Predator effects on faunal community composition in shallow seagrass beds of The Bahamas

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ABSTRACT

Much emphasis has been placed on predator effects that cascade through food webs. Such top-down effects seem to be most common in systems with relatively simple food chains, and rarer in species-rich systems where numerous weak interactions among species can buffer strong top-down effects. Seagrass ecosystems are typically species-rich and characterized by complex food webs, but evidence of top-down effects in these systems has been mixed. We examined effects of predatory fishes on the species richness, biomass, density, and composition of the epifaunal community in a shallow seagrass ecosystem of The Bahamas. We used exclusion experiments at two different spatial scales, and applied mesh sizes that excluded different-sized predator individuals. We found some evidence of species-level top-down effects (i.e., strong interactions within a subset of the community), driving higher biomass in at least one decapod mesopredator. In contrast, community-level predator effects were rather weak, with predator size and spatial scale of experiments displaying no detectable impact on the overall epifaunal community. Multiple factors may have contributed to these patterns, including high species richness, relatively shallow water depth, small-scale spatial variation in habitat features, and the size and abundance of predators. Because of the rapid global decline of seagrasses and their associated fauna, increased knowledge of predator effects on faunal communities of seagrass beds is critical for long-term conservation efforts.

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1. Introduction

Much emphasis has been placed on the cascading effects of predators in food webs (Polis et al., 2000), and strong top-down effects have been documented in many aquatic ecosystems (Strong, 1992). Often these systems are relatively simple, low-diversity, food webs with little omnivory or intraguild predation (Chase, 2000; Finke and Denno, 2005; Fox, 2007; Heck and Valentine, 2007; Polis and Strong, 1996; Shurin et al., 2002, 2006). Examples of strong top-down effects have been well documented in freshwater lentic and marine benthic systems, rocky intertidal zones and kelp forests (Estes et al., 1998; Paine, 1966; Shurin et al., 2002). Conversely, more species-rich ecosystems seem less likely to have such strong top-down effects, largely because of their inherently reticulate food webs with many weak interaction links (McCann et al., 1998; Strong, 1992).

Seagrass beds are species-rich ecosystems that provide food and shelter for numerous ecologically and economically important organisms (Beck et al., 2001; Orth et al., 1984). Evidence of predator effects on food web structure in these ecosystems has been mixed, with some studies suggesting strong (Ambrose, 1984; Douglass et al., 2007; Duffy et al.,

2005; Heck et al., 2000; Hindell et al., 2000; Moksnes et al., 2008), and others weak or no top-down effects on faunal seagrass communities (Gacia et al., 1999; Hindell et al., 2001; Leber, 1985; Moore and Hovel, 2010; Summerson and Peterson, 1984; Valentine et al., 2008). Predator effects in seagrass ecosystems have been suggested to be rather weak because other factors may be more important in structuring food webs, such as landscape context (i.e., the spatial position of a given patch within a larger mosaic of habitats or landscape features, Turner, 1989) or structural complexity of seagrass beds (Leber, 1985; Moore and Hovel, 2010; Orth et al., 1984; Rypel et al., 2007; Summerson and Peterson, 1984). In contrast, high local abundance of predatory fishes may override these factors and result in strong top-down effects (Hindell et al., 2001).

Predator body size range (Costa, 2009) may be another factor mediating the strength of top-down effects in seagrass systems. In terrestrial, freshwater and temperate marine ecosystems, relative predator size has been shown to play an important role in regulating prey communities (Langlois et al., 2006; Magnusson and Williams, 2009; Perez et al., 2009; Radloff and Du Toit, 2004; Rudolf, 2006; Winkler and Greve, 2004). Understanding the divergent effects of large- versus small-bodied predators on top-down regulation of food webs is critical as human activities (e.g., overexploitation, habitat degradation) alter the size structure of marine organisms (Knowlton and Jackson, 2008; Pauly et al., 1998; Worm et al., 2006).

Studies examining predator effects in seagrass beds have focused primarily on subtidal systems with water depths >1 m (Gacia et al., 1999; Heck et al., 2000; Hindell et al., 2000; Leber, 1985; Moore and Hovel, 2010). However, the role of predation may be rather different when predator access is constrained temporally, for instance, by water depth variation during a tidal cycle. In The Bahamas, for example, seagrass beds are common in extremely shallow, subtidal, wetlands with water depths as low as <0.1 m at low tide (Hammerschlag-Peyer and Layman, 2010; Rypel et al., 2007). In these systems, most fish predators can only forage in seagrass beds at high tide, and are restricted to deeper refuge areas, such as sink holes or mangrove-lined channels, during lower tidal levels (Hammerschlag-Peyer and Layman, 2010).

We examined predator effects on the seagrass epifaunal community in a shallow Bahamian wetland system. We employed exclusion experiments at two different spatial scales, and utilized mesh sizes that excluded different-sized predator individuals, to investigate how predatory fishes affected species richness, biomass and density, and community composition of the epifaunal community. Given the high abundance of predatory fishes, especially schoolmaster (*Lutjanus apodus*) and gray snapper (*Lutjanus griseus*), in this study system, we hypothesized strong predator effects on the epifaunal community. Furthermore, because these predators have been observed to shift their diet through ontogeny (Hammerschlag et al., 2010; Hammerschlag-Peyer and Layman, 2012; Starck and Schroeder, 1971), we also expected to see divergent responses between the two exclusion treatments.

