



# Relative influence of habitat complexity and proximity to patch edges on seagrass epifaunal communities

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Habitat structure at many scales influences faunal communities. Although habitat structure at different scales often covaries, studies rarely examine the relative effects of structure at multiple scales on faunal density and diversity. In shallow-water seagrass systems, epifaunal density at local scales generally increases with increased habitat structural complexity (e.g. shoot density per unit area). In turn, structural complexity often varies with other aspects of habitat structure at patch scales, such as proximity to patch edges, which itself modifies ecological processes that structure epifaunal communities. We conducted surveys and a manipulative experiment in the eelgrass *Zostera marina* beds of San Diego Bay, California, USA, to determine (1) whether eelgrass structural complexity, epifaunal density and diversity, and fish (predator) density and diversity vary with proximity to patch edges, and (2) the relative influences of structural complexity, proximity to patch edges and predator presence on epifaunal distribution. Seagrass structural complexity generally increased from patch edges to patch interiors at all sites and in all sampling periods. However, patterns of epifaunal density, diversity, and biomass varied among sites and sampling periods, with density and biomass increasing from patch edges to interiors at some sites and decreasing at others. In the manipulative experiment, we allowed epifauna to colonize sparse or dense artificial seagrass habitat at both the edge and interior of a seagrass patch, and enclosed a subset of experimental units in predator exclusion cages. Overall, proximity to patch edges had a larger influence on epifaunal density and community structure than did structural complexity or predation, with the exception of some common taxa which responded more strongly to either complexity or predator exclusion. Our results emphasize the importance of addressing and evaluating habitat structure at multiple scales to better understand the distribution and interactions of organisms in a particular environment.

Habitat structure strongly influences faunal density, distribution and diversity within ecosystems (MacArthur and MacArthur 1961, Robinson et al. 1995, Lima 1998, Moksnes 2002). Many habitats exist as patches embedded within a heterogeneous matrix of alternative habitat of variable suitability (Forman and Godron 1986), and ecological processes dictating the distribution and abundance of fauna in these habitats may be influenced by structure at multiple spatial scales. At small scales within habitat patches, habitat structural complexity (i.e. the amount, density and configuration of structural elements such as tree branches, grass blades, rocks or kelp fronds) strongly influences processes such as predation and competition that dictate patterns of faunal abundance, survival and community structure (Heck and Crowder 1991). The effects of structural complexity on fauna may be modified, however, by proximity to patch edges, which influences abiotic (e.g. windfall and current scouring: Saunders et al. 1991, Fonseca and Bell 1998) and biotic (e.g. predation and competition: Paton 1994, Remer and Heard 1998) processes. At still larger scales, ecological processes are influenced by position of patches within the landscape (Hovel et al. 2002) and landscape

context (Donovan et al. 1997). Though a great deal of research has been conducted on processes occurring at each of these scales, the relative effects of structure at more than one scale have rarely been assessed simultaneously. To gain a better understanding of the factors affecting the organization of communities in complex landscapes, it is imperative that studies consider the relative and simultaneous effects of habitat structure at different scales on ecological processes (Levin 1992).

Seagrasses are found in shallow marine and estuarine environments worldwide, where they form complex above- and belowground structures that are valuable habitats for many commercially and ecologically important species (Williams and Heck 2001). Seagrass habitat is an ideal model system for studying the effects of habitat structure at multiple scales on faunal communities because structural complexity and patchiness are highly variable within and among locations, the beds occur at spatial scales amenable to manipulation, and because of the strong associations between epifaunal and infaunal organisms and seagrass blades, roots and rhizomes (Robbins and Bell 1994). The majority of studies on habitat structure in seagrass habitat have focused on the effects

of within-patch structural complexity (e.g. shoot density, shoot length, blade surface area or biomass per unit area) on epifaunal communities. Epifaunal density, survival and diversity typically increase with structural complexity, likely due to increased food availability, increased living space, and enhanced refuge from predators (reviewed by Orth et al. 1984, Heck and Crowder 1991). However, proximity to seagrass patch edges also may strongly influence ecological processes (Ries and Sisk 2004, Tanner 2005, Selgrath et al. 2007). The seagrass patch interior, patch edge, and matrix habitat (i.e. adjacent non-seagrass habitat) provide different resources for organisms, which often preferentially inhabit only one of these areas (Tanner 2005). Epifaunal abundance may be elevated at edges due to high settlement rates there (Eggleston et al. 1998) or due to accumulation of organisms moving among patches (Virnstein and Curran 1986). Alternatively, epifaunal abundance may be low at the edge if predation risk is elevated due to predators using edges or adjacent unvegetated habitat as movement corridors, or if epifauna are more visible at an edge (Irlandi et al. 1995, Bologna and Heck 1999).

Seagrass habitat degradation and fragmentation are increasing worldwide (Hemminga and Duarte 2000), creating an urgent need for more information on how simultaneous reductions in structural complexity and increases in patchiness and amount of edge are likely to influence the value of seagrass as a nursery habitat. In addition to human-induced changes in seagrass structure, many naturally occurring processes (e.g. scouring by currents and waves, variation in rhizome elongation, digging animals) influence structure at multiple scales, such that structural complexity, proximity to patch edges, and landscape structure commonly covary (Robbins and Bell 1994). For instance, hard clam *Merccenaria mercenaria* survival decreased with seagrass patchiness, but seagrass structural complexity did as well, making it difficult to determine the relative effects of each level of structure on clam survival (Irlandi 1994). Juvenile blue crab *Callinectes sapidus* survival was highest in large patches when structural complexity covaried with patch size (Hovel and Lipcius 2002), but was highest in small patches when structural complexity was held constant among patch sizes (Hovel and Lipcius 2001).

The goal of our study was to assess the relative influence of two aspects of habitat structure that covary in seagrass habitat – structural complexity and proximity to the patch edge – on the abundance and diversity of epifaunal organisms and their predators. We worked in San Diego Bay, southern California, USA to determine (1) whether seagrass structural complexity varied between the edge and interior of large seagrass patches; (2) whether the density and diversity of epifauna (prey) and fishes (predators) varied with structural complexity or between the edge and interior of patches; and (3) the relative influence of structural complexity, distance from patch edges, and the presence of predators on epifaunal density and community structure.

## Methods

Our study was conducted in the eelgrass *Zostera marina* beds of San Diego Bay, California, USA (32°44'N, 117°10'W)

during the summer of 2007. San Diego Bay is a heavily developed urban estuary used for shipping, military operations, and recreation. Freshwater inflow is low, and hydrodynamic conditions are largely tidally driven (Largier et al. 1997). The front region of the bay is characterized by relatively low water residence times, moderate currents, and low fluctuations in salinity and temperature through the year, whereas higher water residence time in the southern or back region leads to slower currents and greater fluctuations of salinity and temperature. We conducted surveys of the eelgrass, epifauna, and fishes at two sites located in the central region of the bay (south-central bay (SCB), and north-central bay (NCB)) and one site close to the bay mouth (Shelter Island (SI)) during June and August of 2007. We also conducted a manipulative experiment to address the relative influences of structural complexity, distance from the edge and predator presence on epifaunal communities at SI. At all sites eelgrass patches are 20–30 m in width and run parallel to shore for approximately 250 m. Surveys and experiments were conducted at depths of 2–5 m below mean lower low water (MLLW).

