Relative influence of habitat complexity and edges on seagrass epifaunal communities

Eliza C. Moore* and Kevin A. Hovel

Department of Biology
San Diego State University
5500 Campanile Drive
San Diego, CA. 92182

* To whom correspondence should be addressed
The City of San Diego
Metropolitan Wastewater Division – Marine Biology Laboratory
2392 Kincaid Road
San Diego, CA. 92101
Email: mooree@sandiego.gov
FAX: (619) 758-2350

Abstract

Habitat structure at many scales can influence 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 worldwide, epifaunal density at local scales generally increases with increased habitat structural complexity (e.g. shoot density or shoot biomass 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 (i) whether eelgrass structural complexity, epifaunal density and diversity, and fish (predator) density and diversity vary with proximity to patch edges, and (ii) the relative influences of structural complexity, proximity to patch edges, and predator presence on epifaunal density and diversity. 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 from patch edge to interiors at other sites. In the manipulative experiment, we allowed epifauna to colonize sparse or dense artificial seagrass habitat at both the edge and interior of a natural seagrass bed, 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 and predation, with the exception of commonly preyed upon taxa such as grass shrimp *Hippolyte* spp. which was significantly more abundant when predators were excluded. 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.

Keywords: artificial seagrass unit; community structure; covariation; edge; epifauna; habitat complexity; habitat structure; seagrass; *Zostera marina*.

1. Introduction

Habitat structure strongly influences faunal density, distribution, and diversity within ecosystems (MacArthur and MacArthur 1961, Catling and Burt 1995, Robinson et al. 1995, Lima 1998, Moksnes 2002). At local scales (i.e. within habitat patches), habitat structural complexity may be defined as the amount, density, and configuration of structural elements, such as tree branches, grass blades, rocks, or kelp fronds. At the landscape scale, differences in the size, shape, and dispersion of habitat patches create variability in attributes of landscape structure such as total habitat area, amount of edge, and patch connectivity (Fahrig 2003). Although structural complexity and landscape structure both influence ecological processes in many habitats, their relative effects 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, Hovel 2003).

Seagrasses are found in shallow marine and estuarine environments worldwide, where they form complex above- and below-ground structure that is a valuable habitat 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 on faunal communities because structural complexity and landscape structure 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 beds 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 and survival typically increase with structural complexity, likely due to increased food availability, increased living space, and enhanced refuge from predators (see reviews by Orth et al. 1984, Heck and Crowder 1991). Epifaunal diversity and community composition often are positively related to patch-scale seagrass structural complexity as well (Attrill et al. 2000, Sirota and Hovel 2006).

Habitat patch size, patch shape, and landscape configuration are all highly variable in seagrass landscapes (Fahrig 2003). 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 (Ries and Sisk 2004, Tanner 2005, Selgrath et al. 2007). 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 and landscape structure commonly covary (Robbins and Bell 1994). For instance, hard clam (*Mercenaria 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 (i) whether seagrass structural complexity varied between the edge and interior of large seagrass patches; (ii) whether the density and diversity of epifauna (prey) and fishes (predators) varied with structural complexity or between the edge and interior of patches; and (iii) the relative influence of structural complexity, distance from patch edges, and the presence of predators on epifaunal density and community structure in artificial seagrass habitat. Because many of the fishes inhabiting these seagrass beds are commercially and ecologically important, understanding the aspects of habitat structure that influence the abundance of their prey may be useful in seagrass habitat management and restoration (Fonseca et al. 1998).

2. Methods

2.1 Study sites

This study was conducted in the eelgrass (*Zostera marina*) beds of San Diego Bay, California, USA (32º 44’ N x 117º 10’ W; Fig. 1). San Diego Bay is a heavily developed urban estuary used for shipping, military operations, and recreation. Freshwater inflow to this estuary is low, resulting in seasonal hypersalinity (Largier et al. 1997). The front region of the bay is characterized by relatively low water residence times, moderate tidally driven currents, and low fluctuations in salinity and temperature through the year. The southern or back region of the bay is characterized by longer water residence times, lower current speeds, and greater extremes and 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); Fig. 1). We also conducted a manipulative caging 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 MLLW.

2.2 Seagrass, epifaunal, and fish surveys

We conducted surveys to measure seagrass structural complexity and epifaunal density and diversity in July 2006 and in June and August of 2007. We also conducted surveys to measure the diversity and abundance of fishes and fish gut contents in June and August 2007. To determine whether seagrass structural complexity (shoot density, shoot length, and biomass per unit area) varied among locations (edge vs. interior) within seagrass beds at each site, we collected samples within eelgrass patches at the outer edge (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 (15 cm diameter) were taken every 5 m along 40 m transects at each of the three locations running parallel to the edge of the bed (n = 6 in 2006, n = 8 in both June and August 2007). Samples were rinsed through a 6 mm sieve in the field and all retained eelgrass and rhizome material was frozen at 0°C until it was processed at the lab. 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 60º C to a constant weight for estimations of aboveground biomass per unit area. We used a multivariate analysis of variance (MANOVA) to test whether the combined seagrass structural complexity variables (shoot density, length, and biomass) vary with location and site in 2006, or location, site, and sampling period in 2007. 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 (ω^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. Data were transformed when necessary to meet the assumptions of ANOVA.

We sampled for mobile epifauna along each transect by capturing organisms within a small underwater sieve made of 20 cm diameter x 25 cm tall PVC pipe with a mesh bag attached to one end (mesh size ~400 µm). Every 5 m along each transect divers quickly slipped sieves over eelgrass shoots, cut shoots at the sediment surface using scissors, and then placed a 500 µm 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. Epifaunal samples were sorted and individuals in each taxon were counted to obtain densities. Total biomass per sample for six epifaunal categories (fishes, gastropods, crabs, shrimp, peracarid crustaceans, and ostracods/copepods) was obtained after drying epifauna in a drying oven at 60° C for 24 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 guts (see Results). We used ANOVAs to test for differences among location, site, and sampling periods in total epifaunal abundance, species richness, Simpson's index of diversity (D_s), and the biomass of common prey (as determined by gut content analyses).

We used non-metric Multi Dimensional Scaling (MDS) to investigate patterns of epifaunal community composition between sites and bed locations. MDS analyses were conducted on a matrix of Bray-Curtis similarities based on square-root transformed abundances of all taxa to reduce the influence of abundant taxa. Ordination was followed by 2-way analyses of similarity (ANOSIM) and similarity percentages (SIMPER) were calculated to identify particular taxa driving clusters revealed by the MDS and ANOSIM.

To quantify the density and diversity of fishes at the edge and interior of eelgrass beds at each site, we towed a non-destructive beam trawl (1.5 m wide x 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. Though we were able to sample for fishes along the edge and within the interior of patches using the beam trawl, we were not able to distinguish between outer and inner patch edges, and we therefore considered edge samples to be within 2 m of the eelgrass-unvegetated sediment interface, and interior samples to be > 5 m from the interface. Three trawls were conducted within each location (edge and interior) at each site in each of the two sampling periods. Fishes captured in trawls were identified to species and 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 gut content analysis during each sampling period. All identifiable organisms 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 location, site, and sampling period, and conducted MDS and SIMPER analyses as described above to test for variability in community composition. We explored variation in gut content composition using MDS, ANOSIM, and SIMPER. Fish with no identifiable gut contents were excluded from analyses.

2.3 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, location within the patch, and exposure to predators on the density and diversity of epifauna. ASUs are widely used to precisely control structural complexity in seagrass experiments and are colonized by epifauna similarly to living seagrass (e.g. 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 cm x 25 cm) anchored to the sediment. ASUs were placed 5 m apart along the edge of the eelgrass bed (at the sand-seagrass interface) and in the interior of the bed (> 5 m from the sand-seagrass interface) at depths of ca. 3 – 5 m MLLW. Each ASU was one of two simulated shoot densities: sparse (150 shoots m^{-2}) or dense (600 shoots m^{-2}), 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). Cages enclosed the entire ASU and were rectangular (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 were used to control for caging artifacts which may include reduced flow, shading, and addition of structure to the habitat. ASUs were deployed for 28 days and the mesh on all cage and partial cage treatments was cleaned weekly. At the end of deployment all epifauna that colonized each ASU 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_s, and prey biomass varied with location within the patch, complexity, and exposure to predators. We again utilized MDS to compare differences in community composition between treatments.