2. Materials and methods

We examined effects of predatory fishes using exclusion experiments at two spatial (and temporal) scales: 1) "small-scale" (0.77 m² treatment area, 34 days, Figs. 1A), and 2) "medium-scale" (19.6 m² treatment area, 77 days, Fig. 1B). Both manipulations were conducted in the subtidal region of seagrass beds in Jungle Creek (26°21′36″N, 77°00′58″W), a seagrass- and mangrove-dominated tidal wetland, locally called "tidal creek" on the east side of Abaco Island, Bahamas. Jungle Creek is lined by mangroves (predominantly *Rhizophora mangle*) and the most prevalent benthic habitat types are seagrass beds (primarily *Thalassia testudinum*), submerged mangrove prop roots and sand flats. The system has a semi-diurnal tidal regime and mean daily tidal amplitude of ~0.8 m. Most of the seagrass areas have low tide depths <0.1 m. Consequently, fish predators were only able to access the seagrass beds twice daily for ~3–4 h around high tide (depending on individual body size), and were restricted to deeper refuge areas, such as mangrove-lined channels, during lower tidal levels (Hammerschlag-Peyer and Layman, 2010).
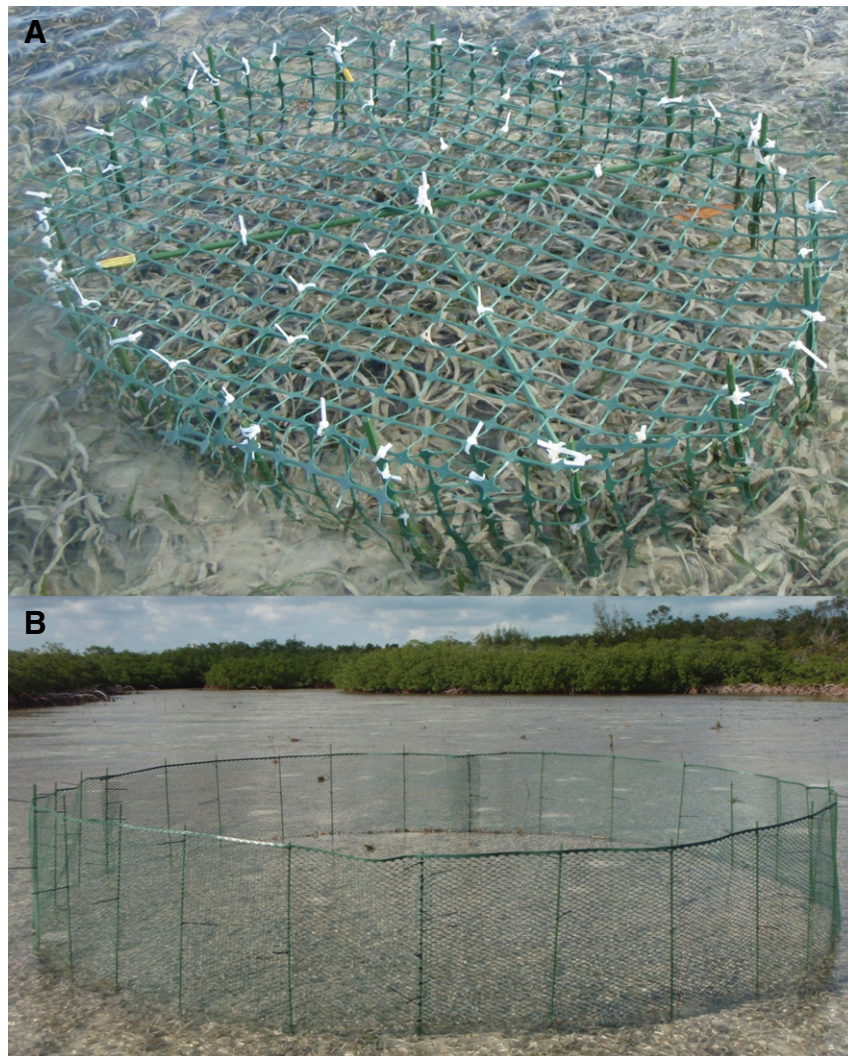
Fig. 1. Pictures of the A) large-predator (LPE) and B) small-and-large-predator (SPE + LPE) exclusion treatments of the small-scale and medium-scale experiment, respectively. Exclusion "cage" dimensions: A) 1.16 × 0.85 × 0.3 m (length × width × height), and B) 5 × 1.2 m (diameter × height). Treatment "cages" in the small-scale experiment were covered because height of cage was lower than water depth at high tide.
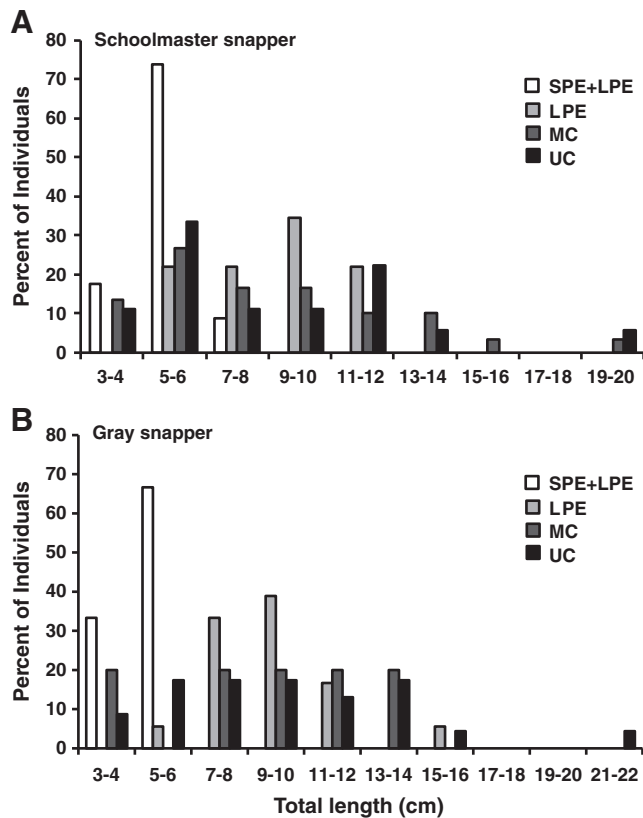
Fig. 2. Size-frequency distribution of A) schoolmaster snapper (*Lutjanus apodus*) and B) gray snapper (*L. griseus*) observed during underwater surveys of the medium-scale experiment in the four different treatments: SPE + LPE = small-and-large-predator exclusion, LPE = large-predator exclusion, MC = manipulated control, and UC = unmanipulated control. Bins included 2 cm total length (TL) starting at 3 cm TL.