## Seagrass, epifauna and fish surveys

To determine whether seagrass structural complexity (shoot density, shoot length and biomass per unit area) varied with distance from the edge within seagrass patches at each site, we collected samples at the outer edge (vegetated substrate at the bayward sand–eelgrass interface), the inner edge (vegetated substrate, 1 m from interface), and within the interior (vegetated substrate, 5 m from interface). Seagrass cores (12 cm  $\phi$   $\times$  15 cm depth) were taken every 5 m along 40 m transects at each of the three distances running parallel to the edge of the bed ( $n = 8$ ). We counted shoots and determined mean shoot length per core by averaging the length of the longest blade per shoot. Shoots were separated from rhizome material and dried at 60°C to a constant weight for estimations of aboveground biomass. We used a multivariate analysis of variance (MANOVA) to test whether the combined seagrass structural complexity variables (shoot density, length and biomass) vary with distance from the edge, site, and sampling period. We followed MANOVAs with separate analyses of variance (ANOVAs) for each dependent variable. For these and all other ANOVAs, we calculated the proportion of variance accounted for by each factor ( $\omega^2$ ; Graham and Edwards 2001) and tested for differences in means using Student–Newman–Keuls (SNK) multiple comparisons. Before analyses were performed, we visually inspected the data for normality and we tested for homogeneity of variances using Cochran's test, transforming the data where necessary.

We sampled for mobile epifauna along each transect by capturing organisms within a small underwater sieve made of 20 cm  $\phi$   $\times$  25 cm tall PVC pipe with a mesh bag attached to one end (mesh size  $\sim$ 400  $\mu$ m). Every 5 m along each transect (away from where seagrass cores were taken) divers quickly slipped sieves over eelgrass shoots, cut shoots at the sediment surface using scissors, and then placed a 500  $\mu$ m screen under the sieve to capture the contents. Contents were stored on ice before transport to the lab where shoots were rinsed in freshwater and shaken to

release epifauna which were frozen for preservation. Epifaunal samples were sorted and individuals in each taxon were counted to obtain densities. Estimates of total biomass per sample for six epifaunal categories (fishes, gastropods, crabs, shrimp, peracarid crustaceans and ostracods/copepods) were obtained after drying epifauna in an oven at 60°C for 48 h. Soft-bodied epifauna (including nematodes and polychaetes) were excluded from analysis due to poor preservation in frozen samples and their relatively low abundance in fish stomachs (Results). We used ANOVAs to test for the effects of distance from the edge, site, and sampling periods on total epifaunal abundance, species richness, Simpson's index of diversity ( $D_s$ ), and the biomass of selected epifaunal species that dominated fish stomach contents.

We used non-metric multi dimensional scaling (nMDS) to investigate patterns of epifaunal community composition between sites and among the three distances from the edge for each sampling period. nMDS analyses were conducted on a matrix of Bray–Curtis similarities based on square-root transformed abundances of all taxa to reduce the influence of a few, highly abundant taxa (Clarke and Warwick 2001). Where data were shown to cluster in nMDS plots, ordination was followed by analyses of similarity (ANOSIM) to further investigate the causes of those patterns. ANOSIM results are shown where pair-wise comparisons had R-values greater than 0.60, indicating strong group differences. The R-statistic is considered more robust to sample-size influence than traditional p-values (Clarke and Warwick 2001).

To quantify the density and diversity of fishes at the edge and interior of eelgrass patches at each site, we towed a non-destructive beam trawl (1.5 m wide  $\times$  0.6 m tall, 6 mm mesh cod end) at a speed of 3 knots for 100 m against tidal flow through the beds in June and September 2007. The precision of the trawl did not allow us to distinguish outer from inner edge, and we thus collected samples within the patch interior and within 2 m of the eelgrass-unvegetated sediment interface. Three trawls were conducted at the edge and three in the interior at each site in each of the two sampling periods. Fishes captured in trawls were identified to species, measured (fork length (FL)) on the boat, and then released. A subset of fish from each species at each site was immediately frozen and later dissected for stomach content analysis during each sampling period. All identifiable organisms in the fish stomachs were processed as described for epifaunal sampling above. We used separate ANOVAs to test for differences in fish abundance, species richness,  $D_s$ , and mean FL between distance from patch edge, site, and sampling period, and conducted nMDS as described above to test for variability in community composition. We also explored variation in stomach content composition using nMDS and ANOSIM as above. Fish with no identifiable stomach contents were excluded from that analysis.

### Caging experiment

We conducted a manipulative experiment using artificial seagrass units (ASUs) at SI in July 2007 to determine the relative effects of structural complexity, distance from the edge, and exposure to predators on the density and

Table 1. (a) p-values and Wilks-lambda statistics (in parentheses) generated from the MANOVA run on the three seagrass structural measures (i.e. shoot density, length, and biomass) from survey samples. (b) p-values and  $\omega^2$  (in parentheses) values from three-way ANOVAs on survey samples. The  $\omega^2$  values are given only for p-values  $< 0.1$  (in bold).

	Sampling period	Site	Distance	Site $\times$ sampling period	Distance $\times$ sampling period	Site $\times$ distance	Site $\times$ distance $\times$ sampling period
(a) MANOVA							
(b) Shoot density <sup>†</sup>	<b>&lt;0.001 (0.8)</b>	<b>&lt;0.001 (0.3)</b>	<b>&lt;0.001 (0.6)</b>	<b>0.018 (0.9)</b>	0.106 (0.9)	<b>0.001 (0.8)</b>	0.180 (0.9)
Shoot length <sup>†</sup>	<b>&lt;0.001 (6.3%)</b>	<b>0.074 (1.6%)</b>	<b>&lt;0.001 (21.1%)</b>	0.167	0.847	0.704	<b>0.079 (2.2%)</b>
Biomass <sup>†</sup>	0.598	<b>&lt;0.001 (59.5%)</b>	<b>&lt;0.001 (4.1%)</b>	0.318	<b>0.007 (1.6%)</b>	<b>&lt;0.001 (5.9%)</b>	0.621
Total epifauna <sup>†</sup>	0.788	<b>&lt;0.001 (25.8%)</b>	<b>&lt;0.001 (25.8%)</b>	<b>0.046 (1.4%)</b>	0.162	0.148	0.617
Richness	<b>0.007 (2.6%)</b>	<b>&lt;0.001 (19.0%)</b>	<b>&lt;0.001 (11.3%)</b>	0.887	<b>0.029 (2.1%)</b>	<b>0.004 (5.0%)</b>	<b>0.064 (2.1%)</b>
$D_s$ <sup>†</sup>	<b>0.004 (4.0%)</b>	<b>&lt;0.001 (8.2%)</b>	<b>0.002 (5.6%)</b>	0.482	0.206	<b>0.007 (5.6%)</b>	<b>0.058 (2.7%)</b>
Prey biomass*	<b>&lt;0.001 (13.5%)</b>	0.848	<b>&lt;0.001 (7.6%)</b>	<b>0.011 (2.1%)</b>	<b>&lt;0.001 (12.3%)</b>	<b>&lt;0.001 (19.4%)</b>	<b>&lt;0.001 (6.8%)</b>
Fish abundance*	0.390	<b>&lt;0.001 (19.8%)</b>	<b>&lt;0.001 (12.9%)</b>	<b>0.030 (2.2%)</b>	0.351	<b>0.041 (2.6%)</b>	<b>0.034 (2.8%)</b>
Richness*	0.324	0.190	<b>0.026 (9.8%)</b>	<b>0.087 (7.3%)</b>	0.124	0.392	0.851
$D_s$	<b>&lt;0.001 (30.8%)</b>	0.764	0.108	<b>0.020 (11.0%)</b>	0.499	0.144	0.633
Fork length*	<b>0.055 (4.1%)</b>	0.561	<b>0.002 (13.9%)</b>	<b>0.001 (20.5%)</b>	<b>0.008 (9.9%)</b>	<b>0.017 (0.0%)</b>	0.137
	<b>&lt;0.001 (30.1%)</b>	<b>0.001 (20.0%)</b>	0.648	<b>0.029 (7.0%)</b>	0.266	0.426	0.156

\*square-root transformed, <sup>†</sup>ln(x+1) transformed, <sup>‡</sup>arcsine transformed

