Predation in subtropical soft-bottom systems: spiny lobster and molluscs in Florida Bay

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ABSTRACT: A 2 yr field experiment conducted in 2 locations in seagrass meadows within Everglades National Park, Florida Bay, tested the hypothesis that variations in physical structure of experimental shelters ('casitas') would affect abundance and composition of the predator guild and, in turn, that these predators would then have measurable and commensurate impacts on the nearby benthic community. Experimental structures (casita frame, mesh-roof casita and full-roof casita) were successful in attracting and aggregating predators as hypothesized, with those structures providing more overhead cover attracting significantly more predators. Although many predators, including the numerically dominant spiny lobster *Panulirus argus*, preyed heavily on or included molluscs in their diets, no significant impacts of predation by spiny lobsters and finfishes on the abundance and species richness of the molluscan assemblage were observed. Regional differences in prey abundance and richness were significant, yet predator effects were similar between locations. Significant location differences in prey abundances, therefore, did not result from differential impacts of prey consumption by casita-associated predators. Predation effects by spiny lobsters and various species of finfishes in Florida Bay were dispersed over time and space and predation was not the primary structuring mechanism for the gastropod and bivalve assemblages in these seagrass and macroalgal habitats. Measurable differences between prey populations in the 2 study locations probably reflect differences in habitat heterogeneity, spatial and temporal variability in predator and prey abundances and distributions, overall high diversity of benthic prey, and ontogenetic shifts in diet and habitat use by predators, all which tend to buffer predatory impacts.

KEY WORDS: Tropics · Soft-bottom systems · Predation · Spiny lobster · Community structure · Florida Bay

INTRODUCTION

The tropics cover more area than any other biogeographical region (Rosenzweig 1995), support a higher percentage of the world's species (Rosenzweig 1995, Blackburn & Gaston 1996), and provide the highest diversity of benthic habitats (Alongi 1990). Additionally, marine biodiversity is higher in benthic systems than in pelagic systems and higher in coastal regions than in open-ocean habitats (Gray 1997). It is not surprising, therefore, that species richness and diversity tend to be high in tropical, coastal, benthic habitats. Although the mechanisms behind the pattern continue

to be debated (Blackburn & Gaston 1996), a tendency for higher diversity in tropical systems is a recognized ecological pattern (Rosenzweig 1995, Blackburn & Gaston 1996).

The role of predation in regulating abundance and diversity of macrobenthic invertebrates in subtropical and tropical systems is predicted to be great, as it is presumed to be more intense in the tropics and generally increases species diversity (Paine 1966, Connell 1978, Sih et al. 1985, Alongi 1989). Additionally, predation is considered to be the most important organizing mechanism in trophically complex communities (Menge & Sutherland 1976). Decreased environmental

stress often corresponds to increased trophic complexity and, under these conditions, predation becomes an increasingly important process (Menge & Sutherland 1987). These factors (i.e. trophic complexity and reduced environmental stress) are characteristics often used to describe tropical communities (Alongi 1989).

The predictability of predation effects or the relative importance of predation impacts by specific predators, considered either singly or in combination with other predators, have not been adequately addressed experimentally within complex marine communities. Evidence for strong predation impacts, in the form of diffuse predation (all predator species contribute significantly and equally to the overall predation effect; Menge & Lubchenco 1981, Menge et al. 1986, Robles & Robb 1993), has been reported for hard-bottom tropical systems (e.g. Menge & Lubchenco 1981, Menge et al. 1986), suggesting that predation plays a primary role in regulating some tropical benthic communities. Soft-bottom systems, however, seem to abide by different rules (Dayton 1984, Wilson 1991) and experimental documentation of the role of predators in soft-bottom communities has proven difficult (Dayton 1984). Attempts to confirm or refute hypotheses regarding predation as a major structuring factor in soft-bottom, subtidal, subtropical or tropical systems are limited, and these studies have produced results ranging from no predation effects, to equivocal results, to intense predation effects (Young et al. 1976, Heck 1977, Young & Young 1978, Mahoney & Livingston 1982, Vargas 1988, Alongi 1989, Edgar 1990b). Lack of significant effects is problematic in that interpretation of negative results is clouded by the uncertainty of whether findings are real or whether the experimental design was inadequate (Barros 2005). However, when results from independent studies suggest that predation is not the primary mechanism producing observed patterns in community structure, then this scenario (i.e. negative results) must also be considered.