The most abundant fish predators in Jungle Creek were schoolmaster (*L. apodus*) and gray snapper (*L. griseus*) (>90% of total predator biomass, Fig. 2) which are generalist species that have been observed to feed primarily on benthic invertebrates and small teleost fishes in these seagrass systems (Hammerschlag-Peyer and Layman, 2012; Hammerschlag-Peyer et al., 2011; Layman and Silliman, 2002; Layman et al., 2007). These species mostly consist of juveniles (schoolmaster: <12.5 cm standard length (SL); gray: <10 cm SL) and sub-adults (schoolmaster: 12.5–25 cm SL; gray: 10–20 cm SL; Hammerschlag-Peyer et al., 2011; Hammerschlag et al., 2010; Yeager and Layman, 2011), likely because larger individuals move to deeper habitats, including coral reefs, as they grow (Nagelkerken et al., 2000; Sheridan and Hays, 2003). Other epibenthic predators observed at the study site were cubera snapper (*L. cynopterus*), sergeant major (*Abudefduf saxatilis*), blennies (Blenniidae), slippery dick (*Halichoeres bivittatus*), mojarras (including *Gerres cinereus* and *Eucinostomus* spp.), and grunts (Haemulidae), all of which were far less abundant than schoolmaster and gray snapper. Jungle Creek is not adjacent to human settlements (Stoner et al., 2011) and thus experiences little fishing pressure.

Four treatments were employed in both the small- and medium-scale experiments: unmanipulated control (UC), manipulated control (MC), large-predator exclusion (LPE, Fig. 1A) and small-and-large-predator exclusion (SPE + LPE, Fig. 1B). The LPE and SPE + LPE consisted of green plastic fence material (Landware®) of 5 × 5 cm and 2 × 2 cm mesh size, respectively (Fig. 1). Presumably, these mesh sizes would exclude larger fishes, yet allow for free movement and recruitment of most epibenthic fauna (*e.g.*, small fishes, crabs, shrimps, snails, mussels). The effectiveness of the predator exclusion treatments was assessed using underwater visual census with mask and snorkel (Brock, 1954;

Layman et al., 2004) during the medium-scale experiment. At high tide, one diver (CAL or JEA) slowly approached the experimental areas from which the entire experimental area could be surveyed. After waiting ~1–2 min for fishes to acclimate to the diver's presence, a snapshot survey (single time point observation) was taken with each fish's identity and size recorded. The surveys were not intended as quantitative estimates of density, but instead for relative size structure of observed fishes in each experimental area. Data were combined across blocks and survey dates to provide an overall relative frequency of fish size classes observed.

These surveys suggested that LPE and SPE + LPE excluded different-sized fish predators (Fig. 2). For example, schoolmaster snapper (*L. apodus*) ≤8 cm total length (TL) and gray snapper (*L. griseus*) ≤6 cm TL were observed feeding in the SPE + LPE treatment, whereas schoolmaster snapper ≤12 cm TL and gray snapper ≤16 cm TL were seen feeding in the LPE treatment (Fig. 2). Individuals that were able to forage in the SPE + LPE treatment were considered to be too small to substantially affect the epifaunal community that we sampled. Specifically, gray and schoolmaster snapper ≤8 cm and ≤6 cm TL, respectively, feed on small (<4 mm) epifaunal organisms (*e.g.*, copepods, small caridean shrimp; Starck and Schroeder, 1971) that were not sampled in this study (see below).

MC treatments included approximately the same amount of fencing material with both mesh sizes, but had gaps on the sides allowing fish predators of all sizes to move freely in and out of the experimental area. UC treatments consisted of no "cage" material (no fencing or rebar stakes, except one stake to mark the treatment location), but were comparable to the other treatments in terms of percent seagrass cover, distance to seagrass edge and water depth.