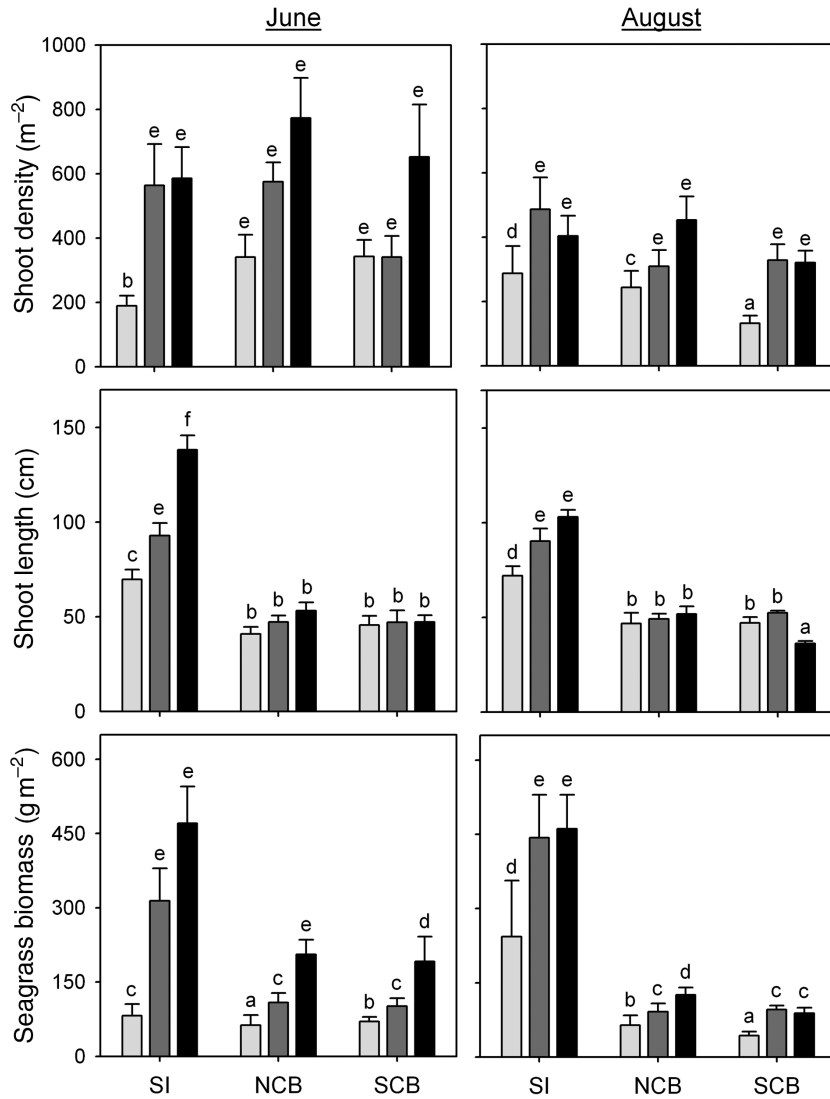


Figure 1. *Zostera marina* shoot density, shoot length, and shoot biomass measured in the seagrass surveys. Error bars represent 1 SE. Letters above bars denote groups separated by SNK post-hoc analysis.

diversity of epifauna. ASUs are widely used to control structural complexity in seagrass experiments and are colonized by epifauna similarly to living seagrass (Healey and Hovel 2004, Moksnes and Heck 2006, Micheli et al. 2008). ASUs consisted of green polypropylene ribbon to simulate eelgrass blades tied to a mesh base (25 × 25 cm) anchored to the sediment. ASUs were placed 5 m apart along the edge of the eelgrass patch (within 0.5 m of the sand–seagrass interface) and in the interior of the patch (> 5 m from the sand–seagrass interface) at depths of ca 3–4 m MLLW. Each ASU was one of two simulated shoot densities: sparse (150 shoots m<sup>-2</sup>) or dense (600 shoots m<sup>-2</sup>), representing extremes observed at this site. Exposure to predators was varied by enclosing a subset of ASUs within predator-exclusion cages, while leaving a second subset open to predators (no cage) and a third subset enclosed within partial cage-controls (n = 5 ASUs/caging treatment/complexity treatment/distance from the edge × three caging treatments × two complexity treatments ×

two distances = 60 ASUs). Cages enclosed the entire ASU and were 71 cm in height with a mesh size of 6 mm to exclude fish predators and allow colonization by epifauna. Cage-controls were partial cages with two open walls, and controlled for potential caging artifacts which may include reduced flow, shading, and addition of structure to the habitat. ASUs were deployed for 28 days, and we cleaned the mesh on all cages and partial cages weekly. At the end of deployment ASUs were collected by slipping a mesh bag over the whole unit (after gentle removal of caging structure where present). On shore, the mesh bags and ASUs were rinsed with freshwater through sieves (500 μm) and all epifauna collected were frozen and processed as above. We used separate three-way ANOVAs followed by SNK multiple comparisons to test whether total epifauna abundance, species richness, D<sub>s</sub>, and prey biomass varied with location within the patch, complexity, and exposure to predators. We again utilized nMDS to compare differences in community composition between treatments.

Table 2. Taxon abundance in survey samples (counts not converted to values per m<sup>2</sup>). Taxa listed by name made up at least 1.0% of the total sampled for at least one sampling period. Additional individuals are listed as 'Other'. G = gastropods, O = ostracods and copepods, P = peracarid crustaceans, S = shrimp.

Taxon	Group	June	August	Total	%
Gammaridea	P	13 942	26 716	40 658	67.9
Caprellidae	P	4421	810	5231	8.7
Copepoda	O	2108	923	3031	5.1
<i>Paracerceis</i> spp.	P	75	2296	2371	4.0
<i>Alia carinata</i>	G	903	788	1691	2.8
<i>Hippolyte californiensis</i>	S	958	546	1504	2.5
<i>Sinelobus stanfordi</i>	P	597	869	1466	2.5
<i>Tectura depicta</i>	G	595	403	998	1.7
<i>Califanthur squamosissima</i>	P	93	767	860	1.4
Ostracoda	O	266	98	364	0.6
Other	n/a	742	1002	1744	2.9

## Results

### Seagrass, epifauna and fish surveys

The results of the MANOVA showed strong evidence for effects of distance from the edge, site, and sampling period on seagrass structural complexity (Table 1a). Significant interaction terms in the MANOVA suggest that structural complexity varied by site dependent on season, mostly due to differences in aboveground biomass (see univariate results below). The effect of distance from the edge depended on site, largely driven by variability in average shoot length.

The results of univariate ANOVAs run on each dependent variable indicated that overall, structural complexity was lower at the outer edge than the inner edge, but was similar between the inner edge and interior (Fig. 1). Patterns generally were similar between the two central bay sites, which differed slightly from SI. Shoot density was consistently lowest at the outer edge at all sites and distance from the edge explained the majority of the variation (Table 1b). Shoot length tended to be lowest at the outer edge, with the exception of SCB in August, but site accounted for more of the variability in shoot length, with SI having the longest shoots (Fig. 1). Aboveground biomass also tended to be lower at the outer edge than at the inner edge and interior, and increased from June to August at SI but decreased from June to August at the central bay sites.

Over the two survey periods approximately 60 000 epifaunal organisms were counted and sorted into a total of 46 taxonomic groups (Table 2). The most abundant taxon, gammarid amphipods, comprised 56%, and 76% of total epifauna in June and August respectively. Although caprellid amphipods have recently been reclassified as a family within the suborder Gammaridea, we considered them independent taxa (Carleton 2007). Overall, there was a significant interactive effect of distance from the edge, site, and sampling period on each measure of community structure (total abundance, species richness,  $D_s$ , and biomass), though the majority of variation was usually explained by

main effects. There was little variation in total epifaunal abundance with distance from the edge in June, except for lower abundance at the outer edge at SCB (Fig. 2). In August, epifaunal abundance was higher in patch interiors at NCB and SCB than at the outer or inner edge. Species richness did not vary with distance from the edge at SI, but was lower at the outer edge than at other distances at NCB in June and lower at the outer edge at SCB in both sampling periods (Fig. 2). Simpson's index of diversity was lower at the outer edge of SI than at the inner edge and interior in June and in August. At NCB and SCB, however,  $D_s$  did not differ with distance from the edge in June, but was higher at the outer and inner edge than in the interior in August. The collective biomass of taxa most commonly found in fish stomach analyses (peracarids, shrimp, ostracods and copepods) tended to increase from the edge to the interior at NCB and SCB. However, prey biomass decreased from the edge to the interior at SI in August (Fig. 2). Finally, we found that patterns of abundance with distance, site, and sampling period varied widely among selected common taxa (Appendix 1).