3. Results

3.1 Seagrass, epifaunal, and fish surveys

Seagrass. MANOVAs for 2006 and 2007 showed strong evidence for effects of location and site on seagrass structural complexity. Overall, structural complexity was lower at the outer edge than the inner edge, but was similar between the inner edge and bed interior (Fig. 2). Shoot density was consistently lowest at the outer edge at all sites during both years of sampling and location explained the majority of the variation (Tables 1 and 2). In 2006, there was a larger difference in shoot density between the outer edge and the inner edge and interior locations at SCB and NCB than at SI (Table 1, Fig. 2). In contrast, in 2007 shoot density was lower at the outer edge than at the other locations at SI in June but not August, and shoot density was lower at the outer edge than at the other locations at SCB in August but not in June (Table 2). Shoot length tended to be lowest at the outer edge in both years, with the exception of SCB in August 2007, but site accounted for more of the variability in shoot length, with SI having longer shoots than NCB and SCB (Fig. 2). Above-ground biomass was consistently lowest at the outer edge and bed location explained most of the variance in 2006. In 2007, above-ground biomass again tended to be lower at the outer edge than at the inner edge and interior, and biomass increased from June to August at SI but decreased from June to August at NCB and SCB.

Epifauna. Over the 3 survey periods approximately 77,000 epifaunal organisms were counted and sorted into a total of 54 taxonomic groups (Table 3). The most abundant taxon, gammarid amphipods, comprised 42%, 56%, and 76% of total epifauna in 2006, June 2007, and August 2007, respectively. For total epifaunal density, in 2006 there was strong evidence of an interactive effect of location and site (Table 1, Fig. 3). Though SNKs revealed no differences among treatments, total epifaunal density decreased from the edge to the interior at SI, and increased from the edge to the interior at NCB and SCB. In 2007, there were few differences in total epifaunal abundance among bed locations in June, except for lower abundance at the outer edge than other locations at SCB, but in August epifaunal abundance was higher in bed interiors at NCB and SCB than at the outer or inner edge (Table 2, Fig. 3).

In 2006 species richness was lower in the interior of SI than at all other locations, including the edge and interior at NCB and SCB, and there was little difference in richness among locations at NCB and SCB. In 2007 species richness did not vary among bed locations at SI, but was lower at the outer edge than at other locations at NCB in June and lower at the outer edge than at other locations at SCB in June and August. In 2006, trends for D_s were similar to trends in species richness from 2006 at all sites, and in 2007 D_s was lower at the outer edge of SI than at any other location at all sites in June, but varied more widely among locations and sites in August. In August, D_s was lower at the outer edge than the inner edge or interior of SI, but was lower in the interior than at the outer or inner edge at NCB and SCB (Fig. 3). The collective biomass of taxa most commonly found in fish gut analyses (peracarids, shrimp, ostracods, and copepods; see below) tended to increase from the edge to the interior at NCB and SCB in both

2006 and 2007. However, prey biomass decreased from the edge to the interior at SI in 2006 and in August 2007 (Fig. 3). Finally, the density of specific taxa (e.g., *Hippolyte* spp., Caprellidae, etc.) found most commonly in samples varied with location, site, and year in a taxon-specific manner (Fig. 4).

MDS ordination of epifaunal communities revealed clear separation of Shelter Island samples from the mid bay sites, but no clear separation among locations in any sampling period (Fig. 5).

Fishes. The overall abundance of fishes was slightly higher in the patch interior than at the patch edge, but this effect explained less than 10% of the total variation, and fish abundance was not strongly related to sampling period or site (Tables 2 and 4, Figure 6). Sampling period explained the most variation in species richness, which was lower overall in September than in June at SI and NCB, but not at SCB. Simpson's index of diversity was similar among groups except for the interior at NCB in September, where diversity was extremely low as 95% of the fish caught were juvenile giant kelpfish (*Heterostichus rostratus*). Average fish size varied between sampling periods and sites. Fish were larger in September than in June and larger at the mid bay sites (NCB and SCB) than at SI.

MDS ordination of the fish community did not generate any clear group clustering. SIMPER analysis revealed the greatest dissimilarity between SI and the mid bay sites was due to dwarf surfperch (*Micrometrus minimus*), which made up approximately 35% of the total catch at SI in June and 65% in September. This species was almost completely absent from the mid bay, with the exception of one individual being caught at NCB in June. NCB tended to have greater numbers of juvenile giant kelpfish and fewer shiner surfperch (*Cymatogaster aggregata*) than SCB. The sampling periods differed mostly in the number of juvenile giant kelpfish, which were more abundant in September (Table 4). Dissimilarity between locations was also caused primarily by juvenile giant kelpfish which on average were more than 3 times as abundant in the interior than at the edge.

We examined the gut contents of 191 fishes (Table 5). Gammarid amphipods made up the majority of the gut contents by abundance for all fish groups except pipefish, whose gut contents primarily included copepods, ostracods, or cumaceans. Bass had the most varied diet, with molluscs making up a large percentage of gut content biomass, and perch and kelpfish had the most specific diets, primarily feeding on gammarid amphipods, other peracarids, and shrimp. Perch, pipefish, and other fish gut contents were primarily gammarid amphipods by biomass. Kelpfish had a large average biomass of fish in their guts, but this represents very few individual fish whose guts were completely filled by the remains of a single fish. Our ANOSIM and SIMPER analyses of each fish group revealed no strong differences in gut contents based on location (results not shown). However, perch caught at the edge had greater amounts of copepods, ostracods, cumaceans, and gammarid amphipods than those caught in the interior, and some relatively rare fishes (including flatfish, blennies, and black croakers) ate proportionally more gammarid amphipods at the edge, as well as molluscs and worms, than in the interior, where more shrimp and non-gammarid peracarids were consumed. Finally, there was strong dissimilarity in gut contents between fishes captured at SI and fishes captured at the two central bay sites, among which gut contents were similar.

3.2 Caging experiment

Nearly 45,000 individual epifauna were collected from ASUs in the caging experiment and were sorted into 42 taxonomic groups (Table 6). As with the epifaunal surveys, gammarid amphipods were the most abundant taxon (73% of individuals). Copepods, the gastropod *Alia carinata*, grass shrimp *Hippolyte* spp., and caprellid amphipods were also among the most abundant taxa. Isopods *Paracerceis* spp. were rare at Shelter Island in the surveys and also in the caging samples (0.23% of total).

Total epifaunal density varied with location and structural complexity, but not with predator access (Table 7, Fig. 7). Collectively, epifauna were denser at the bed edge than at the interior, regardless of structural complexity, and were more abundant in dense ASUs than in sparse ASUs, regardless of location. There was an interactive effect of location 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 than in dense ASUs in the interior of seagrass beds (Fig. 7). D_s was higher in ASUs placed in the interior than at the edge, 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 location, structural complexity, and predator access. Biomass 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 (Table 7, Fig. 7).

Responses of individual taxa to treatments varied. Most taxa were less abundant in sparse than in dense ASUs, but gammarid amphipods also were less abundant in bed interiors than at the edge, as were caprellid amphipods (Table 7, Fig. 8). *Hippolyte* spp. 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. Results of the MDS ordination suggested that the epifaunal community varied strongly between the edge and the interior of seagrass beds (Fig. 9). Bed location differences were largely driven by gammarid abundance (28% dissimilarity), and samples separated to a lesser extent by structural complexity treatment, also driven by gammarid amphipods (25% dissimilarity). There was high overlap between all three predation treatment groups, and the slight differences between caged plots and open were largely driven by gammarid amphipod and *Hippolyte* (23% and 11% dissimilarity respectively).

4. Discussion

In our study we found that (i) seagrass structural complexity generally increased from the edge of patches to the interior of patches; (ii) epifaunal density increased from the edge to the interior of patches at mid-bay sites (NCB and SCB), but decreased from the edge to the interior at our front-bay site (SI); (iii) structural complexity and proximity to patch edges 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 (iv) prey biomass was higher in dense vs. sparse artificial eelgrass, higher in caged plots than in those exposed to predators and in cage-control plots, and higher at the patch edge than in the interior. Overall, our results indicate that local-scale and patch-scale attributes of eelgrass habitat structure covary in San Diego Bay and jointly influence epifaunal and fish density, diversity, and community composition, but that the interactive effects of these factors differ among sites and sampling periods.