2.1. Small-scale experiment

We employed a randomized block design, with each block (n = 4) located ~50 m apart. The blocks were set up June 20th–23rd 2008. Within each block, the four treatments (SPE + LPE, LPE, MC, and UC) were randomly assigned to four *a priori* identified sub-sites. The exact treatment locations were selected in an attempt to minimize differences in water depth, distance to seagrass edge and percent cover of *T. testudinum* (≥80%), since these factors have previously been shown to affect faunal seagrass communities and predation rates (Moore and Hovel, 2010; Orth et al., 1984; Rypel et al., 2007).

The SPE + LPE, LPE and MC treatments were constructed in an oval shape (1.16 × 0.85 × 0.3 m, maximum length × maximum width × height) using plastic fencing material, rebar stakes and plastic ties (Fig. 1A). Sixteen 0.6 m-long and 1 cm-thick rebar stakes were spaced in equal intervals and the fencing material of the entire oval was pushed ~5 cm into the substrate. Compared to SPE + LPE and LPE, MC had one large gap on each side of the simulated exclosure to allow the free movement of all organisms in and out of the experimental area. Since the fencing height was ~0.3 m (lower than the water depth at high tide), the top of each cage was covered using two crossing 1.2 m-long rebar stakes and fencing material.

After 34 days, an oval throw trap (1.16 × 0.85 × 1 m, length × width × height), with solid plastic sides, was placed over each treatment area during low tide. After removal of the fencing material and rebar stakes, we recorded percent cover of *T. testudinum* within the throw trap. The area enclosed in the throw trap was sampled with two dip nets (4 mm and 10 mm mesh) until three consecutive dips yielded no organisms. Since the smallest dip net had a mesh size of 4 mm, we collected epibenthic organisms that were retained by this mesh size. All sampled organisms were immediately put on ice and later frozen. In the laboratory, organisms were sorted and identified to the lowest taxonomic level possible. We then measured, dried (60 °C), and weighed each organism to obtain dry biomass (g m^{-2}). For all mollusks, only the soft tissue was measured for biomass.

2.2. Medium-scale experiment

A randomized block design was employed in the second experiment, with distances between blocks 130–530 m. Treatments (SPE + LPE, LPE, MC, and UC) were constructed from February 13th–16th 2009 (one block per day). The treatment "cages" were constructed as 5 m-diameter circles with 1.8-m rebar stakes spaced in 0.5-m intervals (Fig. 1B). The same fencing material was applied as in the small-scale experiment and was pushed ~5 cm into the substrate after cage construction. The height of the fencing (~1.2 m) exceeded the height of the highest spring tides, and thus tops were not necessary. No birds were observed in or around any experimental area during the study period, as bird densities are relatively low in these creek systems (Chacin et al., in review). The "cage" of the MC treatment had a 1-m opening every ~2 m to allow the free movement of organisms of all sizes in and out the experimental area. Using the same throw trap as in the small-scale experiment, we collected three subsamples per treatment after 77 days of deployment (3 subsamples × 4 treatments × 4 blocks = 48 subsamples). Data collection and sample processing were performed as in the small-scale experiment.

2.3. Data analysis

All data were tested for normality (Shapiro–Wilk test) and homogeneity of variance (Bartlett test) in R version 2.12.2 (R-Development-Core-Team, 2008). Data that failed to meet these assumptions were transformed and reassessed.

For both experiments, we examined the effect of treatment and block on 1) species richness (# of species m^{-2}), 2) biomass (g m^{-2}), 3) density (# of individuals m^{-2}), and 4) composition of epifaunal community. For the medium-scale experiment, the three sub-samples of each treatment were averaged to obtain a mean value for each response variable. The averaging of sub-samples can provide the same results as nested analyses if the analyses are completely balanced and performed at the lowest experimental scale (Montgomery, 2009). Hence, the sample size was n = 4 (4 samples/treatment/block) for both exclusion experiments. We omitted sea cucumbers (Holothuria sp., n = 27, total dry weight = 250 g), sponges (Porifera, total dry weight = 1026 g), and one large spider crab (Majidae, total dry weight = 23 g) from the analyses because these taxa were unlikely prey of the excluded predators and their high biomass may have skewed analyses.

2.4. Univariate analyses

First, we tested for cage effects by comparing 1) species richness, 2) biomass and 3) density between the manipulated (MC, caged area) and unmanipulated control (UC, uncaged area) following Hindell et al. (2001). These comparisons were a priori planned to test for differences among caging levels. With this approach, if controls do not differ significantly (i.e., no cage effect), exclusion treatments are compared to the average of the manipulated and unmanipulated controls. If the controls differ significantly (i.e., cage effect), the exclusion treatments are compared to the manipulated controls. Effects of treatment and block on the response variables were then analyzed using randomized-block ANOVA. If significant effects among treatments or blocks were found, Tukey's post-hoc test was applied.

2.5. Multivariate analyses

For community structure analysis, rare taxa (<3% of total biomass and density, respectively) were omitted (Clarke and Warwick, 1994). Taxa used for the community structure analysis are shown in Table 1. Biomass and density of taxa were ln(x + 1)- and sqrt(x + 1)-transformed, respectively, and similarity matrices on biomass and density data were constructed using standardization and the Bray–Curtis similarity

coefficient. Treatment and block effects were separately tested on biomass and density data of the epifaunal taxa using ANOSIM without replication (i.e., Spearman rank correlation method, with test statistic = ρ) in PRIMER 5.2.9 (Clarke and Warwick, 1994). Statistical significance was tested at $\alpha = 0.05$.