Visual inspection of nMDS ordination of epifaunal communities revealed clear separation of SI samples from the two central bay sites (Fig. 3). Results of the ANOSIM on June data revealed SI differing strongly from NCB ( $R = 0.73$ ,  $p < 0.001$ ) and SCB ( $R = 0.81$ ,  $p < 0.001$ ). This pattern persisted in August, with SI differing from NCB ( $R = 0.94$ ,  $p < 0.001$ ) and SCB ( $R = 0.91$ ,  $p < 0.001$ ). Clustering by distance from the edge was weaker, though in August ANOSIM revealed differences between the outer edge and interior ( $R = 0.62$ ,  $p < 0.001$ ).

The abundance of fishes was slightly higher in the patch interior than at the edge but this effect explained less than 10% of the total variation in the ANOVA model and SNK post-hoc analyses revealed no significant differences (Table 1, 3). Fish abundance was not strongly related to sampling period or site. Sampling period explained the most variation in species richness, which was lower overall in September than in June at SI and NCB. Simpson's index of diversity was similar among groups except for the interior at NCB in September, where  $D_s$  was extremely low as 95% of the fish caught were juvenile giant kelpfish *Heterostichus rostratus*. Fish were larger in September than in June and larger at the central bay sites than at SI (Table 1). nMDS ordination of the fish community did not generate any clear group clustering (results not shown).

We examined the stomach contents of 191 fishes (Table 4). Gammarid amphipods made up the majority of the contents by abundance for all fish groups except pipefish, whose stomachs primarily contained copepods, ostracods or cumaceans. Overall, there were no strong differences in fish diets between the edge and the interior, but there was some dissimilarity in diet between fishes captured at SI and fishes captured at the two central bay sites, reflective of differences between these sites in epifaunal community composition (results not shown).

### Caging experiment

Nearly 45 000 individual epifauna were collected from ASUs in the caging experiment and were sorted into 42

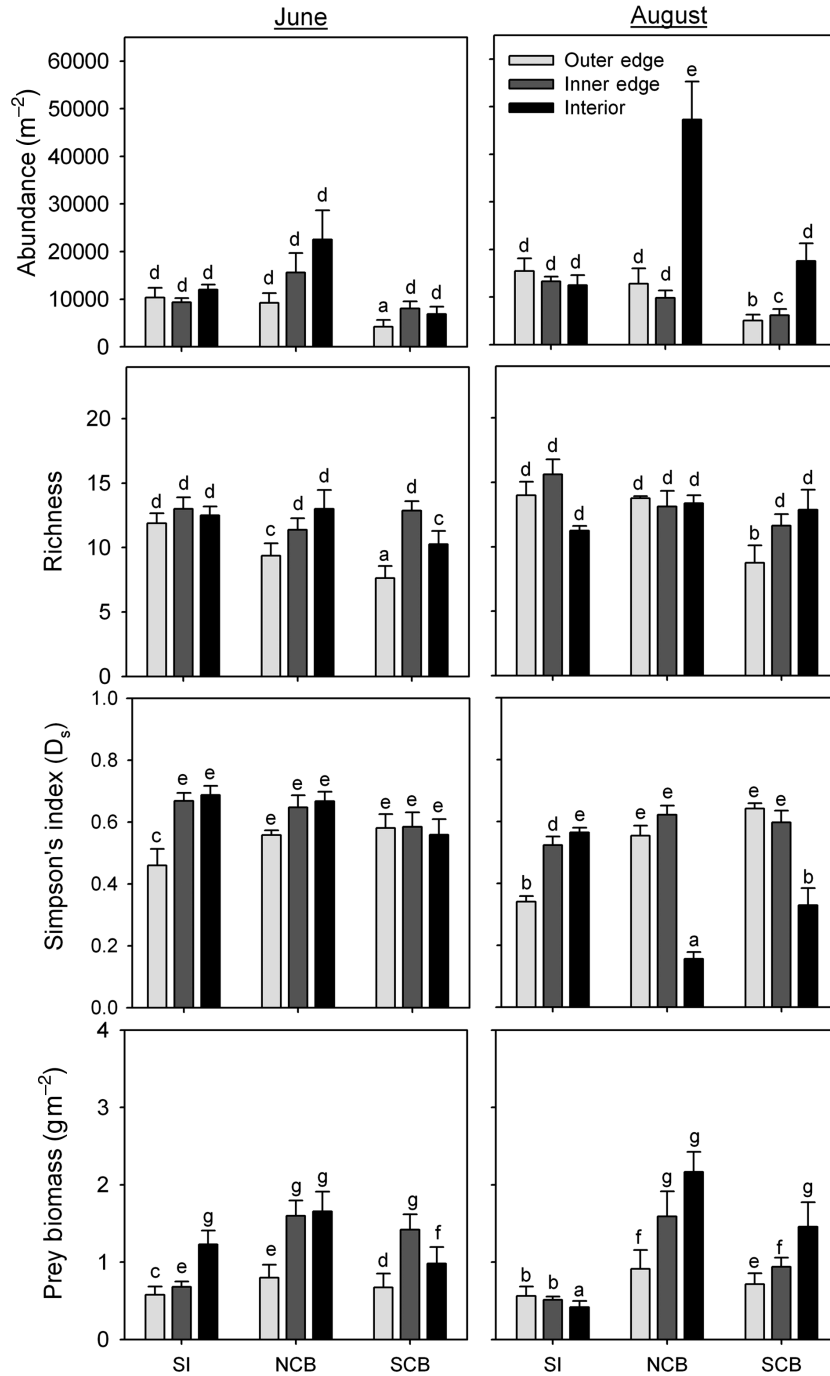


Figure 2. Epifaunal abundance, richness (number of distinct taxa), Simpson's index of diversity ( $D_s$ ), and biomass of prey ( $\text{g m}^{-2}$ ) calculated from epifauna surveys. Error bars represent 1SE. Letters above bars denote groups separated by SNK post-hoc analysis.

taxonomic groups. As with the epifaunal surveys, gammarid amphipods were the most abundant taxon (73% of individuals). Overall, distance from the edge and complexity had stronger effects on the epifaunal community than did predator access. Distance from the edge accounted for more variability than did structural complexity in total epifaunal density, species richness, and  $D_s$  (Table 5). Collectively, epifauna were more abundant at the patch edge than at the interior, regardless of structural complexity, and were more abundant in dense ASUs than in sparse ASUs,

regardless of distance from the edge (Fig. 4). There was an interactive effect of distance from the edge and structural complexity on taxon richness: there was no difference in richness between the sparse and dense ASUs at the edge, but richness was lower in sparse ASUs in the interior of seagrass beds. Simpson's index of diversity was higher in ASUs placed in the interior, and there was a weak trend for higher  $D_s$  in open plots than in cages and cage-control plots. Finally, prey biomass varied with distance from the edge, structural complexity, and predator access. Biomass

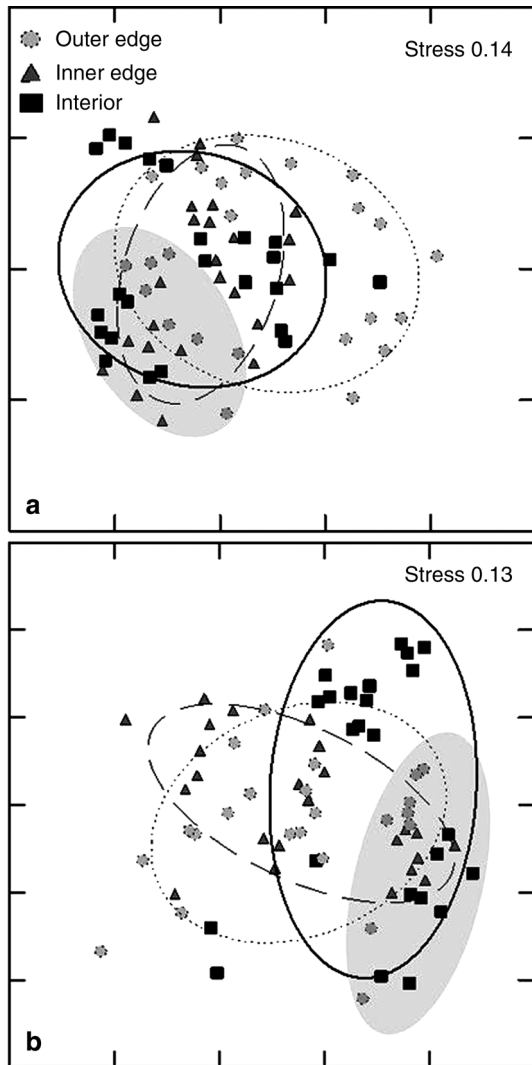


Figure 3. nMDS plots based on a Bray–Curtis similarity matrix of square-root transformed abundances of all taxa seen in (a) June, and (b) August epifauna samples. Distances of points represent relative similarity in community composition. Symbols represent patch location values and confidence ellipses are drawn around 1 standard deviation of the group centroid. The shaded ellipse is drawn around all Shelter Island points, the only site that clustered separately.

was higher in caged ASUs than in open and cage-control ASUs, higher in dense plots than in sparse plots, and higher at the edge than in the interior.

Responses of individual taxa to treatments varied. Most taxa were less abundant in sparse than in dense ASUs, but gammarid and caprellid amphipods were also less abundant in patch interiors than at the edge (Table 5, Fig. 5). *Hippolyte californiensis* were far more abundant in caged (predator-excluded) ASUs than in open and cage-control ASUs, and slightly more abundant in dense than in sparse ASUs. nMDS ordination suggested that the epifaunal community varied most strongly between the edge and interior plots, with a one-way ANOSIM on this distance effect generating a higher R-value than the other main effects ( $R = 0.39$ ,  $p < 0.001$ ; Fig. 6).

## Discussion

Local-scale measures of seagrass structural complexity (e.g. shoot density, shoot biomass per unit area and shoot length) strongly influence epifaunal abundance and diversity via their effects on food availability and refuge value (Heck and Orth 1980, Bell and Westoby 1986, Sirota and Hovel 2006; but see Attrill et al. 2000). Proximity to seagrass patch edges also influences epifaunal abundance (Bologna and Heck 2002, Tanner 2005) and may influence faunal survival as well (Bologna and Heck 1999, Selgrath et al. 2007). Our study is the first to experimentally eliminate covariation between seagrass local-scale structural complexity and proximity to patch edges to isolate the relative and interactive effects of these two scales of structure on epifaunal communities. We found that (1) seagrass structural complexity generally increased from the edge of patches to the interior; (2) effects of distance from the edge on epifaunal community structure were common but differed between sites and sampling periods; (3) structural complexity and proximity to patch edge both strongly influenced epifaunal density and diversity in the manipulative experiment, and both had larger effects on epifaunal density and diversity than did predator access; and (4) prey biomass was higher in dense than in sparse artificial eelgrass, higher in caged plots than in those exposed to predators, and higher at the patch edge than in the interior. Overall, our results indicate that local-scale and larger, patch-scale attributes of eelgrass habitat structure covary in San Diego Bay and jointly influence epifaunal and fish density, diversity, and community composition, and that the interactive effects of these factors differ among sites and sampling periods.

Edge effects on community composition and species interactions are well documented in a variety of systems, particularly in anthropogenically altered forest landscapes (Desrochers and Fortin 2000). Organisms that utilize edge habitat may benefit from access to the adjacent habitat for foraging (i.e. access to supplemental resources), but may also face greater exposure to predators. For birds, elevated levels of nest parasitism and predation often occur within 50 m of forest patch edges (Gates and Gysel 1978, reviewed by Paton 1994) due to heavy use of surrounding matrix habitat (e.g. farmland) by parasites and predators. Predation on skinks *Lampropholis delicata* and *L. guichenoti* by avian predators led to lower skink abundance near forest edges in Australia, where avian predators used structures adjacent to patches such as telephone posts and wires as perches while searching for prey (Anderson and Burgin 2008). Prey survival also may be reduced along edges in seagrass habitat: scallop *Argopecten irradians* survival was low in patchy seagrass habitat in North Carolina, likely due to predators such as crabs and whelks using unvegetated sediment between patches as corridors (Irlandi et al. 1995), and scallop survival also was lower along seagrass patch edges than within interiors in Florida (Bologna and Heck 1999). Because epifaunal densities often are higher at the edge of seagrass patches than within the interior (Bologna and Heck 2002, Tanner 2005, this study), seagrass patch edges may be critical areas for transfer of secondary production to higher trophic levels (Bologna and Heck 2002).

Table 3. Total counts of fishes caught in trawl samples. Species listed made up at least 1.0% of the total catch for June (n = 18) and September (n = 18) respectively.

Common name	Scientific name	June	September	Total	%
Giant kelpfish	<i>Heterostichus rostratus</i>	268	412	680	43.9
Dwarf surfperch	<i>Micrometrus minimus</i>	143	153	296	19.1
Shiner surfperch	<i>Cymatogaster aggregata</i>	218	7	225	14.5
Black surfperch	<i>Embiotoca jacksoni</i>	39	28	67	4.3
Spotted sand bass	<i>Paralabrax maculatofasciatus</i>	52	8	60	3.9
Black croaker	<i>Cheilotrema saturnum</i>	12	37	49	3.2
Kelp bass	<i>Paralabrax clathratus</i>	31	7	38	2.5
Pipefish	<i>Syngnathus</i> spp.	25	11	36	2.3
Barred sand bass	<i>Paralabrax nebulifer</i>	17	8	25	1.6
Round ray	<i>Urolophus halleri</i>	6	19	25	1.6
CA halibut	<i>Paralichthys californicus</i>	11	5	16	1.0
Blenny	<i>Hypsoblennius</i> spp.	10	5	15	1.0
Other	n/a	13	3	16	1.0

Though we found that taxa comprising a large portion of the diet of predatory fishes (e.g. amphipods) were more abundant along seagrass patch edges than within interiors, we found little evidence that trophic transfer is higher along seagrass patch edges at our sites (i.e. no interactive effect of predator access and proximity to edges on epifaunal biomass in our manipulative experiment). Likewise, we did not detect major differences in fish (predator) abundance or diet between the patch edge and interior. Fishes captured in our beam trawl are vulnerable to predation by larger fishes and birds and may have to balance prey capture success, which may be higher in less complex habitat at the edge, with seeking refuge from their own predators by spending less time at the patch edge. A recent review of patterns of nekton abundance in seagrass habitat also reported little evidence that fishes display distinct patterns of distribution throughout patches (Connolly and Hindell 2006). An exception in our study was that juvenile giant kelpfish, a cryptic species in eelgrass habitat, were consistently more abundant in patch interiors than near edges. This species can often be seen drifting, hanging vertically in the water where they become camouflaged among the eelgrass blades, and likely utilize the interior of the patch for concealment.

Our manipulative experiment allowed us to examine the relative effects of distance from the edge, seagrass structural complexity, and predator access on the epifaunal community. For many variables (e.g. total epifaunal abundance,

species richness and D<sub>1</sub>) and taxa (e.g. gammarid and caprellid amphipods, tanaids), distance from the edge accounted for more of the variability among plots than did structural complexity or predator access (Table 5). We found few differences between sparse and dense ASUs along the edge, suggesting that epifauna may preferentially occur at that location, regardless of structural complexity variability within the patch (Tanner 2005). Several mechanisms may account for this. Within seagrass systems, organisms dispersing among patches may remain within the habitat they first encounter (the nearest refuge hypothesis: Virnstein and Curran 1986, Tanner 2005) leading to higher abundance along patch edges than in patch interiors. Similarly, when dispersing larvae in the water column encounter the structure of a seagrass bed, they may ‘settle and stay’ regardless of microhabitat characteristics, thereby also leading to higher faunal abundance at the patch edge (Bologna and Heck 2002). This suggests that species richness also should be higher along patch edges than in patch interiors, which was not the case in our study. In addition to movement and dispersal behavior, the feeding mode of an organism likely influences its abundance at habitat edges. Many marine invertebrates that rely on currents to deliver planktonic food may exhibit higher abundance or growth along patch edges where currents are typically stronger (Bologna and Heck 1999, Peterson et al. 2004). In seagrass habitat in St Joseph Bay, Florida, epifaunal density was higher along patch edges than interiors, despite the

Table 4. Percent composition of fish stomach content analyses by abundance. COC = copepods, ostracods and cumaceans. Molluscs include bivalves and gastropods, and worms include polychaetes and nematodes. All values greater or equal to 1.0% of the average stomach contents for each group are in bold.

Fish group	n	Fork length, mm (SE)	Gammarid amphipods%	Other peracarids%	Shrimp%	Crabs%	COC%	Molluscs%	Worms%	Fish%
Bass	34	146.74 (9.05)	<b>56.9</b>	<b>24.2</b>	<b>6.2</b>	<b>1.5</b>	0.8	<b>9.0</b>	<b>1.2</b>	0.1
Kelpfish	74	100.49 (3.28)	<b>89.8</b>	<b>6.0</b>	<b>3.3</b>	0.0	0.5	0.1	0.0	0.2
Perch	39	75.82 (4.48)	<b>56.8</b>	<b>9.0</b>	0.6	0.1	<b>31.8</b>	<b>1.4</b>	0.2	0.0
Pipefish	17	137.06 (10.26)	<b>33.9</b>	0.6	<b>3.7</b>	0.0	<b>61.9</b>	0.0	0.0	0.0
Other	27	94.30 (5.36)	<b>93.1</b>	<b>4.3</b>	0.7	0.1	0.8	0.2	0.7	0.0

Table 5. p-values and  $\omega^2$  (in parentheses) values from three-way ANOVAs on caging experiment data. The  $\omega^2$  values are given only for p-values < 0.1 (in bold).

	Distance	Complexity	Predation	Distance × complexity	Distance × predation	Complexity* predation	Distance × complexity × predation
Total epifauna*	<0.001 (35.6%)	<0.001 (21.6%)	0.109	0.346	0.276	0.564	0.154
Richness†	<0.001 (19.1%)	<b>0.001 (12.7%)</b>	0.157	<b>0.038 (3.7%)</b>	0.650	0.876	0.392
D <sub>s</sub> ‡	<0.001 (32.8%)	0.297	<b>0.052 (4.3%)</b>	0.853	0.875	0.212	0.717
Prey biomass*	<b>0.004 (5.5%)</b>	<0.001 (26.0%)	<0.001 (27.0%)	0.163	0.316	0.527	0.366
Gammaridea*	<0.001 (44.5%)	<0.001 (14.2%)	0.193	0.523	0.243	0.352	0.171
Copepoda†	0.990	<b>0.002 (12.3%)</b>	0.817	<b>0.023 (6.1%)</b>	0.258	0.824	0.573
<i>Alia carinata</i> *	0.328	<0.001 (25.1%)	<b>0.011 (8.7%)</b>	0.851	0.395	0.869	0.911
<i>Hippolyte californiensis</i> †	0.492	<0.001 (16.4%)	<0.001 (49.4%)	0.368	0.607	0.744	0.747
<i>Leptocheilia dubia</i> †	<b>0.001 (14.5%)</b>	<b>0.004 (9.5%)</b>	0.297	<b>0.098 (2.2%)</b>	0.187	0.499	0.378
Caprellidae†	<0.001 (66.9%)	0.207	0.286	0.700	0.706	0.500	0.955

\*square-root transformed

† ln(x+1) transformed

‡ arcsine transformed

fact that seagrass biomass and shoot density were higher in patch interiors (Bologna and Heck 2002). Similarly, epifaunal density was higher at seagrass-sand edges than in seagrass patch interiors in South Australia, despite the fact that seagrass biomass per unit area increased from the edge to the interior (Tanner 2005). In our study, caprellid amphipods were typically more abundant along patch edges than in patch interiors, regardless of shoot density. These amphipods feed by sweeping the water column with enlarged gnathopods while grasping seagrass blades with modified abdominal appendages (Brusca and Brusca 2002) and they may benefit from greater food delivery to the canopy near the patch edge (Bologna and Heck 1999, Peterson et al. 2004).

Though much of the variance in community structure and taxon abundance was explained by distance from the edge and structural complexity in our study, predator access strongly affected epifaunal biomass (reduced biomass in open plots and cage-controls compared to caged plots) and the abundance of the grass shrimp *H. californiensis*, which was well represented in predator stomachs. Grass shrimp were more abundant in patch interiors than at patch edges in our epifaunal survey, and results of our manipulative experiment suggest that these shrimp prefer patch interiors due to the protective function of dense eelgrass shoots found there. Although gammarid amphipods were the most abundant taxa in fish stomachs, their high abundances across caging treatments, and in surveys, suggest their distribution is not predator-limited.

Few studies have examined how faunal diversity and community composition vary with proximity to patch edges. We found that D<sub>s</sub> was higher in patch interiors than at the edge at SI, and that this difference was not due to variability in seagrass structural complexity with distance from the edge. Community composition also varied between patch edges and interiors. These results may in part be due to the fact that gammarid amphipods, which were least abundant within patch interiors, were the most abundant taxonomic group in our samples. The caging experiment also revealed that distance from the patch edge influences relationships between taxon richness and structural complexity. Richness did not vary with structural complexity at the edge, but did

within the interior of seagrass patches, where richness was higher in dense than in sparse ASUs.

Edge effects often depend on landscape context. For instance, in forests of the American midwest, higher nest predation rates at edges vs. patch interiors occurred in fragmented landscapes, but not in contiguous areas (Donovan et al. 1997). In Rhode Island, effects of proximity to cobble patch edges on juvenile American lobster abundance and survival varied with the type of adjacent habitat (e.g. seagrass vs unvegetated sediment; Selgrath et al. 2007). Though all seagrass patch edges bordered unvegetated sediment in our study, we found that effects of structural complexity and proximity to patch edges on fauna varied between sites within sampling periods, as well as between sampling periods. Relationships between habitat structure and epifaunal community structure differed strongly between our front-bay site (SI) and our two central bay sites (NCB and SCB) suggesting that estuarine-scale processes also influence the epifaunal communities within San Diego Bay. Gradients in tidal flux, water retention time, temperature, salinity, and other factors with distance from the bay mouth may influence larval delivery and community-level interactions as well as the size of the ‘ecological edge’ of a patch (Largier et al. 1997). Additionally, recruitment pulses are common for many of the epifaunal species present in our samples (Bologna and Heck 2002, Sirota and Hovel 2006), which can lead to large fluctuations in epifaunal abundance between sampling periods. Moreover, the biomass and structure of the eelgrass itself changes seasonally; long reproductive shoots are produced in early summer, and blades become increasingly fouled by bryozoans and epiphytes from mid to late summer. It is important to note that our study did not include replicate patches within different regions in San Diego Bay, and that we therefore were unable to determine the primary causes of variability among sites. Experiments that include replicate patches within sites along an estuarine gradient (Jenkins et al. 1998) are necessary to determine how landscape context influences the effects of habitat structure at multiple spatial scales.

In summary, the results of our surveys and experiment suggest that the organisms living in the seagrass beds of

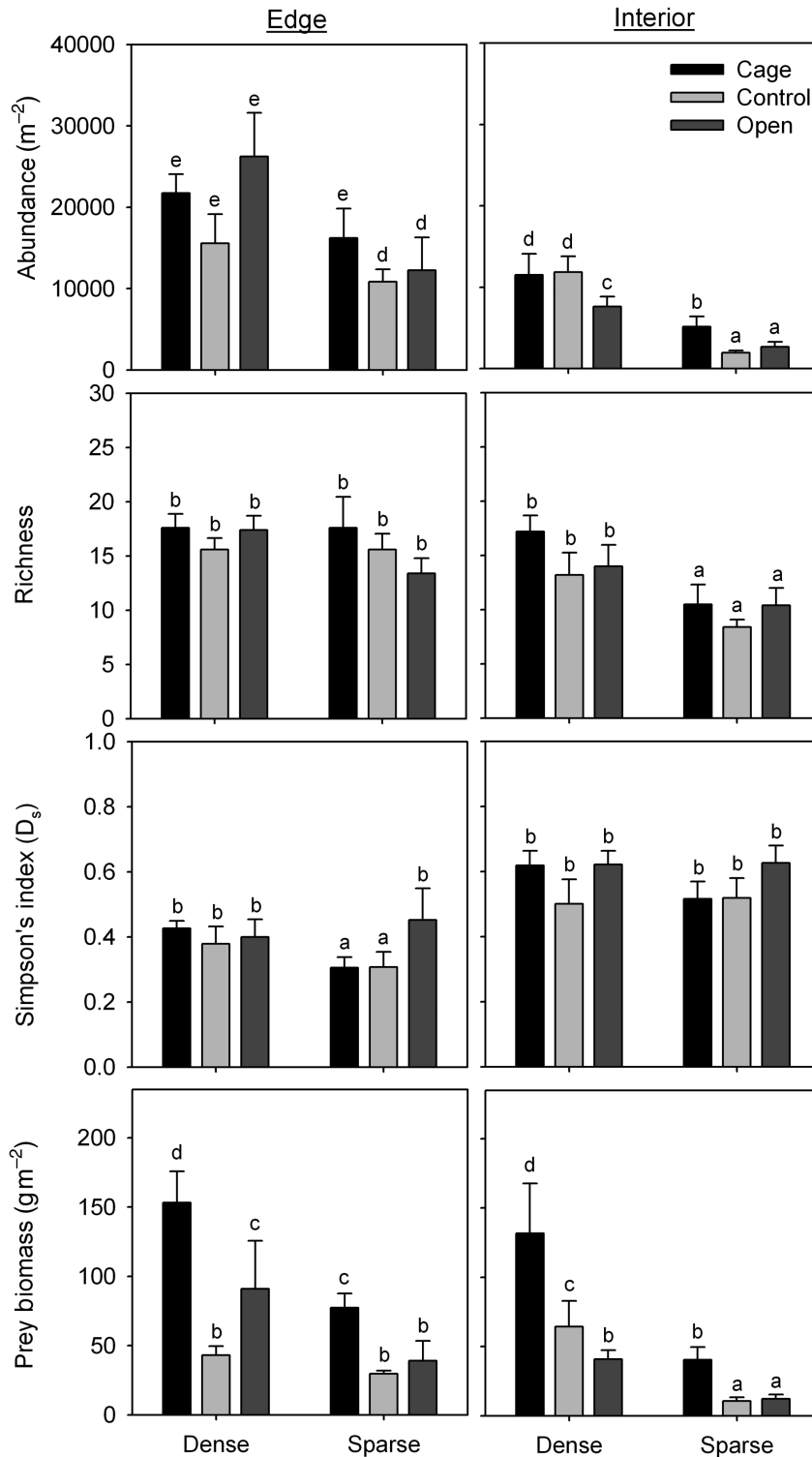


Figure 4. Epifaunal abundance, richness (number of distinct taxa), Simpson's index of diversity ( $D_s$ ), and biomass of prey ( $\text{g m}^{-2}$ ) calculated from caging experiment. Error bars represent 1 SE. Letters above bars denote groups separated by SNK post-hoc analysis.

San Diego Bay respond not only to local-scale, within-patch measures of habitat complexity but also to larger scale attributes of structure such as proximity to patch edges. We also found that relationships between epifaunal and seagrass habitat structure vary by site, and that some taxa seemed to be strongly influenced by factors

outside the scope of our study. Future research addressing faunal responses to variation in other aspects and scales of habitat structure will add to the growing knowledge of the environmental and ecological phenomena maintaining the diverse communities found in seagrass beds and other ecosystems.

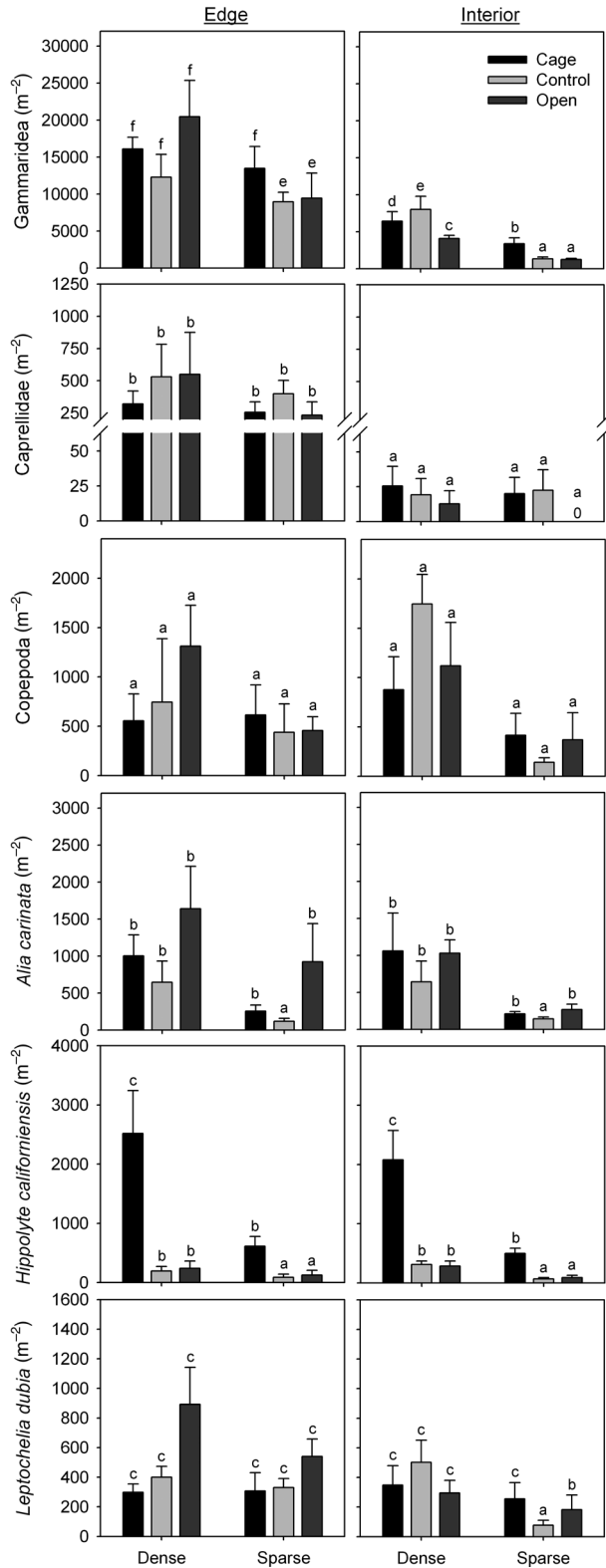


Figure 5. Abundance data for the six most abundant taxa in caging experiment. Error bars represent 1 SE. Letters above bars denote groups separated by SNK post-hoc analysis.

