stevens Act. However, the proximity of seagrass to the shoreline makes this important habitat vulnerable to extensive anthropogenic disturbances, including sedimentation from coastal development, eutrophication from urban and agricultural runoff, trampling, and scarring due to boating and fishing (Sargent et al. 1995). Many efforts are underway worldwide to restore seagrass, and better assessments of the success of restoration are needed. For instance, ecologists, resource managers, and policy makers regularly gauge the health of a restored habitat by measuring only seagrass plant growth and survival, or by using a few univariate community measures such as total faunal abundance, species richness, and species diversity. Although community responses to habitat treatments were inconsistent in our study, there were generally positive relationships between eelgrass habitat amount and epifaunal density and diversity, and surface area appeared to explain patterns of epifaunal density and diversity more often than did shoot density and shoot length. This suggests that biomass, which is relatively easy to measure and has a strong positive relationship with shoot surface area, may be used by managers as an indicator of epifaunal density and diversity. The abundance of fishes, including the recreationally important giant kelpfish, also appears to be strongly linked to shoot surface area. However, because different epifaunal species have different responses to seagrass habitat structure, if a target organism is included in a conservation or mitigation plan, separate quantification of the organism's response to

habitat structure will be necessary. Additionally, our study showed that the majority of plots with the highest abundances were also the plots with the lowest diversity, due to a few dominant species strongly influencing the epifaunal community. Thus, different management goals (e.g. enhancing diversity, species richness or the abundance of target organisms) may require different conservation and restoration strategies.

It is important to point out that this study investigated the influence of habitat structure on both epifaunal communities and individual species in relatively small, isolated plots. Though seagrass patches of this size are common in locations of high hydrodynamic activity, seagrasses also form extensive, continuous beds, and care should be taken when extrapolating our results to a larger scale. In addition, seagrass beds are structurally heterogeneous unlike the standardized ASUs in this experiment, and structural components vary with many environmental and habitat characteristics including patch size, hydrodynamic regime, depth, and location within a bed. The use of artificial habitat allowed us to standardize potentially confounding variables while systematically manipulating others. However, both the structure and quality of the artificial habitat are not equal to a natural seagrass bed. Epiphyte cover and nutrient availability are 2 examples of natural components that are not simulated or controlled for in the ASUs.

In conclusion, our results and those of others (e.g. Parker et al. 2001, Jenkins et al. 2002) suggest that individual habitat characteristics (shoot length and shoot density), in addition to available surface area, may influence epifaunal density and diversity in seagrass habitats. Not surprisingly, epifaunal responses to structure appear to differ with site and through time, and thus the most information on faunal responses to seagrass structure will be generated from studies incorporating multiple sites, seasons, and years.

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