3. Results

We identified 60 species from 49 families in the small-scale experiment, and 68 species from 57 families in the medium-scale experiment. In total, we collected 951 (357 g) and 4927 (1025.6 g) individuals in the small- and medium-scale experiments, respectively. The dominant organisms in terms of biomass and density (averaged across all treatments and blocks) found in both experiments are given in Tables 2A and 2B. No cage effects were found on species richness, total biomass, and total density in both experiments (p > 0.05). Hence, exclusion treatments were compared to the average of the manipulated and unmanipulated controls (herein referred to as average control, AC).

3.1. Univariate analysis

There was a treatment effect on species richness in the medium-scale experiment (ANOVA: $F_{2,3} = 5.32$, $P = 0.047$; Table 3, Fig. 3D). Tukey's post-hoc test revealed that the SPE + LPE was lower than the AC treatment, although only marginally (Tukey: $P = 0.053$; Fig. 3D). Organism density was different among blocks in the small- and medium-scale experiment (Table 3), with density being higher in Block 4 than in Block 3 in the small-scale experiment (Fig. 4A), though only marginally significant (Tukey: $P = 0.052$). In the medium-scale experiment, total density was significantly higher in Block 2 compared to Block 1 (Tukey: $P = 0.04$, Fig. 4B) and Block 4 (Tukey: $P = 0.04$, Fig. 4B). No treatment or block effects were observed on biomass in either experiment or for species richness in the small-scale experiment (Table 3).

Table 1
Taxa (marked "x") that contributed ≥3% to the overall biomass and density and were included in the community analysis (relative biomass and density for the small-scale and medium-scale exclusion experiment). Taxa are organized phylogenetically.

Scientific name	Common name	Small-scale		Medium-scale	
		Biomass	Density	Biomass	Density
Cerithium spp.	Sea snail		x	x	x
Gastropoda[a]	Sea snails other than Cerithium spp.		x	x	x
Codakia spp.	Marine mussel	x	x		x
Lucina spp.	Marine mussel				x
Bivalvia[b]	Marine mussels other than Codakia spp. and Lucina spp.			x	x
Phascolion sp.[c]	Hermit sipunculid		x	x	x
Oligochaeta	Annelids				x
Amphipoda	Amphipods		x		
Alpheus sp.	Snapping shrimp	x	x	x	x
Palaemonetes sp.	Grass shrimp		x		x
Squilla sp.	Mantis shrimp		x		
Panopeus sp.	Mud crab	x	x	x	x
Xanthidoidae	Mud crabs other than Panopeus sp.			x	x
Portunidae	Swimming crabs			x	
Pitho sp.	Urn crab	x	x	x	
Dromidia sp.	Decorator crab			x	
Majidae[d]	Spider crabs				x
Ophiurida	Brittle stars		x	x	x
Anguilliformes	Eels			x	
Gobiidae/Blenniidae	Gobies and Blennies	x	x	x	x
Pomacentridae	Damselfish	x			

[a] Modulus sp., Tegula sp., Bulla sp. and Cerodrillia sp.
[b] Galeommatidae, Tellinidae, and Glycymeris spp.
[c] Unsegmented worm that inhabits abandoned shells, in this study mostly in Cerithium spp. shells.
[d] Pitho sp., Dromidia sp., and Mithrax sp.

Table 2A
Dominant organisms in terms of biomass (averaged across all treatments and blocks) in the small- and medium-scale experiment.

Experiment	Rank	Species	Common name	Biomass (g m^{-2})	Percent of overall biomass
Small-scale	1	*Panopeus* sp.	Mud crab	6.2	44
	2	*Pitho* sp.	Urn crab	3	21
	3	Gobiidae	Gobies	2	14
	4	*Alpheus* sp.	Snapping shrimp	1	7
Medium-scale	1	*Panopeus* sp.	Mud crab	4.2	41
	2	*Phascolion* sp.	Hermit sipunculid	1	10
	3	Portunidae	Swimming crabs	0.9	9
	4	*Cerithium* spp.	Cerith snails	0.8	8

Table 2B
Dominant organisms in terms of density (averaged across all treatments and blocks) in the small- and medium-scale experiment.

Experiment	Rank	Species	Common name	Density (# ind. m^{-2})	Percent of overall density
Small-scale	1	*Alpheus* sp.	Snapping shrimp	18	25
	2	*Palaemonetes* sp.	Grass shrimp	14	20
	3	*Phascolion* sp.	Hermit sipunculid	11	15
	4	*Cerithium* spp.	Cerith snails	5	7
Medium-scale	1	*Phascolion* sp.	Hermit sipunculid	85	60
	2	*Cerithium* spp.	Cerith snails	18	12
	3	*Alpheus* sp.	Snapping shrimp	9	7

3.2. Multivariate analysis

There were neither treatment effects nor block effects in community structure on biomass in the small-scale experiment (Table 4). Similarly, we found no treatment or block effect on biomass or density data in the medium-scale experiment (Table 4).

Although predator effects were generally not observed across the entire community, individual species responses were identified. For example, biomass of *Pitho* sp., the species with the second highest biomass in the small-scale experiment (Table 2A), differed significantly among treatments (ANOVA: F = 14.1, df = 2, P = 0.005), exhibiting higher biomass in the SPE + LPE treatment compared to the LPE (Tukey: P = 0.004) and control (AC; Tukey: P = 0.04) treatments in the small-scale experiment (Fig. 5).