Many studies have shown seagrass structural complexity strongly affects epifaunal organisms (e.g. Heck and Orth 1980, Bell and Westoby 1986, Sirota and Hovel 2006; but see Attrill et al. 2000), but far fewer have tested whether proximity to patch edges (i.e. location) influences epifaunal density, diversity, or survival. In seagrass habitat in St. Joseph Bay, Florida, epifaunal density was higher along patch edges than in patch interiors, despite the fact that seagrass biomass and shoot density were higher in patch interiors than along edges (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 seagrass beds near the Isles of Scilly, England, infaunal community composition differed between the edge and the interior of both small (< 15 m diameter) and large (> 30 m diameter) seagrass patches (Bowden et al. 2001). Though these studies, like ours, indicate that proximity to patch edges influences epifaunal community composition, none manipulated structural complexity within patches to test the relative effects of structural complexity and location on epifaunal density and diversity. The results of our manipulative experiment indicate that structural complexity and location independently influence taxon density, and for some taxa, that density is more strongly tied to either structural complexity or location. For example, the grass shrimp *Hippolyte* spp. was more abundant in patch interiors than at patch edges, but our caging experiment combined with high *Hippolyte* spp. abundance in fish guts indicated that these shrimp prefer patch interiors due to the protective function of dense eelgrass found there. In contrast, caprellid amphipods were far more abundant along patch edges than in patch interiors, and location, rather than simulated shoot density, explained the majority of variation in caprellid abundance. These amphipods are relatively sedentary and 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 in higher water flow near the patch edge (Bologna and Heck 1999, Peterson et al. 2004).

Edge effects on community composition and species interactions are well documented in terrestrial systems, particularly for bird communities (e.g., Paton 1994, Desrochers and Fortin 2000). Ornithologists have shown elevated levels of nest parasitism and predation within 50 m of forest edges compared to deeper in forest interiors (reviewed by Paton 1994). In Australia, Anderson and Burgin (2008) found lower abundances of skinks at forest edges compared to the interior, and higher abundances and predation rates of avian predators at the edge. In this system, the birds may prefer to inhabit the edge as they utilize man-made structures (e.g. telephone posts, wires) outside of the forest as perches while scanning for prey at the forest edge. There is also evidence that tree recruitment is higher at tropical forest edges, and unique light regimes at edges can result in unique plant communities, thus habitat structure (Laurance et al. 1998).

We know far less about the effects of patch edges on ecological processes in marine ecosystems. Within seagrass habitat, proximity to patch edges may influence epifaunal density and diversity in several ways. Organisms dispersing among patches may remain within the habitat they first encounter (the "nearest refuge" hypothesis: Virnstein and Curran 1986, Bologna and Heck 2002, Tanner 2005). Similarly, when passive 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). Also, as noted above for caprellid amphipods, planktonic food delivery to the seagrass canopy may be greater near patch edges, just as food delivery to the benthos may be greater in patch interiors as currents attenuate with distance into the patch (Gambi et al. 1990, Bologna and Heck 1999).

We found that faunal distribution patterns related to shoot density and location varied between sites within sampling periods, as well as between sampling periods. Although our surveys were not replicated within regions of the bay, relationships between habitat structure and epifaunal community structure differed strongly between our front-bay site (SI) and our two mid 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 (Largier et al. 1997). These parameters generally are more variable at SI than in the mid bay due to greater amounts of ocean and bay water mixing, and this variability likely contributed to the variability seen in faunal abundances at SI over time despite relatively consistent eelgrass structural complexity at this site. Additionally, recruitment pulses are common for many of the epifaunal species present in our samples (Sirota and Hovel 2006), which can lead to large fluctuations in epifaunal abundance between sampling periods. Recruitment rates may vary with eelgrass structural complexity (Sirota and Hovel 2006), potentially altering relationships between epifaunal density and diversity and eelgrass habitat structure through time. 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 early to late summer.

Though low structural complexity at patch edges was a consistent feature of seagrass beds at all sites, location had different effects on epifaunal density and biomass at SI vs. NCB and SCB. Prey density and biomass tended to increase going into the patch at NCB and SCB but decrease going into the patch at SI in 2006 and August 2007. High secondary production at patch edges may result in high rates of trophic transfer to fishes that consume epifauna (Bologna and Heck 1999, 2002). In St. Joseph Bay, Florida, predation on scallops *Argopecten irradians* was higher along seagrass patch edges compared to patch interiors (Bologna and Heck 1999). However, scallop growth rates were higher along seagrass patch edges, likely due to increased food delivery. Fishes captured in our beam trawl are vulnerable to predation by larger fishes and sea birds and may have to balance prey capture success, which may be higher in the sparser grass at the edge, with seeking refuge from predators by spending less time at the patch edge. However, we were unable to detect major differences in fish abundance or diet between the patch edge and interior. Fish species in our surveys are highly mobile and may forage throughout the bed, even if they preferentially inhabit one location over another. A recent review of nekton patterns of abundance in seagrass beds also reported little evidence for fishes showing distinct patterns of distribution throughout the bed (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.

The caging experiment allowed us to compare the relative influences of structural complexity and location on the epifaunal community. Although total epifaunal density and species richness varied both with location and complexity, location explained more of the variation. This may be due to the overwhelming majority of taxa being peracarids (gammarid amphipods in particular), which do not follow the expected positive correlation with complexity but instead have been consistently shown as more abundant at the patch edge (Bologna and Heck 2002, Tanner 2005). Diversity of epifauna was not influenced by complexity but seemed largely dependent on location, though on average it was only marginally higher in patch interiors than at the edge. Copepods (which included calanoid, cyclopoid, and harpactecoid species) and the tanaid *Leptochelia dubia*, more often considered as part of the plankton and infauna, respectively (Brusca and Brusca 2002), were found in high abundances in the caging experiment but are not likely to be strongly tied to habitat structure. It was not surprising then that location and simulated shoot density explained very little of their distribution. In contrast abundant taxa that are highly associated with seagrass blades, such as the gastropod *Alia carinata* and caprellid amphipods, were influenced strongly by shoot density and location, respectively.

Surprisingly, predator exclusion had much less of an effect on the density of most taxa than did structural complexity and location. The exclusion of predators had the most influence on *Hippolyte* spp. distribution which was not surprising given its frequency in the stomachs of fish collected during surveys, and the well documented predator avoidance behavior by similar species (Main 1987). Although gammarid amphipods were the most abundant taxa in fish guts, their high abundances across caging treatments, and in surveys, suggest their distribution is not predator-limited.

The results of our surveys and experiment suggest that the organisms living in the eelgrass beds of San Diego Bay respond not only to local-scale, within-patch measures of habitat complexity but also to larger scale attributes of structure like proximity to patch edges, and that relationships between epifaunal and seagrass habitat structure vary by site, region within bay, and sampling period. However, many taxa seemed to be strongly influenced by factors outside the scope of our study. Future research addressing faunal responses to variation in other aspects of habitat structure will add to the growing knowledge of the environmental and ecological phenomena maintaining the diverse communities found in seagrass beds.

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Table 1: P-values and ω^2 (in parentheses) values from 2-way ANOVAs on 2006 survey samples. The ω^2 values are given only for p-values < 0.1, which are also in bold. Due to sample loss (n = 6 reduced to n = 3) in the epifauna survey, data were unbalanced and ω^2 values were not calculated. Transformations used to meet analysis assumptions are given where applicable.

		Factors		
Variable	Transformation	Site	Location	Site*Location
Shoot density*	Square-root	**0.096 (8.6%)**	**<0.001 (72.0%)**	**0.058 (1.9%)**
Shoot length*	Square-root	**<0.001 (66.3%)**	**<0.001 (24.8%)**	0.248
Biomass†	Ln(x+1)	**0.003 (21.1%)**	**<0.001 (65.7%)**	**0.007 (2.4%)**
Epifaunal abundance†	Ln	**0.066**	**0.055**	**0.065**
Richness*	Square-root	0.593	0.136	**0.002**
D_s‡	Arcsine	**<0.001**	**0.030**	0.156
Prey biomass†	Ln	**0.062**	**0.001**	**0.023**
Gammaridea†	Ln	**<0.001**	**<0.001**	**0.002**
Caprellidae†	Ln(x+1)	**0.006**	**0.033**	**0.054**
Paracerceis spp. †	Ln(x+1)	**<0.001**	0.827	**0.001**
Copepoda†	Ln(x+1)	0.337	0.554	**0.076**
*Alia carinata**	Square-root	**<0.001**	0.115	0.403
Hippolyte spp.†	Ln(x+1)	**<0.001**	**<0.001**	0.291

* Square-root transformed
† Ln(x+1) transformed
‡ Arcsine transformed

Table 2: P-values and ω^2 (in parentheses) values from 3-way ANOVAS on 2007 survey samples. The ω^2 values are given only for p-values < 0.1, which are also in bold. Transformations used to meet analysis assumptions are given where applicable.