Subtropical seagrass beds of Florida Bay provide an excellent arena for testing impacts of predation in regulating macrobenthic invertebrate prey abundances. These soft-bottom areas are highly productive, support diverse populations of large, mobile predators and their prey, and can be easily manipulated to test for predation effects. These habitats serve as primary nursery and foraging grounds for various finfishes and invertebrate populations. The Caribbean spiny lobster *Panulirus argus*, a high level predator, utilizes the Florida Bay system from settlement to subadult stage of its life cycle. *P. argus* is a numerically dominant species that feeds preferentially on gastropods and bivalves throughout its residency in seagrass beds (Herrnkind et al. 1975, Kanciruk 1980, Colinas-Sánchez & Briones Fourzán 1990,

Espinosa et al. 1991, Cox et al. 1997). The spiny lobster is a logical candidate for consideration as an important predator in this system, given its persistent occurrence at moderate to high relative abundances. In their respective habitats, other species of spiny lobsters (*Jasus lalandii*: Griffiths & Seiderer 1980, Barkai & McQuaid 1988; *P. interruptus*: Tegner & Levin 1983, Robles & Robb 1993; *P. cygnus*: Joll & Phillips 1984, Edgar 1990a,b) have been implicated as ecosystem regulators. Previous research at experimental sites within Florida Bay (Proft 1995) quantified impacts of predation on macrobenthic prey assemblages and suggested that molluscan abundance was significantly reduced when spiny lobsters were present at artificially high densities. Whether predation impacts by lobsters occur on molluscan assemblages when lobster densities are closer to naturally occurring levels has not been addressed. Therefore, a manipulative experiment was designed in a Florida Bay seagrass/macroalgal system to quantify overall predation effects on molluscs by spiny lobsters and other molluscivorous predator species.

MATERIALS AND METHODS

Field sites and experimental design. The field experiment was designed to test the hypothesis that variations in physical structure of artificial shelters, ('casitas', lit. 'small house') would attract different members of the structure-oriented predator guild, and that these components would then have measurable and differential impacts on the nearby benthic community. In an effort to replicate and then manipulate more natural conditions, casitas were utilized as an alternative to cages. Casitas have been used successfully to simulate shelter and attract lobsters in habitats where they naturally occur (Eggleston et al. 1990, Briones-Fourzán et al. 2000, R. N. Lipcius & D. B. Eggleston unpubl. data). By placing casitas in seagrass beds, the space beneath the casitas did not fill with sand, and thus a habitat critical for lobsters was not eliminated (Briones-Fourzán et al. 2000). Also, the artifactual influence of casitas on hydrodynamics should be minimal within seagrass beds since flows are already naturally slow and the emergent structure should not create much additional effect on a hydrodynamic regime already influenced by emergent vegetation (Ólafsson et al. 1994).

Since spiny lobsters are numerically dominant benthic predators in Florida Bay seagrass beds, shelters were designed primarily to manipulate spiny lobster abundance by modifying physical properties of the shelter to create a den preference gradient. Characteristics of a preferred spiny lobster den include presence

of a shaded cover, multiple entrances, and low roof height (Eggleston et al. 1990). Abundances of predatory fishes at casita sites were also hypothesized to vary based on shelter requirements of individual species. Thus, the relative composition of this predator guild could be manipulated and the relative impact of predation by spiny lobsters and finfishes could be assessed. This experiment utilized 4 treatments: (1) control (no structure)—no attraction value to predators and no enhancement of predator abundances; (2) casita frame (no roof)—designed to attract only those fishes that are generally attracted to structure, but that otherwise have no overhead shelter requirements; unattractive to spiny lobsters due to the lack of overhead cover, (3) mesh-roof casita (frame covered with 3.8 cm diamond mesh vexar)—designed to attract most of the fish assemblage but not spiny lobsters due to the lack of a completely opaque overhead cover, and (4) full-roof casita (frame covered with 0.32 cm aluminum sheet metal)—designed to attract the entire casita predator guild (including spiny lobsters and finfishes) by providing full overhead cover.

Casita design was a modification of large casitas (scaled for lobsters 65 to 80 mm carapace length, CL) described in Eggleston et al. (1990). All casitas were constructed of 7.6 cm PVC frames (100 cm length × 60 cm width × 7 cm opening height). The opening height was increased to 7 cm to ensure that the complete size range of lobsters (20 to 95 mm CL) observed in the area could utilize the structure. Each PVC pipe was filled with concrete to eliminate additional shelter (i.e. inside the pipe) and to add weight to the structure and minimize movement induced by tide and waves. Results from a pilot study demonstrated that concrete-filled frames were sufficiently weighted and remained stationary even during severe weather events. Control treatments were marked by a partially buried cement block, which could be located easily but which did not provide shelter for the organisms being studied. Casitas were constructed and all treatments deployed in July 1993.