4. Discussion

Predators may play fundamental roles in regulating population dynamics and community structure (Sih et al., 1985). Strong top-down effects, including community-level cascades (Polis, 1999), typically garner the most attention, yet may be limited to ecosystems with low species diversity, little omnivory, and/or strong, concurrent interactions between trophic levels (Estes et al., 1998; Ferretti et al., 2010; Heck and Valentine, 2007; Polis and Strong, 1996; Shurin et al., 2002; Strong, 1992). Although seagrass beds are species-rich systems, strong predator effects have been identified in some cases (Ambrose, 1984; Heck et al., 2000; Hindell et al., 2000; Moksnes et al., 2008). We extend the assessment of predator effects on food web structure to shallow seagrass ecosystems, focusing especially

Table 3
Results of analysis of variance (ANOVA) for the small- and medium-scale exclusion experiments. Treatments consisted of large-predator exclusion, small-and-large-predator exclusion, and average control (average of manipulated and unmanipulated control; see text for more details), and, in each experiment, four blocks were employed. Bold P-values indicate statistically significant findings (P < 0.05).

		Small-scale		Medium-scale	
		F	P	F	P
Species richness	Treatment	5.09	0.05	5.32	**0.047**
	Block	3.51	0.09	4.53	0.06
Total biomass	Treatment	1.79	0.25	4.8	0.06
	Block	0.08	0.97	1.5	0.31
Total density	Treatment	0.76	0.51	0.38	0.7
	Block	4.9	**0.047**	6.31	**0.03**

on the potential effects associated with predators of different sizes. Contrary to our initial hypotheses, our findings suggest (1) weak predator effects in these seagrass ecosystems, and (2) no effect of predator size on faunal community structure and composition. We discuss several factors that might underlie our findings.
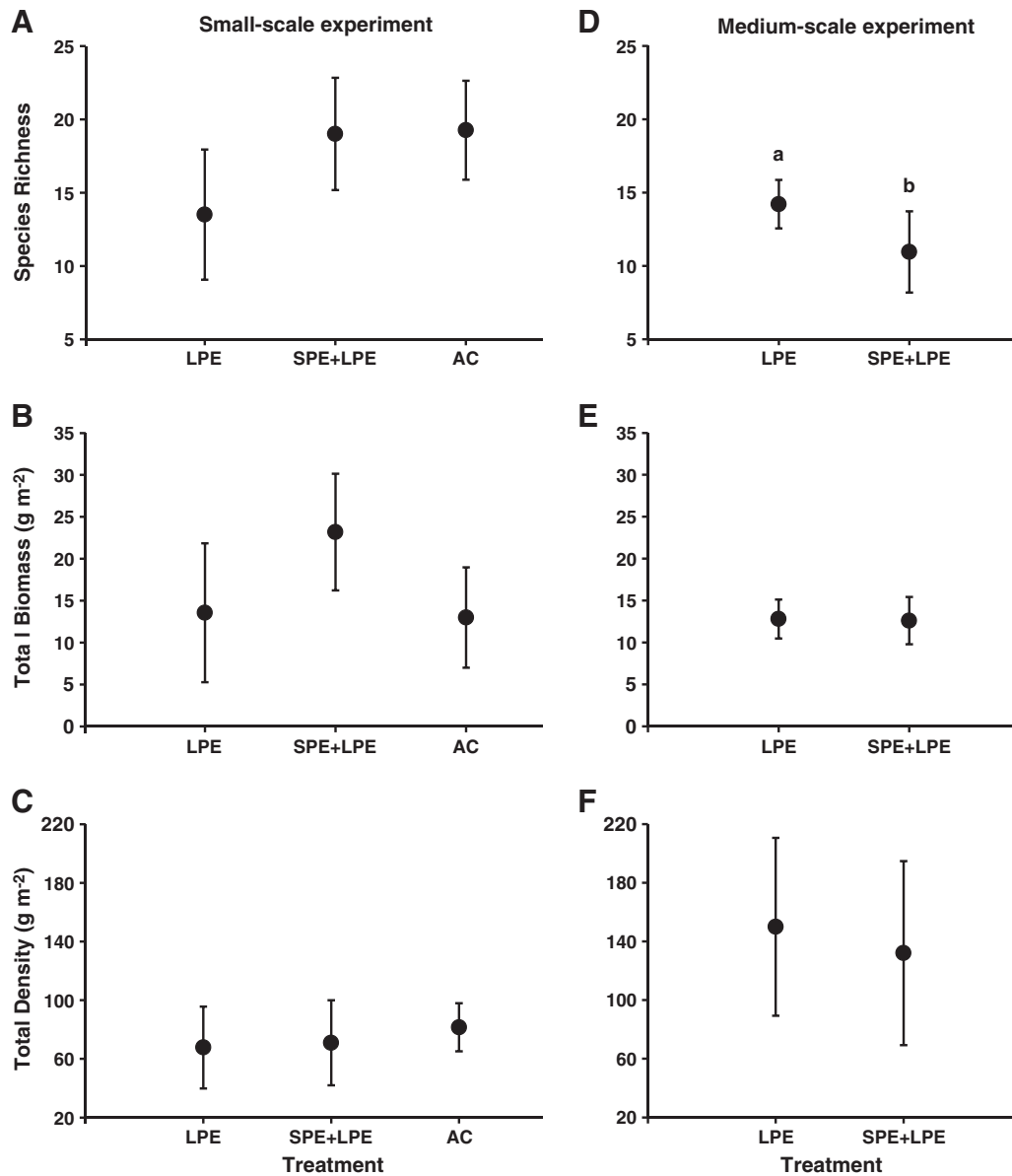
Two of the characteristics that often define systems with weak top-down effects are high species richness and high incidence of omnivory (Edwards et al., 2010; Fox, 2007; Strong, 1992), both of which are apparent in the shallow Bahamian seagrass systems. For example, at least 60 species were collected in our benthic throw traps alone, not including the diverse assemblage of meiofauna that we did not sample (<4 mm). Likewise, omnivory is typically high in seagrass ecosystems (Jaschinski et al., 2008; Livingston, 1982; Marguillier et al., 1997). In the present study, the two most common fish mesopredators (gray snapper and schoolmaster snapper), as well as many of their prey items (*e.g.*, crabs and small teleosts), are generalists that feed on a variety of prey items (Hammerschlag et al., 2010; Hammerschlag-Peyer and Layman, 2012; Silliman et al., 2004; Starck and Schroeder, 1971; Yeager and Layman, 2011). Consequently, it is possible that predator effects in our study system were dampened, at least to a certain degree, by myriad weak and reticulated interactions among species.