	Factors						
Measure	Sampling period	Site	Location	Site* Sampling period	Location* Sampling period	Site* Location	Site* Location* Sampling period
Shoot density†	**<0.001 (6.3%)**	**0.074 (1.6%)**	**<0.001 (21.1%)**	0.167	0.847	0.704	**0.079 (2.2%)**
Shoot length†	0.598	**<0.001 (59.5%)**	**<0.001 (4.1%)**	0.318	**0.007 (1.6%)**	**<0.001 (5.9%)**	0.621
Biomass†	0.788	**<0.001 (25.8%)**	**<0.001 (25.8%)**	**0.046 (1.4%)**	0.162	0.148	0.617
Total epifauna†	**0.007 (2.6%)**	**<0.001 (19.0%)**	**<0.001 (11.3%)**	0.887	**0.029 (2.1%)**	**0.004 (5.0%)**	**0.064 (2.1%)**
Richness	**0.004 (4.0%)**	**<0.001 (8.2%)**	**0.002 (5.6%)**	0.482	0.206	**0.007 (5.6%)**	**0.058 (2.7%)**
D_s ‡	**<0.001 (13.5%)**	0.848	**<0.001 (7.6%)**	**0.011 (2.1%)**	**<0.001 (12.3%)**	**<0.001 (19.4%)**	**<0.001 (6.8%)**
Prey biomass*	0.390	**<0.001 (19.8%)**	**<0.001 (12.9%)**	**0.030 (2.2%)**	0.351	**0.041 (2.6%)**	**0.034 (2.8%)**
Gammaridea†	**<0.001 (4.1%)**	**<0.001 (18.4%)**	**<0.001 (10.3%)**	0.225	**0.001 (4.4%)**	**<0.001 (9.0%)**	**0.006 (3.8%)**
Caprellidae†	**<0.001 (25.8%)**	**<0.001 (19.8 %)**	**0.040 (1.3%)**	**<0.001 (6.7%)**	0.174	**0.003 (3.6%)**	0.108
Paracerceis spp. †	**<0.001 (41.5%)**	**<0.001 (27.0%)**	**<0.001 (1.5%)**	**<0.001 (14.6%)**	**<0.001 (1.8%)**	0.163	0.882
Copepoda†	**<0.001 (3.7%)**	**<0.001 (40.0%)**	**<0.001 (9.4%)**	**0.003 (3.1%)**	0.101	0.305	0.249
*Alia carinata**	**0.006 (0.5%)**	**<0.001 (82.1%)**	**<0.001 (3.8%)**	**0.001 (1.0%)**	0.580	**0.001 (1.3%)**	0.614
Hippolyte spp. *	**<0.001 (9.6%)**	**<0.001 (5.1%)**	**<0.001 (35.1%)**	**0.020 (1.7%)**	0.273	**0.015 (2.5%)**	**0.001 (4.4%)**
Fish abundance*	0.324	0.190	**0.026 (9.8%)**	**0.087 (7.3%)**	0.124	0.392	0.851
Richness*	**<0.001 (30.8%)**	0.764	0.108	**0.020 (11.0%)**	0.499	0.144	0.633
D_s	**0.055 (4.1%)**	0.561	**0.002 (13.9%)**	**0.001 (20.5%)**	**0.008 (9.9%)**	**0.017 (0.0%)**	0.137
Fork length*	**<0.001 (30.1%)**	**0.001 (20.0%)**	0.648	**0.029 (7.0%)**	0.266	0.426	0.156

* Square-root transformed
† Ln(x+1) transformed
‡ Arcsine transformed

Table 3: Taxon abundance in survey samples. Taxa listed made up at least 1% of the total sampled for at least one sampling period. This includes 98.2%, 99.3%, and 99.2% of the total individuals for 2006 (N = 51), June (N = 72), and August (N = 72) 2007 respectively. Grouping as follows: G, Gastropods; O, Ostracods and Copepods; P, Peracarid crustaceans; S, Shrimp.

			2007	
Taxon	Group	2006	June	August
Gammaridea	P	7186	13942	26716
Caprellidae	P	349	4421	810
*Paracercei*s spp.	P	2449	75	2296
Copepoda	O	1359	2108	923
Alia carinata	G	697	903	788
Hippolyte spp.	S	729	958	546
Tanais spp.	P	349	597	869
Leptochelia dubia	P	1217	97	168
Ostracoda	O	987	266	98
Tectura depicta	G	190	595	403
Colanthura squamosa	P	276	93	767
Assiminea californica	G	323	116	177
Unidentifiable shrimp	S	259	130	75
Paranthura elegans	P	300	12	67
Lacuna unifasciata	G	73	131	42
Bulloid snails	G	20	7	151
Crepidula spp.	G	33	64	49
Alia sp.	G	131	7	3

Table 4: Fish caught in trawl samples. Taxa shown made up at least 1% of the total catch and account for 99.0% and 99.7% of the total individuals for June (N =18) and September (N = 18) 2007 respectively. Fish were not sampled in 2006.

Common name	Scientific name	June	September
Giant Kelpfish	*Heterostichus rostratus*	268	412
Dwarf Surfperch	*Micrometrus minimus*	143	153
Shiner Surfperch	*Cymatogaster aggregata*	218	7
Black Surfperch	*Embiotoca jacksoni*	39	28
Spotted Sand Bass	*Paralabrax maculatofasciatus*	52	8
Black Croaker	*Cheilotrema saturnum*	12	37
Kelp Bass	*Paralabrax clathratus*	31	7
Pipefish	*Syngnathus* spp.	25	11
Barred Sand Bass	*Paralabrax nebulifer*	17	8
Round Ray	*Urolophus halleri*	6	19
CA Halibut	*Paralichthys californicus*	11	5
Blenny	*Hypsoblennius* spp.	10	5
Spotted Kelpfish	*Gibbonsia elegans*	5	1

Table 5: Percent composition of fish gut content analyses, (A) by abundance and (B) by dry weight. Average fork length of fishes is given, plus the standard error. COC stands for copepods, ostracods, and cumaceans. Molluscs include bivalves and gastropods. Worms includes polychaetes and nematodes. Fish remains in gut contents were unidentifiable. All values greater or equal to 1% of the average gut contents for each group are in bold.

A)

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

B)

Fish group	**n**	**Fork length, mm (SE)**	**Gammarid amphipods**	**Other peracarids**	**Shrimp**	**Crabs**	**COC**	**Molluscs**	**Worms**	**Fish**
Bass	26	153.88 (10.97)	**3.6%**	**9.6%**	**11.8%**	**7.9%**	0.1%	**55.2%**	**1.0%**	**10.8%**
Kelpfish	64	101.08 (3.49)	**30.6%**	**6.5%**	**11.4%**	0.2%	0.0%	0.0%	0.0%	**51.2%**
Perch	33	77.36 (5.07)	**99.1%**	0.4%	0.1%	0.1%	0.1%	0.2%	0.1%	0.0%
Pipefish	14	138.00 (11.88)	**69.0%**	**2.7%**	**23.2%**	0.0%	**5.0%**	0.0%	0.0%	0.0%
Other	25	97.52 (5.24)	**67.6%**	**18.9%**	**2.6%**	**2.2%**	0.3%	**3.5%**	**4.9%**	0.1%

Table 6: Taxon abundance in caging samples (N = 60). Taxa listed made up at least 1% each of the total individuals collected and represent 97.6% of the total individuals. Groupings as follows: G, Gastropods; O, Ostracods and Copepods; P, Peracarid crustaceans; S, Shrimp.

Taxon	Group	Abundance
Gammaridea	P	32907
Copepoda	O	2749
Alia carinata	G	2485
Hippolyte spp.	S	2221
Leptochelia dubia	P	1384
Caprellidae	P	747
Tanais spp.	P	529
Ostracoda	O	516
Crepidula spp.	G	257

Table 7: P-values and ω^2 (in parentheses) values from 3-way ANOVAS on caging experiment data. The ω^2 values are given only for p-values < 0.1, which are also in bold. Transformations used to meet analysis assumptions are given where applicable.

	Factors						
Measure	Location	Complexity	Predation	Loc.*Comp.	Loc.*Pred.	Comp.*Pred.	Loc.*Comp.*Pred.
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%)**	**0.001 (12.7%)**	0.157	**0.038 (3.7%)**	0.650	0.876	0.392
D_s[‡]	**<0.001 (32.8%)**	0.297	**0.052 (4.3%)**	0.853	0.875	0.212	0.717
Prey biomass[*]	**0.004 (5.5%)**	**<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[†]	0.99	**0.002 (12.3%)**	0.817	**0.023 (6.1%)**	0.258	0.824	0.573
Alia carinata[*]	0.328	**<0.001 (25.1%)**	**0.011 (8.7%)**	0.851	0.395	0.869	0.911
Hippolyte spp. [†]	0.492	**<0.001 (16.4%)**	**<0.001 (49.4%)**	0.368	0.607	0.744	0.747
Leptochelia dubia[†]	**0.001 (14.5%)**	**0.004 (9.5%)**	0.297	**0.098 (2.2%)**	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

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Figure 1: Map of San Diego Bay showing study sites. A) Shelter Island (front bay), B) NCB (mid bay), and C) SCB (mid bay).