Two locations in seagrass meadows within the boundaries of Everglades National Park were selected as experimental locations (Fig. 1). The 2 study locations were set approximately 12 km apart in different basins within Florida Bay, and were representative of distinct sub-environments (Nizinski 1998). Location 1 is characterized by high macrophyte diversity and biomass, fine sediments, low concentrations of nitrogen, high concentrations of phophorus, high turbidity, and high salinity, whereas Location 2 is characterized by low macrophyte diversity and biomass, coarse sediments, high concentrations of nitrogen, low concentrations of phophorus, low turbidity, and variable salinity. Experimental locations were separated by seagrass-
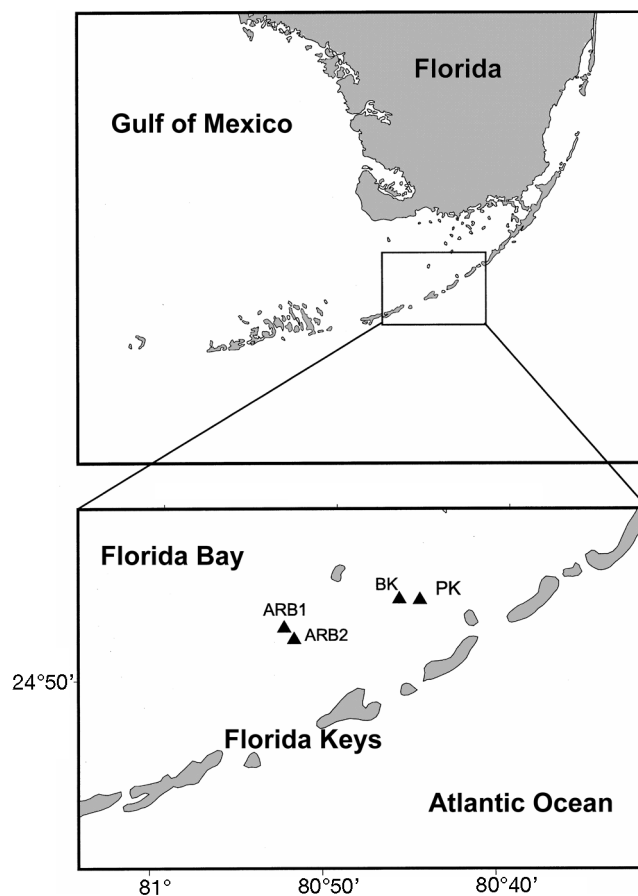

Fig. 1. Map of south Florida including Florida Bay and Florida Keys. Enlargement illustrates general area of experimental locations with sampling sites

covered sand banks, thereby eliminating any interaction between them.

Four experimental sites were then created (Fig. 1); 2 at Location 1 (ARB1 and ARB2) and 2 at Location 2 (PK and BK). Sites were separated within locations by at least 1 km to eliminate interaction between them. Each site consisted of 4 replicates of each treatment, randomly interspersed over 2.4 ha. Each structure was situated 50 m from adjacent structures in an attempt to eliminate interactions between treatments within sites. Thus, sites were replicated within location and treatments were replicated within site.

Placement of casitas in food-rich seagrass beds allowed for the exploitation of available food resources by lobsters (Sosa-Cordero et al. 1998, R. N. Lipcius & D. B. Eggleston unpubl. data). Lobsters tend to be residential in areas of abundant food and shelter (Herrnkind 1980). Previous studies in Florida Bay (Proft 1995, R. N. Lipcius & D. B. Eggleston unpubl. data) demonstrated that lobsters fed in areas where artificial structure was provided, thereby reducing for-

aging distance. However, halos (areas of decreased prey abundances caused by direct or indirect impacts of structure-associated predator activities on the surrounding benthos) have been reported at or immediately adjacent to structures (e.g. Davis et al. 1982, Ambrose & Anderson 1990, Langlois et al. 2005). Ramos-Aguilar (1992) observed that juvenile lobsters foraged near the casita that they were occupying during the first few hours of feeding before moving to the surrounding seagrass beds and sand flats. Since decreased abundances of prey items are expected immediately adjacent to casitas once the structures are occupied, and physical factors associated with the structure itself may either enhance or reduce abundances of benthic organisms (Davis et al. 1982, Ambrose & Anderson 1990), sampling points located 3 m distant from the casita were selected. Observations and results from preliminary studies indicated that 3 m from casitas was an adequate distance to measure impacts of resident predators on prey abundance in the surrounding seagrass habitat yet reduce confounding influences from predator disturbance and physical factors. Since molluscs in general, and gastropods in particular, are primary prey items for *Panulirus argus* (Herrnkind et al. 1975, Kanciruk 1980, Lalana et al. 1987, Colinas-Sánchez & Briones-Fourzán 1990, Espinosa et al. 1991, Cox et al. 1997), only the abundance and diversity of gastropods and bivalves were examined in this study.