Other factors may also have driven weak predator effects in this system. For example, in Bahamian wetlands, predation risk has been shown to increase with water depth, suggesting that predation in certain areas of seagrass beds primarily occurs during a short temporal window around high tide (Rypel et al., 2007). During lower tidal levels, predators in shallow Bahamian systems are restricted to deeper refuge areas, *e.g.*, mangrove-lined channels (Hammerschlag-Peyer and Layman, 2010). In contrast, most other studies examining predator effects on seagrass faunal communities have been conducted in deeper systems where predators have continuous access to prey (Gacia et al., 1999; Heck et al., 2000; Hindell et al., 2000; Leber, 1985; Moore and Hovel, 2010). In shallow systems, the predation window is limited, perhaps diminishing predator effects on the epifaunal community.

Furthermore, heterogeneity in community structure and composition seemed to be generally high in our study, as suggested by the significant block effects in both experiments (Table 3). This heterogeneity was likely driven by microhabitat features of the selected sites. For instance, sponges, whose distribution is often determined by subtle hydrologic characteristics (Droscher and Waringer, 2007), have been shown to provide shelter and food for other macroinvertebrates, enhancing their local abundance and biomass (Gaino et al., 2004; Klitgaard, 1995;

Fig. 3. Species Richness (A and D), Total Biomass (B and E), and Total Density (C and F) of the small-scale (A–C) and medium-scale (D–F) experiments. LPE = large-predator exclusion, SPE + LPE = small-and-large-predator exclusion, AC = average control (*i.e.*, average of manipulated and unmanipulated controls; see text for more details). Error bars represent standard deviation. (a, b) indicate statistically significant (*P* < 0.05) differences between treatments (based on Tukey's post-hoc test), which were only found in Panel D.

Magnino and Gaino, 1998; Rützler, 1976; Saito et al., 2001; Tsurumi and Reiswig, 1997; Turon et al., 2000). In our study, sponge biomass may have contributed to significant block effects on total densities (Table 3), as total density of epifaunal taxa tended to increase with sponge biomass (Fig. 4B). Likewise, other microhabitat features may also have played critical roles in shaping the epifaunal community structure. For instance, epiphytes and macroalgae, whose distribution is often driven by local nutrient and light characteristics (Allgeier et al., 2011), have been found to augment the spatial complexity of seagrass beds or to be important food sources for several taxa (Bologna and Heck, 1999; Gacia et al., 1999; Sala, 1997; Tomas et al., 2005). Indeed, previous research proposed that epifaunal communities, especially those composed of grazing invertebrates, were more likely to be limited by resources than by grazing effects (Edgar, 1993; Edgar and Aoki, 1993).

Although our findings reveal overall weak community-level predator effects, some species-level cascades (Polis, 1999), whereby predators regulate the abundance of a subset of the available prey taxa (Berlow et al., 1999, 2004; Neutel et al., 2002), were documented. For example, biomass of the decapod mesopredator, *Pitho* sp. (small-scale experiment), which is

a common prey of gray and schoolmaster snappers (Hammerschlag-Peyer and Layman, 2012; Starck and Schroeder, 1971), was higher in the SPE + LPE than in the LPE and control (AC) treatments (Fig. 5). *Pitho* sp., which is a smaller-sized crab (carapace length: 19 ± 4 mm, mean ± SD, n = 66), is likely preyed on by smaller predators, and thus might have sought refuge in the SPE + LPE treatment (Fig. 5). Hence, these findings suggest that species-level top-down controls may exist within the community.

In contrast to our hypothesis, one of the most consistent patterns in our findings was the lack of differences in the responses to the two treatments, SPE + LPE and LPE. It is possible that the predator size range (*e.g.*, schoolmaster snapper: 3–20 cm TL, gray snapper: 3–22 cm TL, Fig. 2) might have been too narrow to show significant differences between SPE + LPE and LPE treatments. In Bahamian tidal creeks, larger predators are rare and the most abundant mesopredators (*e.g.*, Lutjanidae) are typically composed of juvenile and sub-adult individuals (Fig. 2), with larger individuals likely moving to deeper water habitats (Nagelkerken et al., 2000; Sheridan and Hays, 2003). Furthermore, according to our underwater visual surveys, small
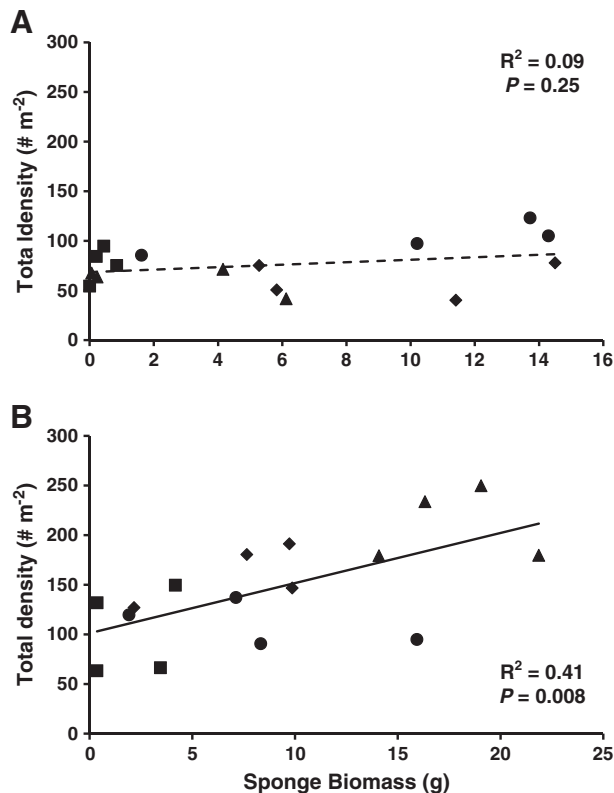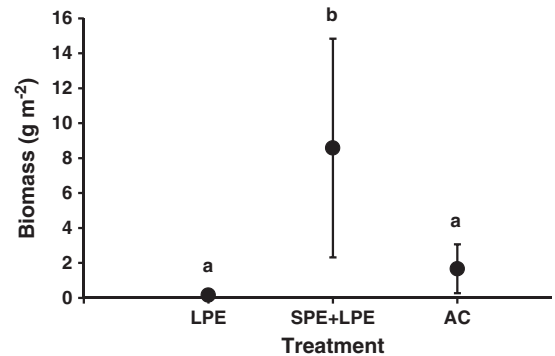
Fig. 4. Linear regression between total density and sponge biomass in the A) small-scale and B) medium-scale exclusion experiment. Block 1 = squares, block 2 = triangles, block 3 = diamonds, block 4 = circles. Dashed regression line represents a non-significant trend ($P \geq 0.05$), and solid line statistically significant relationship ($P < 0.05$).

Fig. 5. Total Biomass of *Pitho* sp. (urn crab) in the small-scale exclusion. LPE = large-predator exclusion, SPE + LPE = small-and-large-predator exclusion, AC average control (*i.e.*, average of manipulated and unmanipulated controls; see text for more details). Error bars represent standard deviation. (a, b) indicate statistically significant ($P < 0.05$) differences between treatments (based on Tukey's post-hoc test).

of predator effects on faunal communities of seagrass beds are critical for long-term conservation efforts. Our study contributes to this body of literature and suggests that shallow, species-rich, seagrass communities may have rather weak community-level predator effects, and that other factors may be more important in structuring these seagrass communities.

Acknowledgments

juvenile schoolmaster (<12.5 cm SL) and gray (<10 cm SL) snapper seemed to be more abundant than sub-adult individuals (schoolmaster: 12.5–25 cm SL; gray: 10–20 cm SL; Fig. 2). Consequently, as local abundance of predators can potentially affect the strength of top-down effects (Hindell et al., 2001), we would expect that higher abundances of larger snappers (or other predatory fishes) in these systems may have resulted in divergent responses between the predator exclusion treatments. Finally, one possible caveat of this study could be the lack of quantitative predator abundance data. Hence, the weak top-down effects observed could also reflect potential weak differences in predation pressure among treatment and control plots.

Although much ecological emphasis has been placed on the role of predation on food web structure, there is a notable lack of consistency in how important top-down effects are in structuring seagrass communities. As such, more research is warranted regarding the specific factors that affect the strength of top-down control. Moreover, in light of the rapid global decline of seagrasses and their associated fauna (Hughes et al., 2009; Orth et al., 2006), a better understanding

Table 4
Results of analysis of similarity (ANOSIM) without replication (*i.e.*, Spearman rank correlation method, with test statistic = ρ) for the small- and medium-scale exclusion experiments. Treatments consisted of large-predator exclusion, small-and-large-predator exclusion, and average control (average of manipulated and unmanipulated control; see text for more details), and, in each experiment, four blocks were employed.

		Small-scale		Medium-scale	
		ρ	P	ρ	P
Total biomass	Treatment	−0.048	0.57	−0.095	0.65
	Block	−0.105	0.67	−0.095	0.63
Total density	Treatment	−0.105	0.65	0.029	0.52
	Block	0.01	0.41	0.114	0.27

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