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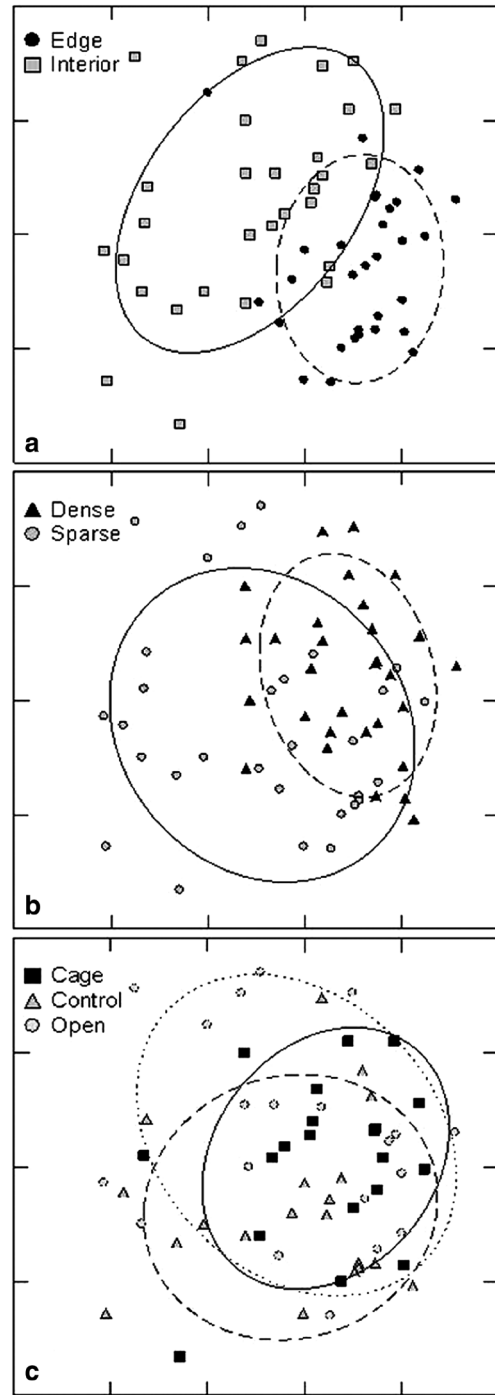


Figure 6. nMDS plots based on a Bray–Curtis similarity matrix of square-root transformed abundances of all taxa seen in caging samples. Distances of points represent relative similarity in community composition. Symbols and standard deviation confidence ellipses distinguish (a) distance from the edge (edge ellipse dashed), (b) complexity (dense ellipse dashed), and (c) predation (cage ellipse solid, control ellipse dashed, open ellipse dotted). Plot stress 0.15.

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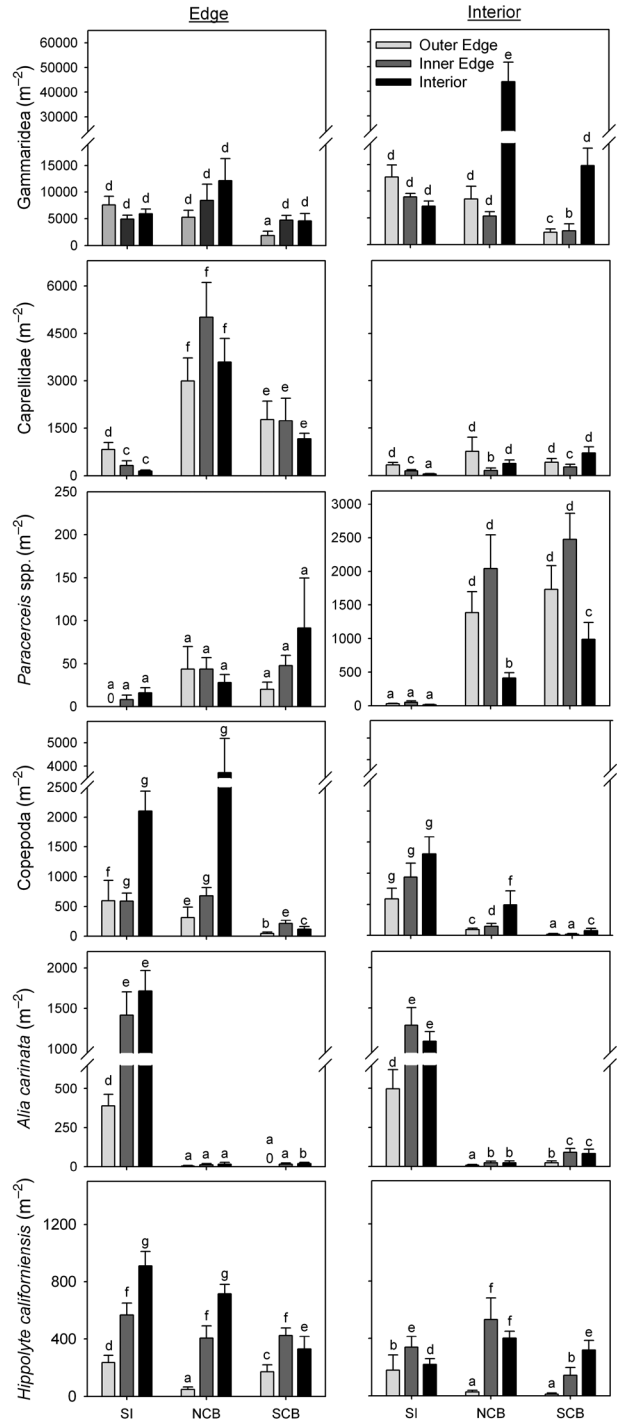
Appendix 1a. p-values and  $\omega^2$  (in parentheses) values from three-way ANOVAS on individual taxa in the survey samples. The  $\omega^2$  values are given only for p-values  $< 0.1$  (in bold). Transformations used to meet analysis assumptions are given where applicable.

Measure	Sampling period	Site	Distance	Site $\times$ sampling period	Distance $\times$ sampling period	Site $\times$ distance	Site $\times$ distance $\times$ sampling period
Gammaridea <sup>†</sup>	<b>&lt;0.001</b> (4.1%)	<b>&lt;0.001</b> (18.4%)	<b>&lt;0.001</b> (10.3%)	0.225	<b>0.001</b> (4.4%)	<b>&lt;0.001</b> (9.0%)	<b>0.006</b> (3.8%)
Caprellidae <sup>†</sup>	<b>&lt;0.001</b> (25.8%)	<b>&lt;0.001</b> (19.8%)	<b>0.040</b> (1.3%)	<b>&lt;0.001</b> (6.7%)	0.174	<b>0.003</b> (3.6%)	0.108
Paracercis spp. <sup>†</sup>	<b>&lt;0.001</b> (41.5%)	<b>&lt;0.001</b> (27.0%)	<b>&lt;0.001</b> (1.5%)	<b>&lt;0.001</b> (14.6%)	<b>&lt;0.001</b> (1.8%)	0.163	0.882
Copepoda <sup>†</sup>	<b>&lt;0.001</b> (3.7%)	<b>&lt;0.001</b> (40.0%)	<b>&lt;0.001</b> (9.4%)	<b>0.003</b> (3.1%)	0.101	0.305	0.249
<i>Alia carinata</i> <sup>*</sup>	<b>0.006</b> (0.5%)	<b>&lt;0.001</b> (82.1%)	<b>&lt;0.001</b> (3.8%)	<b>0.001</b> (1.0%)	0.580	<b>0.001</b> (1.3%)	0.614
<i>Hippolyte californiensis</i> <sup>*</sup>	<b>&lt;0.001</b> (9.6%)	<b>&lt;0.001</b> (5.1%)	<b>&lt;0.001</b> (35.1%)	<b>0.020</b> (1.7%)	0.273	<b>0.015</b> (2.5%)	<b>0.001</b> (4.4%)

\*square-root transformed

<sup>†</sup> ln(x+1) transformed

# arcsine transformed



Appendix 1b. Abundance data for the six most common taxa in the survey samples. Axes are the same scale for a particular taxon except *Paracercis* spp. which has individually labeled axes. Error bars represent one standard error. Letters above bars denote groups separated by SNK post-hoc analysis.