Figure 2: Shoot density, length, and biomass measured in the seagrass surveys. Error bars represent one standard error. Letters above bars denote groups separated by SNK post-hoc analysis.

Figure 3: Epifaunal abundance, richness (number of distinct taxa), Simpson's Index of Diversity (D_s), and biomass of prey (mg) calculated from epifauna surveys. Left column graphs are data from 2006; center and right columns are June and August 2007 respectively. Error bars represent one standard error. Letters above bars denote groups separated by SNK post-hoc analysis.

Figure 4: Abundance data for the 6 most abundant taxa in epifauna surveys. Left column graphs are data from 2006; center and right columns are June and August 2007 respectively. Y-axes are the same for a particular taxon, except for *Paracerceis* spp. (axes are individually labeled). Error bars represent one standard error. Letters above bars denote groups separated by SNK post-hoc analysis.

Figure 5: MDS plots based on a Bray-Curtis similarity matrix of square-root transformed abundances of all taxa seen in (a) 2006, (b) June, and (c) August 2007 epifauna samples. Distances of points represent relative similarity in community composition. Symbols represent bed location values and confidence ellipses are drawn around 1 standard deviation of the group centroid (dotted – outer edge, dashed – inner edge, solid – interior). The shaded ellipse is drawn around all Shelter Island points, the only site that clustered separately.

Figure 6: Results of fish trawls. Error bars represent one standard error. Letters above bars denote groups separated by SNK post-hoc analysis.

Figure 7: Total richness (number of distinct taxa), Simpson's Index of Diversity (D_s), and biomass of prey (mg) calculated from caging experiment. Left column graphs are data from edge plots and right columns are interior plots. Error bars represent one standard error. Letters above bars denote groups separated by SNK post-hoc analysis.

Figure 8: Abundance data for the 6 most abundant taxa in caging experiment. Left column graphs are data from edge plots and right columns are interior plots. Error bars represent one standard error. Letters above bars denote groups separated by SNK post-hoc analysis.

Figure 9: MDS 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) location (dashed – edge, solid – interior), b) complexity (dashed – dense, solid – sparse), and c) predation (solid – cage, dashed – control, dotted – open) treatments. Plot stress 0.15.

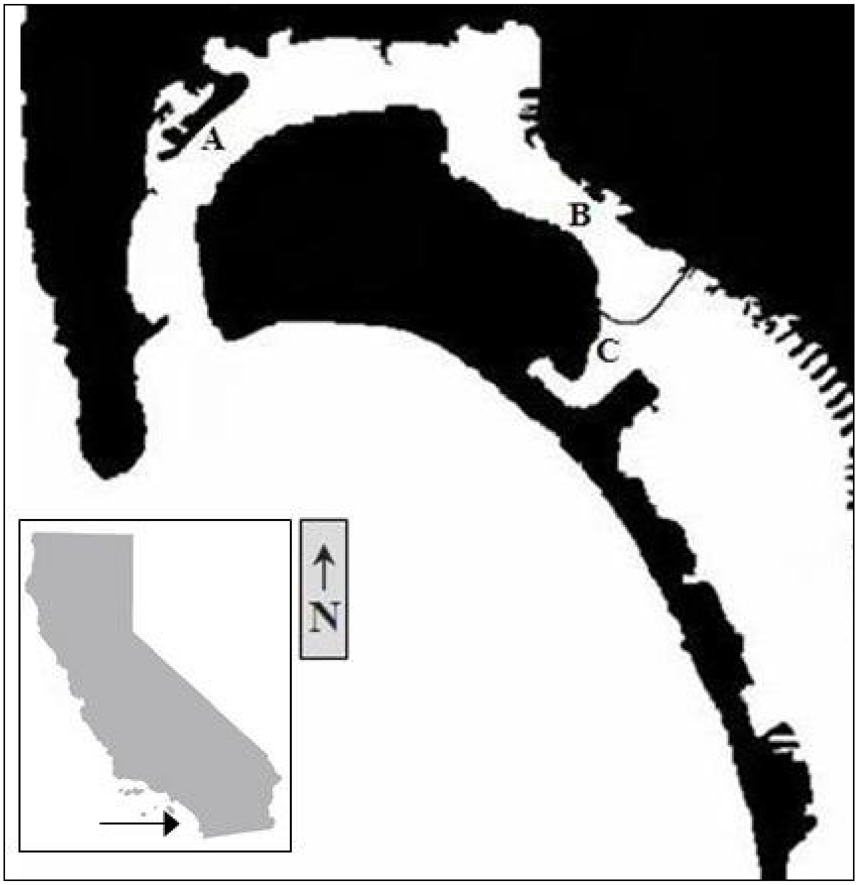
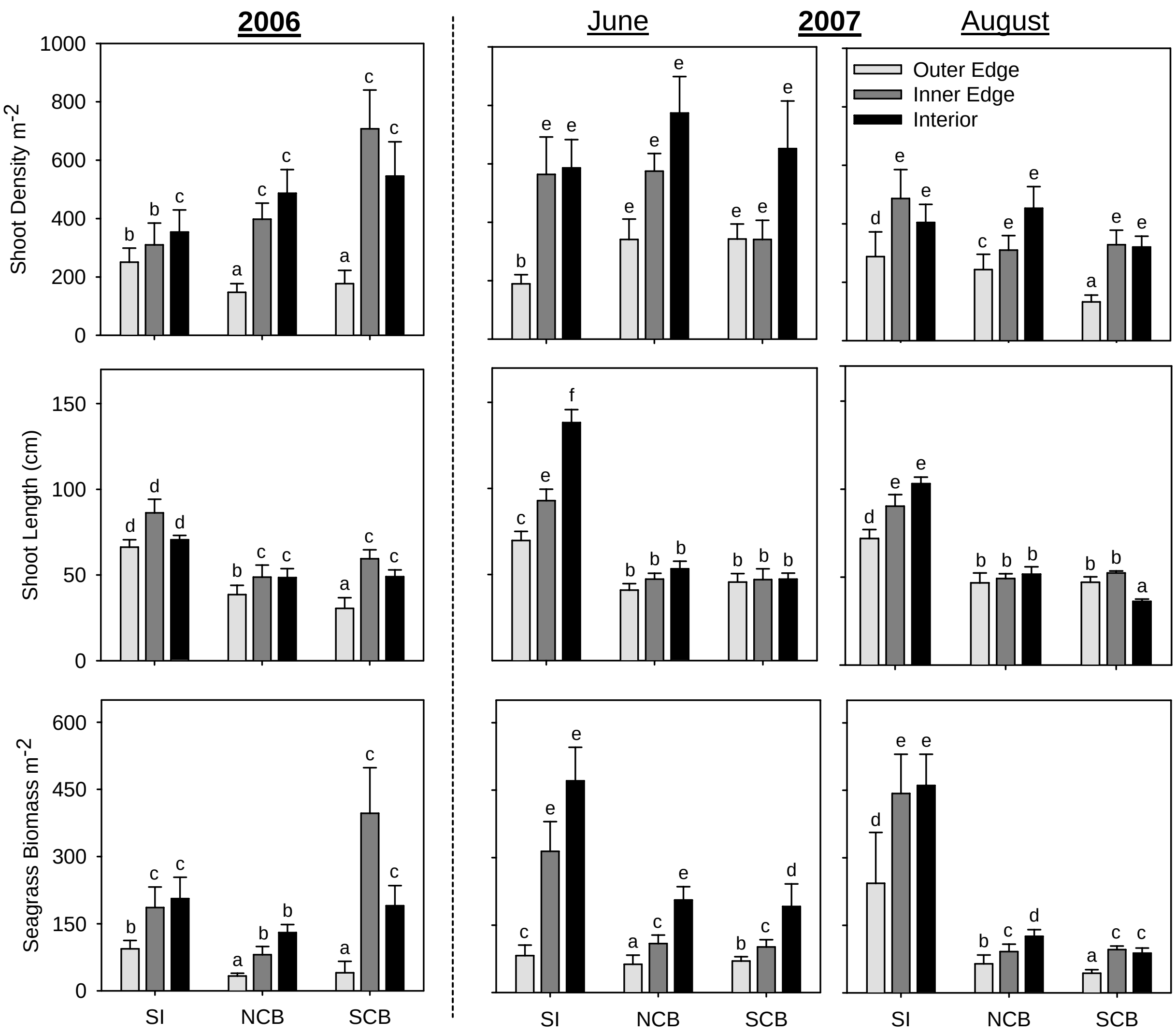


Figure 1.


2006
June
2007
August
Outer Edge
Inner Edge
Interior
Shoot Density m-2
1000
800
600
400
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0
b b c
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d e e
c e e
a e e
Shoot Length (cm)
150
100
50
0
d d d
b c c
a c c
c e f
b b b
b b b
d e e
b b b
b b a
Seagrass Biomass m-2
600
450
300
150
0
b c c
a b b
a c c
c e e
a c e
b c d
d e e
b c d
a c c
SI
NCB
SCB

Figure 2.

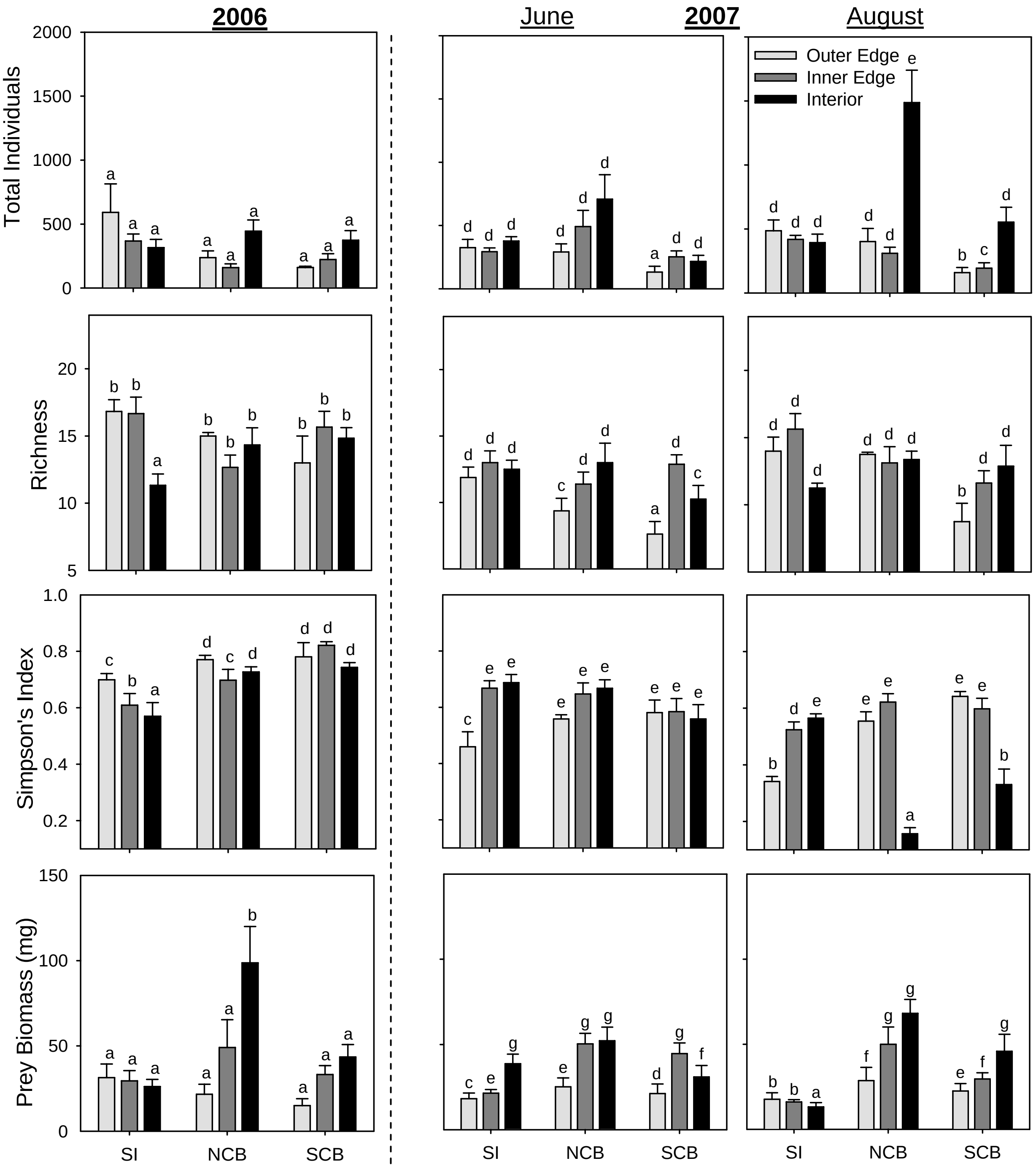
2006
June
2007
August
Total Individuals
2000
1500
1000
500
0
Outer Edge
Inner Edge
Interior
a a a a a a a a a
d d d d d d a d d
d d d d d e b c d
Richness
20
15
10
5
b b a b b b b b b
d d d c d d a d c
d d d d d d b d d
Simpson's Index
1.0
0.8
0.6
0.4
0.2
c b a d c d d d d
c e e e e e e e e
b d e e e a e e b
Prey Biomass (mg)
150
100
50
0
a a a a a b a a a
c e g e g g d g f
b b a f g g e f g
SI
NCB
SCB
SI
NCB
SCB
SI
NCB
SCB

Figure 3.

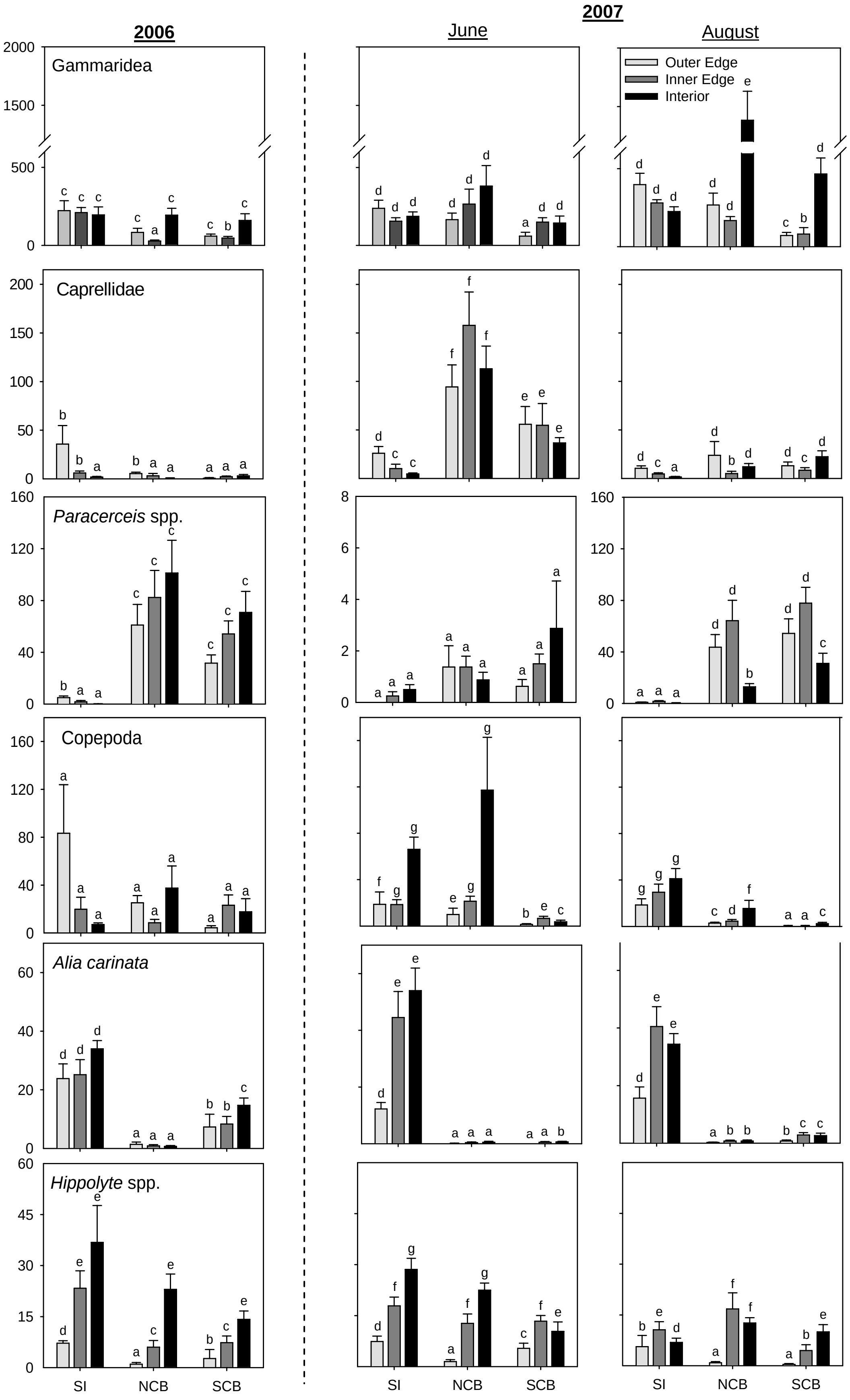
2007
2006
June
August
Outer Edge
Inner Edge
Interior
Gammaridea
2000
1500
500
0
c c c
c a c
c b c
d d d
d d d
a d d
d d d
d d e
c b d
Caprellidae
200
150
100
50
0
b b a
b a a
a a a
d c c
f f f
e e e
d c a
d b d
d c d
Paracerceis spp.
160
120
80
40
0
b a a
c c c
c c c
8
6
4
2
0
a a a
a a a
a a a
160
120
80
40
0
a a a
d d b
d d c
Copepoda
160
120
80
40
0
a a a
a a a
a a a
f g g
e g g
b e c
g g g
c d f
a a c
Alia carinata
60
40
20
0
d d d
a a a
b b c
d e e
a a a
a a b
d e e
a b b
b c c
Hippolyte spp.
60
45
30
15
0
d e e
a c e
b c e
d f g
a f g
c f e
b e d
a f f
a b e
SI
NCB
SCB
SI
NCB
SCB
SI
NCB
SCB

Figure 4.

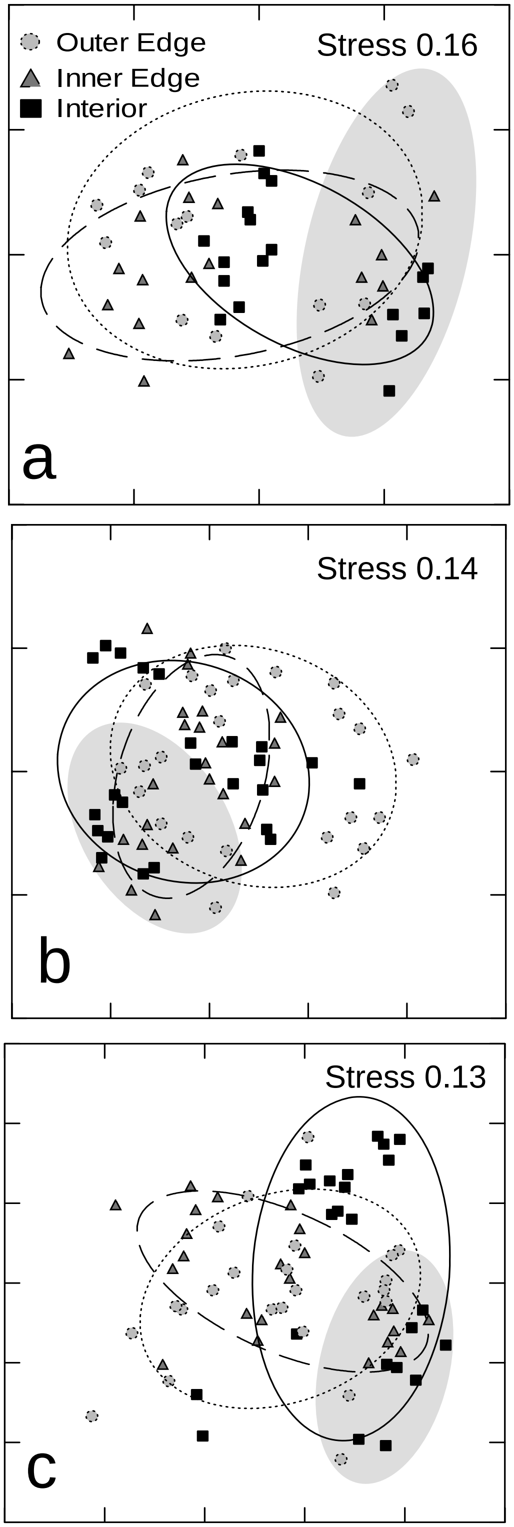
Outer Edge
Inner Edge
Interior
Stress 0.16
a
Stress 0.14
b
Stress 0.13
c

Figure 5.

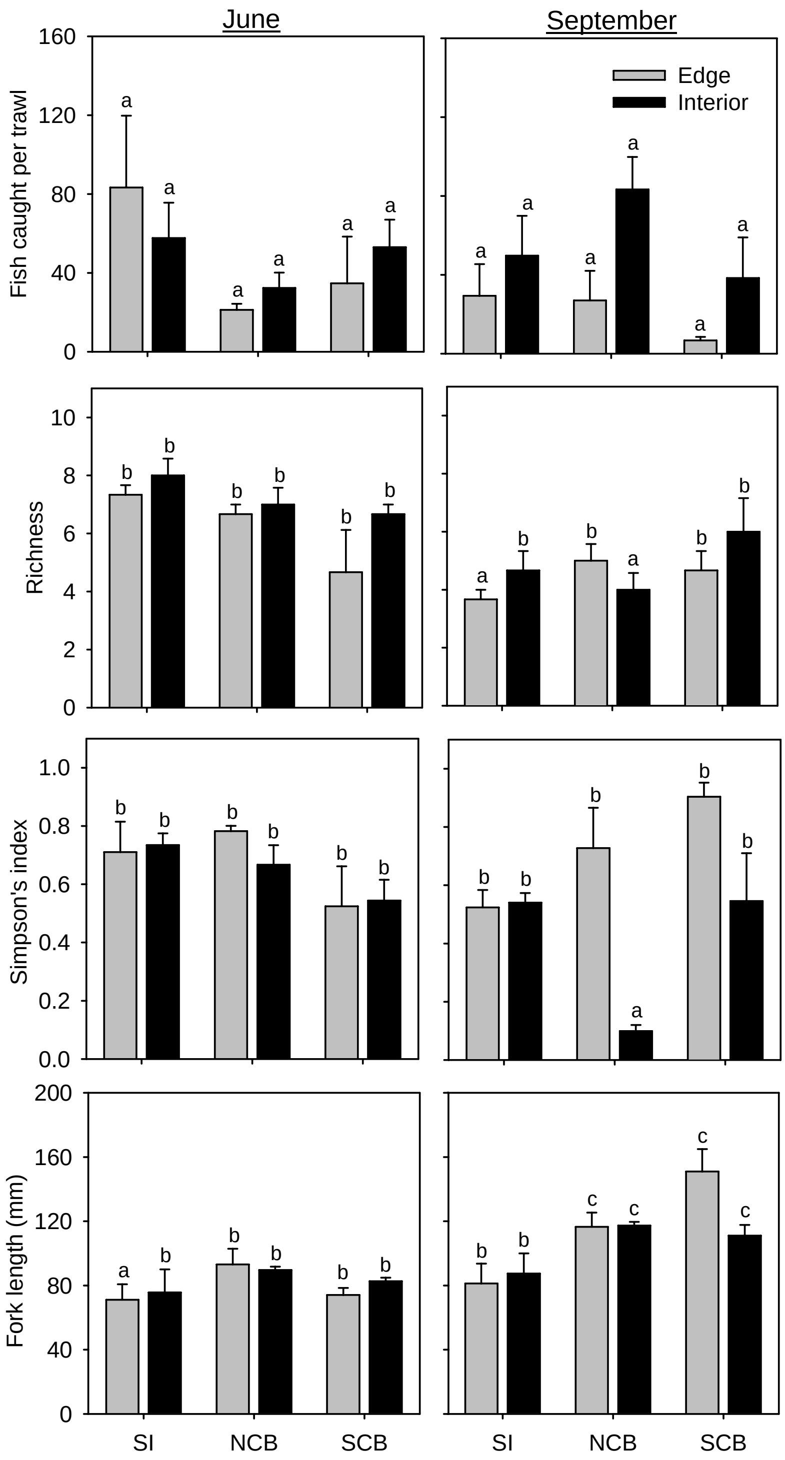
June
September
Edge
Interior
Fish caught per trawl
Richness
Simpson's index
Fork length (mm)
SI
NCB
SCB
SI
NCB
SCB

Figure 6.