Sampling. During each sampling period the predator guild and macrobenthic community were characterized and quantified at each experimental treatment. Time zero samples were collected when treatments were deployed (July 1993). Sampling occurred quarterly during the first year (November 1993, February 1994, May 1994, August 1994), then twice (February 1995, August 1995) the following year.

Visual surveys using SCUBA, modified after techniques outlined in Hixon & Beets (1989), were conducted during each experimental treatment to determine composition and abundance of the predator guild associated with each structure. Species were identified and individuals counted. The size of spiny lobsters and finfishes associated with each experimental treatment was estimated using a t-square calibrated in 1 cm sections.

Predators quantified at each treatment were characterized based on their potential to impact the molluscan assemblage. Although all potential fish and invertebrate predators were identified and counted, only known molluscivores are reported here. Spiny lobsters of sizes greater than 20 mm CL were included in the lobster category. Individuals of any fish species known to include molluscs in their diets (Randall 1967) were counted as molluscivorous fishes, unless evidence was available that the size of individuals observed at experimental structures had alternative food habits. For example, only larger individuals (≥10 cm total length, TL) of *Haemulon aurolineatum* include gastropods in their diets; individuals in the size range observed (2 to 7 cm TL) at experimental structures feed mainly on very small crustaceans (copepods; Sedberry 1985). *H. aurolineatum* in this study, therefore, were considered to be non-molluscivores.

Subsequent to visual surveys, benthic suction samples were taken to assess molluscan abundance and taxonomic composition on each sampling date. Each suction sample was taken from a random location, 3 m distant from 1 each of a randomly chosen treatment replicate on each sampling date. Individual treatments could conceivably be selected more than once. In total, 112 samples were analyzed.

The benthic suction sampling procedure was a modification of methods used by Orth & van Montfrans (1987). Each sample consisted of 30 s duration suction into a 1 mm mesh sampling bag that collected sediment, vegetation and organisms from within a 0.05 m^2 area (a 25.4 cm diameter sampling ring, fitted with a 1 mm mesh top to eliminate escape of mobile organisms). Approximately the same amount of sediment was suctioned each time because the Florida Bay basin in experimental locations is generally characterized by a thin sediment layer overlying a limestone foundation (M. S. Nizinski pers. obs.). Samples were then sieved through 2 mm wire mesh to reduce the amount of sediment to be processed by eliminating the majority of sand and finer sediments from the sample. Material washed through the mesh was macroscopically examined for molluscs. The remaining sample was frozen for later processing.

The mesh size utilized should depend upon the spatial scale of interest, grade of deposit, and the organisms examined. Although numerous studies (e.g. Bachelet 1990, James et al. 1995) focused mostly on soft-bodied organisms such as polychaetes have suggested that smaller mesh sizes may conserve information, those studies also agreed that standardization of sieve mesh size across a diverse array of experimental designs is difficult. A similar study examining macrobenthic abundance and composition in seagrass areas used by juvenile spiny lobster (Lalana et al. 1987) utilized a 2 mm sieve. Since the present study was designed to estimate available food (i.e. molluscs) and to examine impacts of lobster predation on local, readily available molluscan prey, molluscs >2 mm were targeted as these were most likely to be exploited by juvenile and adult spiny lobsters. These organisms are retained on 1 to 2 mm sieves (M. Nizinski unpubl. data).

Benthic samples were visually sorted in the laboratory. All organisms were retained and preserved in 10% formalin and subsequently transferred to 70% ethanol for long-term storage. All gastropod shells

were carefully examined to ensure that a gastropod was actually residing in the shell. Presence of an operculum was the best evidence but, when necessary, the lip of the shell was broken to verify the presence of a gastropod within the shell. Empty shells were not included in the analyses. Once sorted, molluscs were then enumerated and categorized into taxonomic groups. Molluscs were later identified to the lowest taxonomic level possible using authoritative keys and comparative material housed at the Delaware Natural History Museum, Wilmington, Delaware, and the Division of Molluscs, National Museum of Natural History, Smithsonian Institution, Washington, DC. The majority of identifications were verified by collaborative exchange with an expert taxonomist (P. Mikkelsen) formerly at the Delaware Natural History Museum. