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Impact of differential predation potential on eelgrass (*Zostera marina*) faunal community structure

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Abstract The trophic structure of fauna within eelgrass beds (*Zostera marina*) was assessed at two sites in Little Egg Harbor, New Jersey, USA during the summer of 1999. Although the sites were similar with respect to both *Z. marina* shoot density and plant biomass, they differed significantly in the relative distribution of large predatory fish (e.g., *Cynoscion regalis*, *Paralichthys dentatus*, *Morone saxatilis*). Site One, Marsh Elder, was characterized by a significantly greater catch per unit effort for large predators than Site Two, Shelter Island. Gut content analysis provided direct evidence of trophic linking and significant declines between these fish and four of the five most abundant organisms collected in throw traps used to analyze the density of large benthic prey/small predators. The densities of grass shrimp (*Palaemonetes* spp. *Hippolyte zostericola*), blue crab (*Callinectes sapidus*), and small predatory fish (e.g., *Syngnathus fuscus*, *Opsanus* spp., *Tautoga onitus*) were significantly reduced at Marsh Elder, potentially as a direct impact of large predatory fish. In turn, the differences in the density of small predators observed between sites produced either a significant positive or negative effect on the distribution of small benthic prey (e.g., polychaetes, amphipods), resulting in a two-step trophic cascade within the system. Additionally, an analysis of similarities defined each site independently for both large prey/small predators and small benthic prey community structure. Although the mechanism which produced the differences in the distribution of large predatory fish remains unknown, their impact on faunal community structure mediated not only the distribution of their potential prey, but also subsequent lower trophic levels.

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Introduction

Large-scale assessments of marine communities have produced many hypotheses that address the processes dictating community structure. Included among these are disturbance, production, predation, herbivory, and competition. Although each of these processes has been demonstrated to

significantly impact the structure of some marine communities, unifying theories in marine ecology are generally lacking. A great deal of research has focused on the assessment of top-down and bottom-up forces in marine communities (Steele 1998; Menge 2000; Reid et al. 2000). The dramatic impacts that coastal eutrophication has had on communities worldwide is well documented (Twilley et al. 1985; Cambridge et al. 1986; Short et al. 1995; Tomasko et al. 1996). By altering the trophic structure of primary producers in a system, large-scale changes in faunal community structure has occurred as well. Additionally, the depletion and decline of large predatory species in the world's oceans has had trickle-down effects, altering the trophic structure of food webs in some communities (Pauly et al. 1998; Jackson et al. 2001; but see Steele 1998).

Theoretical investigations have shown that by manipulating the trophic structure of a system, direct and indirect effects of predation are felt on lower trophic levels, but with potentially diminished strength (Herendeen 1995; Leibold 1996). Specifically, when predators are included in systems, they directly affect the abundance of their prey through consumption. Indirectly, they affect lower trophic levels by reducing consumption pressure and allowing lower trophic levels (e.g., phytoplankton) to flourish (Carpenter et al. 1985; Carpenter and Kitchell 1993). In the absence of large predators, the abundance of small predators may increase or their behavior may change, thereby causing a decline in the abundance of prey fauna (Mittelbach et al. 1995). Although this has been documented in natural systems and procedurally shown through manipulative experiments in freshwater communities, evidence of these large-scale trophic inversions in marine systems have been difficult to identify. It is clear that top predators can have significant impacts on marine communities (see Menge 2000; Jackson et al. 2001), but an assessment of the predatory forces structuring seagrass communities has as yet not been clearly demonstrated (but see Heck et al. 2000).

Seagrass communities are important nursery grounds for many vertebrate and invertebrate species (Heck et al. 1997) and are among the most studied communities in marine systems (see

Hemminga and Duarte 2000 and references within). However, few investigations have been able to demonstrate community structuring forces by predators. While some investigations have focused on independent predator-prey interactions and the propensity of a predator to reduce prey population density (Seitz and Lipcius 2001), community-wide impacts of predators on lower trophic levels have been difficult to quantify. However, inference from other research clearly indicates that the presence or absence of large predators creates top-down impacts in marine communities (Menge 2000; Jackson et al. 2001), even though no definitive results from seagrass communities have demonstrated this potential. The research reported here addresses the potential impacts that large predators may have in a temperate seagrass system by assessing seagrass habitat characteristics and faunal distribution of three generalized trophic levels.

Study site

Research was conducted in Little Egg Harbor, New Jersey, USA, which is located in the central portion of the Mid-Atlantic Bight. Trophic web assessment was carried out during the summer of 1999 at two sites: Marsh Elder (39°35.2′N, 74°14.2′W) and Shelter Island (39°34.5′N, 74°15.5′W); these sites are situated approximately 1 km apart. Each site was characterized by expansive *Zostera marina* habitat and had been previously investigated with respect to plant and benthic faunal community structure (Bologna et al. 2000; Bologna 2006).

Materials and methods

Plant demography

To assess differences in *Z. marina* shoot density and plant biomass between sites, 15.24-cm-diameter cores ($0.01824\ \text{m}^2$) were collected ($n=8$, per site) during July and August of 1999 at Marsh Elder and Shelter Island (Table 1). The coring device was pushed into the substrate to a depth of 25 cm, capped, and removed from the sediment.

Table 1 Experimental study design

Target organisms[a]	Gear type[b]	Marsh Elder[c]	Shelter Island[c]
Large predatory fish	Gill net	11	12
Small predatory fish and invertebrates	Throw trap	12	13
Large prey	Throw trap	12	13
Small benthic prey	Benthic core	8	8
Plant demography	Benthic core	8	8

[a] Organisms targeted include large predatory fish, small vertebrate and invertebrate predators, and large and small prey

[b] Gear type includes experimental gill nets with varying mesh sizes, 1-m^2 throw traps and 15.24-cm benthic cores

[c] Values under sites represent total sampling effort for each gear at each site

Samples were processed in the field by separating plant material from the core and then freezing the samples. The remaining sediment and animal material was preserved in 95% isopropanol and stained with Rose Bengal (see section on benthic prey assessment). In the laboratory, *Z. marina* shoots were counted and plant biomass was dried to a constant weight at 60°C, then ashed at 500°C for 8 h to determine ash-free dry weight (AFDW). Algae (epiphytic and macro) and detritus were also separated from samples in order to assess overall vegetation patterns between sites. Algae and detritus were dried and ashed in the same manner as described for *Z. marina*. Shoot abundance data were square-root transformed, and vegetation biomass data were log transformed before analysis. Shoot density and biomass were compared between sites using a PROC TTEST model (Littell et al. 1991) with $\alpha=0.05$.

Large predator assessment

To determine the relative distribution of large predatory fish within each study region, experimental gill nets were deployed during July and August 1999. These nets consisted of five regions varying in mesh size. Each region was 7.62 m long and 2.44 m deep and consisted of five individual panels within the net and sections having 2.54-, 3.8-, 5.08-, 6.35- or 7.62-cm mesh gill net openings. Gill nets were deployed at various locations within each site and during a variety of tidal stages during the day to assess the large-scale trophic structure of each site. Nets were allowed to fish between 1 and 2 h. Early deployments were for 2 h, but during retrieval several fish caught in the nets had been scavenged by blue crabs. Consequently, net deployment time was reduced to 1 h to limit loss to crabs. A total of 11 gill-net deployments occurred at Marsh Elder and 12 deployments occurred at Shelter Island (Table 1). The number of fish recovered, species identification, and total length were recorded for each net deployment. A catch per unit effort (CPUE) was calculated and standardized for in-field deployment time (no. of fish h^{-1}). CPUE was compared between sites using a *t*-test on square-root transformed data.

The feeding preference of each collected fish was assessed through an examination of stomach and digestive tract contents. Each predatory fish was returned to the laboratory, re-measured, and dissected immediately. Gut contents of individual fish were identified to the lowest possible taxa.

Large prey-small predator assessment

The abundance of large prey organisms and small predators was assessed using 1-m^2 throw traps. During July and August, throw traps were deployed haphazardly at Marsh Elder ($n=12$) and Shelter Island ($n=13$). After deployment, throw traps were sampled using a 1-m bar seine with a 1-mm mesh. The throw traps were swept consecutively until the bar seine yielded no organisms. This was repeated until three successive passes yielded no organisms. Samples were held on ice and brought to the laboratory. All organisms were identified to the lowest possible taxa and enumerated. Faunal density between sites was compared using a *t*-test. Count data were square-root transformed before analysis to eliminate heteroscedacity. The significance level for all analyses was determined at $\alpha=0.05$.

Benthic prey assessment

Faunal abundance and species composition were assessed using the cores collected for the assessment of plant demography. Eight replicate cores (15.24 cm in diameter) were collected at each site. The cores were used to assess epibenthic and infaunal prey. Specifically, the nonplant portion of these cores was sieved to retain organisms > 710 µm, preserved in 95% isopropanol, and stained with Rose Bengal. Crustaceans and molluscs were identified to the lowest possible taxonomic level, while polychaetes and oligochaetes were condensed into a broad category, annelids. Total faunal density and identified taxonomic group density were analyzed using a *t*-test. Count data were square-root transformed before analysis to eliminate heteroscedacity. The significance level for all analyses was determined at α=0.05.

Community level response

To determine overall differences in faunal community structure between sites, an analysis of similarities (ANOSIM) and a non-metric multidimensional scaling plot (MDS) were conducted on throw trap and benthic core data using the algorithms in PRIMER 5.2 software. The significance level for the analyses was determined at 0.1% sample significance (Clarke and Gorley 2001). Post-ANOSIM, a similarity of percentages (SIMPER), was conducted to assess the relative relatedness of samples from different sites.

Results

Plant demography

The assessment of plant demography between sites revealed no significant differences in shoot density (t_{14}=0.41, $p > 0.68$) or plant biomass ($t = 1.8$, $p > 0.09$). Shoot density was greater at Marsh Elder, while plant biomass was greater from Shelter Island (Fig. 1). No differences were observed in algal biomass ($t = 1.37$, $p = 0.19$) or plant detritus ($t = 0.36$, $p = 0.72$).
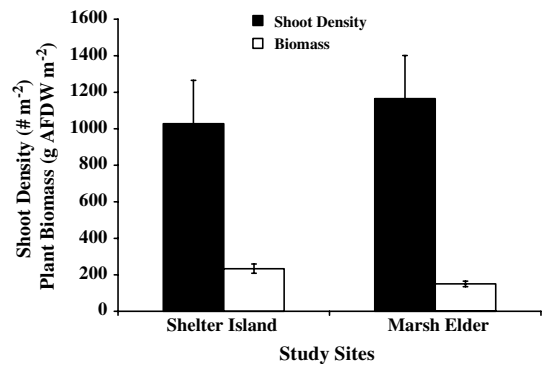

Fig. 1 Plant demography of *Zostera marina*. Values represent average plant biomass and shoot density from cores collected at each site expressed as average value per square meter (± SE)

Large predators

The abundance of predatory fish and the richness of the species were greater at Marsh Elder than at Shelter Island. A total of 28 fish was collected by the experimental gill nets, including species such as weakfish (*Cynoscion regalis*), summer flounder (*Paralichthys dentatus*), striped bass (*Morone saxatilis*), tautog (*Tautoga onitis*), northern puffer (*Sphoeroides maculatus*), bluefish (*Pomatomus saltatrix*), and croaker (*Micropogonias undulatus*). All species, except tautog, were collected at Marsh Elder, while only weakfish and tautog were collected from Shelter Island. Catch Per Unit Effort was significantly greater at Marsh Elder than at Shelter Island (t_{21}=3.0, $p < 0.007$; Fig. 2a).

The analysis of predator feeding preference (Table 2) indicated that weakfish fed heavily on blue crabs (*Callinectes sapidus*) with additional food resources, including grass shrimp (*Palaemonetes* spp., *Hippolyte zostericola*), sand shrimp (*Crangon septemspinosa*), silversides (*Menidia menidia*), and Atlantic awning clams (*Solemya velum*). The diet of the summer flounder diet was similar to that of the weakfish (Table 2), but also included pipefish (*Syngnathus fuscus*) as a major portion of the identified diet. Interestingly, the stomach contents of the striped bass contained only grass shrimp. Of the remaining four individuals, blue crabs had scavenged both bluefish and croaker and, consequently, the stomach contents could not be assessed. However, the
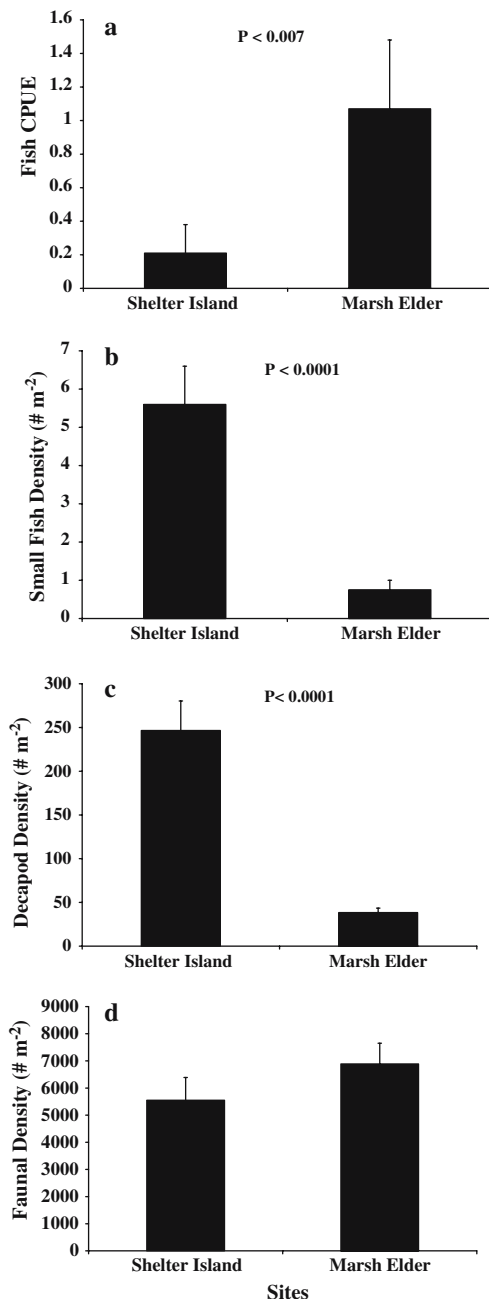
Fig. 2 Comparative abundance of major trophic components of the *Z. marina* community as determined from each of the collection techniques. Values are expressed as averages ± SE. **a** Large predatory fish (gill net), **b** small predatory fish (throw trap), **c** decapods (throw trap), **d** small benthic prey (core). Note: the *Y*-axis varies for each graph

northern puffer stomach contained blue crabs, while the tautog contained one grass shrimp and 14 amphipods.

Large prey-small predator abundance

Dramatic differences were seen between sites with regards to the abundance of large benthic prey and the abundance and species richness of small fish predators (Table 3; Fig. 2b, c). Specifically, densities of grass shrimp (*Palaemonetes* spp. and *Hippolyte zostericola*) were significantly greater at Shelter Island than at Marsh Elder (t_{23}=5.7, $p < 0.0001$), and densities of blue crabs (*Callinectes sapidus*) were almost threefold greater at Shelter Island (t=1.96, p=0.06). The only significant deviation from this pattern was for sand shrimp (*Crangon septemspinosa*), which showed significantly greater densities at Marsh Elder than at Shelter Island (t=2.9, $p < 0.008$). Overall, the density of small benthic predatory fishes was significantly greater at Shelter Island (t=4.5, $p < 0.0001$; Fig. 2b) as was average species richness and total species richness (Table 3). Densities of individual fish species also differed between sites with significantly greater densities recorded at Shelter Island for *Syngnathus fuscus* (t=3.6, $p < 0.001$), *Tautog onitus* (t=2.4, $p < 0.03$) and *Opsanus tau* (t=2.2, $p < 0.04$).

Small prey

The density of small benthic prey varied among individual taxa between sites (Table 4), but was generally greater at Marsh Elder (Fig. 2d). In fact, prey densities were significantly greater at Marsh Elder for the crustaceans – *Ampelisca* spp. (t_{14} = 3.16, $p < 0.007$), Phoxocephalidae (t=2.75, $p < 0.015$), and *Cyathura polita* (t=4.6, $p < 0.0004$) – and for the broad category Annelida (t=2.3, $p < 0.04$; Table 4). Additionally, total Isopod density (e.g., *Erichsonella* spp., *Idotea* spp.) and total Decapod density (e.g., Xanthidae, *Callinectes sapidus*, *Libinia* spp.) were significantly greater at Marsh Elder than at Shelter Island (t=3.5, $p < 0.003$; t=4.17, $p < 0.001$, respectively). Only Caprellid amphipods showed significantly greater densities at Shelter Island (t=5.2, $p < 0.0001$).

Community level response

Results from the ANOSIM revealed the existence of significant differences in the

Table 2 Predator feeding analysis[a]

Predator	n	Size SL (cm)	Grass shrimp (*Palaemonetes* spp. and *Hippolyte* spp.)	*Callinectes sapidus*	*Syngnathus* spp.	Miscellaneous taxa
Cynoscion regalis	14[b]	47.1 ± 6.8	1.13 ± 2.5	2.63 ± 2.1	0	*Crangon septimspinosa*, *Menidia* spp., *Solemya velum*
Paralichthys dentatus	8[c]	28.4 ± 6.8	3.86 ± 3.4	0.28 ± 0.5	0.28 ± 0.5	*Crangon septimspinosa*, *Menidia* spp.
Morone saxatilis	3	38.2 ± 3.4	51.0 ± 32.2	0	0	

[a]Data presented are based on the most abundant predators identified in the study. Values represent the average number of a prey items in the digestive tract (mean ± SD). Miscellaneous taxa represent items present in at least one individual fish for a given species, but not sufficiently abundant to classify as a separate food item

[b]Three *Cynoscion regalis* stomachs were devoid of food, but included for average prey abundance

[c]One *Paralichthys dentatus* stomach was devoid of food, but included for average prey abundance

Table 3 Density distribution[a] of taxa collected by 1-m[2] throw traps

Species	Marsh Elder	Shelter Island
Palaemonetes spp.***	26.8 ± 4.7	190.3 ± 27.3
*Hippolyte zostericola***	5.7 ± 0.9	51.8 ± 7.9
Crangon septemspinosa[b]**	4.7 ± 0.8	1.2 ± 0.8
Callinectes sapidus	0.9 ± 0.25	2.6 ± 0.8
Carcinus maenas	0.08 ± 0.08	0
Hemigrapsus sp.	0	0.3 ± 0.17
Xanthidae	0.17 ± 0.17	0.23 ± 0.17
Libinia spp.	0	0.07 ± 0.07
*Syngnathus fuscus***	0.67 ± 0.26	3.8 ± 0.8
*Tautoga onitis**	0	0.8 ± 0.3
Opsanus spp.*	0	0.3 ± 0.13
Pseudopleuronectes americanus	0	0.3 ± 0.17
Ophidion marginatum	0	0.07 ± 0.07
Apeltes quadracus	0	0.23 ± 0.17
Gobiosoma bosci	0.08 ± 0.08	0
Total abundance***	39.1 ± 5.1	252.2 ± 34.1
Average species richness*	4.3 ± 0.19	5.6 ± 0.4

Asterisks after species represent significant differences in means between sites: *$p < 0.05$, **$p < 0.01$, ***$p < 0.001$

[a]Values represent mean number of individuals per throw trap ± SE

[b]Significantly greater values from Marsh Elder compared to Shelter Island

community level fauna between sites based on the throw trap data (Global $R=0.87$, $p < 0.01\%$) and the benthic core data ($R=0.68$, $p < 0.1\%$). The MDS plots show low levels of stress (0.08 and 0.16, respectively) and complete spatial separation for both data sets (Fig. 3). These results demonstrate that the faunal communities between sites were different. The SIMPER analysis showed an average dissimilarity of 59.1% for the benthic core and a 72.1% dissimilarity for the throw traps.

Discussion

The effects of top-down forces in marine communities have often related to the impacts that predators – or the lack thereof – have on the distribution of lower trophic levels. Perhaps one of the best known trophic structuring relationships is the impacts of sea star predation in intertidal communities, which gave rise the ecological concept of the keystone predator (sensu Paine 1966). In this case, changes in the distribution of a single species resulted in significant

Table 4 Benthic prey abundance[a]

Species	Marsh Elder	Shelter Island
Aoridae	26.4 ± 6.6	16.8 ± 7.5
Ampelisca spp.*	10.1 ± 2.7	2.0 ± 1.0
Melitidae	2.0 ± 1.3	9.7 ± 5.3
Phoxocephalidae*	5.4 ± 1.6	1.0 ± 0.4
Haustoriidae	0.4 ± 0.4	0.9 ± 0.5
Lysianassidae	0.5 ± 0.5	0.3 ± 0.2
Caprellidae[b]*	1.1 ± 0.6	16.9 ± 3.9
Cyathura polita⁎	3.4 ± 0.9	0.1 ± 0.1
Ostracoda	3.4 ± 2.2	4.6 ± 1.5
Annelida*	54.5 ± 11.8	28.1 ± 7.0
Total gammarid amphipods	45.1 ± 11.2	34.3 ± 9.4
Total Isopoda*	8.6 ± 1.3	3.8 ± 0.8
Total Decapoda*	2.1 ± 0.5	0.4 ± 0.2
Total abundance	125.6 ± 13.9	101.2 ± 15.3
Species richness	13.0 ± 1.32	13.75 ± 1.05

Asterisks represent significant differences in means between sites at*$p < 0.05$

[a]Assessment of the relative abundance of the major taxonomic groups collected in benthic cores, as well as the summary for gammarid amphipods, Isopoda, Decapoda, and total prey abundance. Values represent mean number of individuals per core ± SE

[b]Significantly greater values from Shelter Island compared to Marsh Elder
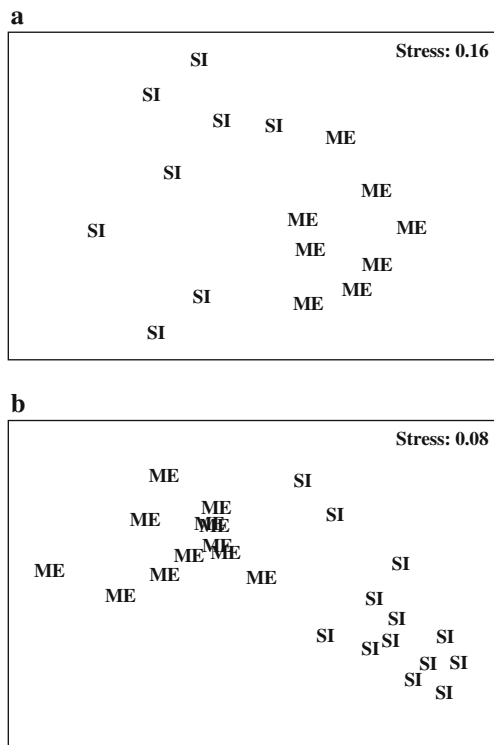
Fig. 3 Non-metric MDS configuration of the faunal community structure between sites. **a** Results based on throw trap data, **b** results based on benthic core data. *SI* Shelter Island, *ME* Marsh Elder Island

community shifts. While a discussion of keystone species would lead to examples from numerous studies (Duggins 1983; Kaufman 1992; Menge et al. 1997), their impacts have generally been seen from hard substrate and macroalgal communities (see reviews by Elner and Vadas 1990; Menge 2000). Given that marine communities are complex with multiple trophic levels, substantial omnivory, and organisms potentially feeding at several trophic steps, it has proven to be very difficult to describe top-down effects in other marine communities (see Heck et al. 2000; Seitz and Lipcius 2001). The response of a community to the elimination of a top predator has often led to other members of the guild filling in and re-establishing the general community structure, until those species are significantly reduced in stock to cause major changes in the ecosystem (Jackson et al. 2001).

Trophic structure assessment in the system reported here yielded intriguing results. While algal biomass and plant demography did not differ between sites (Fig. 1), the difference in large predatory fish CPUE showed significant predation potential impacts on the community as a whole. The presence of these fish had the potential to reduce the density of large invertebrate

prey and the density of small predatory fish (Table 3; Fig. 2b, c). This response in trophic structure alteration was similar to those seen associated with regions that have undergone overfishing of large predatory species (see Dayton et al. 1995). The subsequent differences between the sites studied with respect to small predatory fish and invertebrates provide a proximal process which may be determining the differences in small benthic prey. While total benthic prey abundance did not differ significantly between sites (Fig. 2d), several important taxonomic groups did show significant declines in density. Specifically, annelid worms and several crustacean taxonomic groups showed significantly greater densities at Marsh Elder than at Shelter Island (Table 4). While these differences in individual taxa between the sites is compelling, the substantial differences seen in overall faunal community structure is striking (Fig. 3). The ANOSIM revealed that significant differences existed between sites for both small predators/large prey and small benthic prey. As such, these differences demonstrate that despite similar floral characteristics, faunal community structure was vastly different between these sites. The most probabilistic mechanism causing this divergence in community structure is the difference in the abundance of large predatory fish at Marsh Elder. Consequently, the relative abundance of predatory fish at each site provides evidence of top-down control of faunal communities in this seagrass system (sensu Herendeen 1995; Leibold 1996), and the results presented are very similar to the trophic inversions seen in fresh water systems (Mittelbach et al. 1995).

The assessment of predator gut contents indicated that striped bass, weakfish, and summer flounder fed heavily upon crustacean prey (Table 2). Based on the distribution of these predators between sites (Fig. 2a), this alone provides a proximal mechanism to describe the differences in density of blue crabs, grass shrimp, and pipefish (Table 3; Fig. 2c). However, food habits of the identified top predators cannot explain the differences in the relative abundance of small predatory fishes between sites. Although summer flounder did feed on pipefish, the remaining predatory fish did not appear to be

feeding on these smaller fish (Table 3). This does not mean that these smaller fish were not part of their diet, but rather they were not represented in the fish sampled. Possible explanations of these differences in density between sites may be predator avoidance. Mittlebach and Chesson (1987) showed that in the presence of large predators, sunfish emigrated to regions of low predator abundance. Consequently, it may be possible that the abundant large predators at Marsh Elder may have had a direct effect on small predatory fish through consumption and an indirect effect of causing them to emigrate elsewhere. Regardless of the mechanism, these predators would exert top-down control of lower trophic levels.

In previous marine studies, top-down effects were determined by comparing areas where large predatory organisms have been eliminated and comparing the resultant trophic structure with regions which have had only limited reduction in predator abundance (Sala et al. 1998). In some cases, clear impacts were visible on the overall community structure (see Menge et al. 1994; Pauly et al. 1998), while in others, generalist feeders became abundant without creating a disruption in the community structure (see Menge 2000). Perhaps the most perplexing observation in the present study is that these two sites differed so dramatically in the CPUE of predatory fish. The demography of the *Z. marina* habitat did not differ significantly, but epibenthic prey densities at Shelter Island were almost an order of magnitude greater. This would indicate that food limitation was not a factor in determining the distribution of the predatory fish. Consequently, I was unable to determine the mechanism that created this difference in large predator abundance. It is possible that differences in temperature, salinity, current velocity, sediment size, or some other abiotic factor may have impacted on the distribution of predatory fish. Regardless of the mechanism creating the site differences in predator abundance, the resultant changes in community structure were evident, and the overall impact that these predators had on the system was undeniable.

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