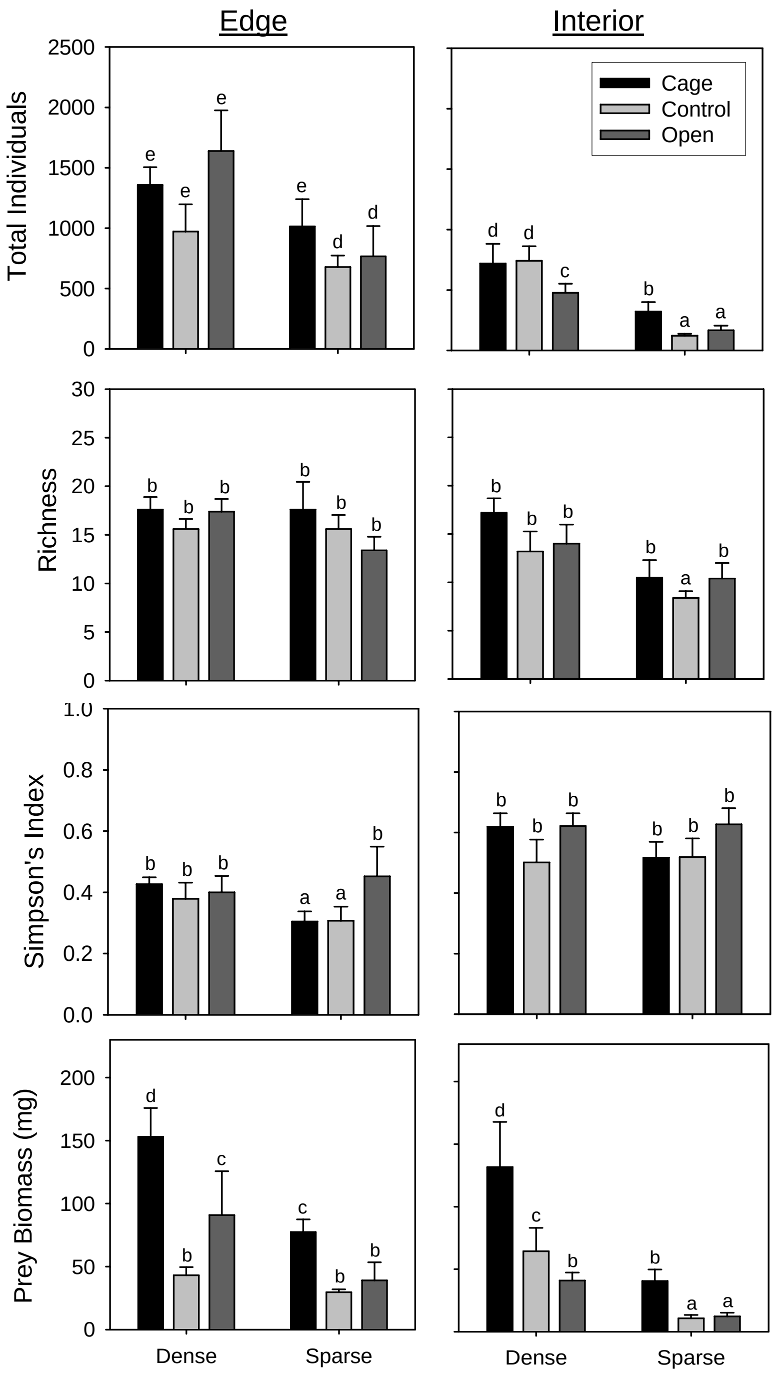Edge
Interior
Cage
Control
Open
Total Individuals
2500
2000
1500
1000
500
0
e
e
e
e
d
d
d
d
c
b
a
a
Richness
30
25
20
15
10
5
0
b
b
b
b
b
b
b
b
b
b
a
b
Simpson's Index
1.0
0.8
0.6
0.4
0.2
0.0
b
b
b
a
a
b
b
b
b
b
b
b
Prey Biomass (mg)
200
150
100
50
0
d
b
c
c
b
b
d
c
b
b
a
a
Dense
Sparse
Dense
Sparse

Figure 7.

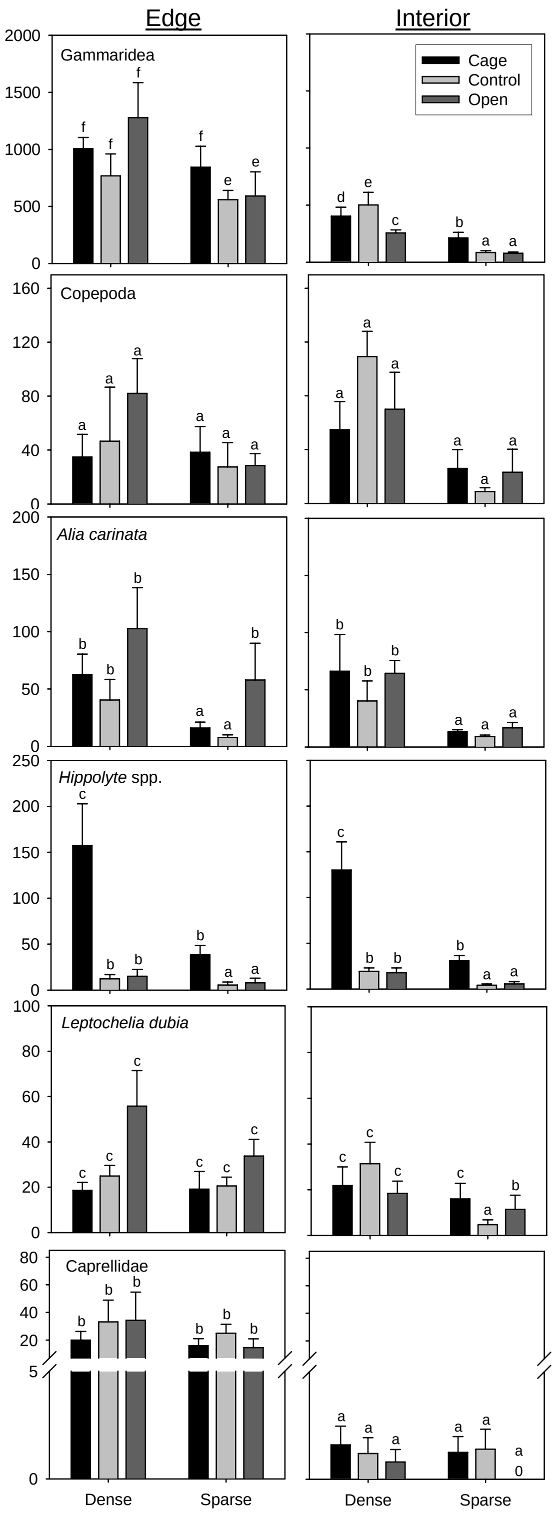
Edge
Interior
Cage
Control
Open
Gammaridea
2000
1500
1000
500
0
f
f
f
f
e
e
d
e
c
b
a
a
Copepoda
160
120
80
40
0
a
a
a
a
a
a
a
a
a
a
a
a
Alia carinata
200
150
100
50
0
b
b
b
a
a
b
b
b
b
a
a
a
Hippolyte spp.
250
200
150
100
50
0
c
b
b
b
a
a
c
b
b
b
a
a
Leptochelia dubia
100
80
60
40
20
0
c
c
c
c
c
c
c
c
c
c
a
b
Caprellidae
80
60
40
20
5
0
b
b
b
b
b
b
a
a
a
a
a
a
0
Dense
Sparse
Dense
Sparse

Figure 8.

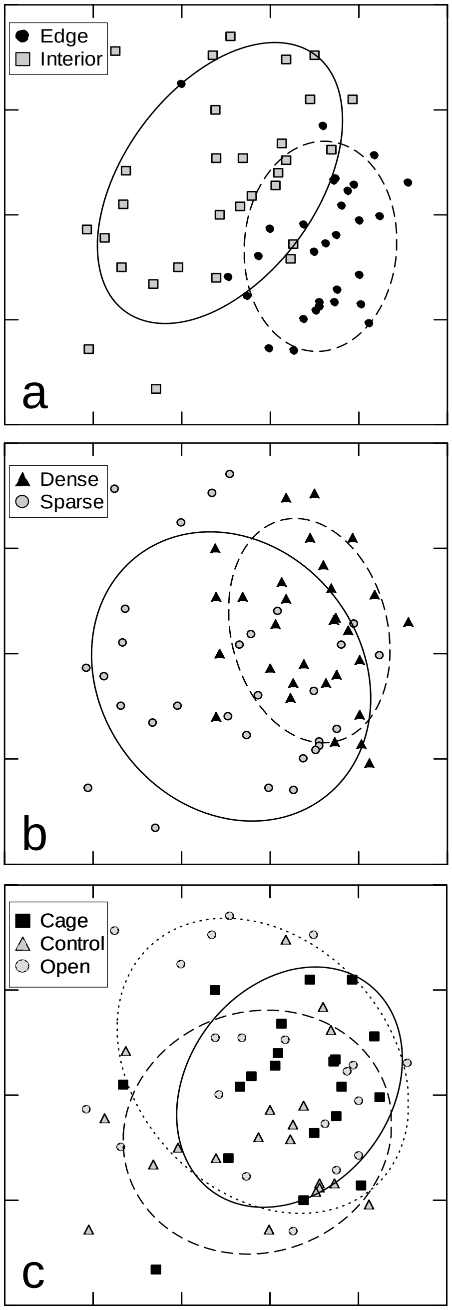

Figure 9.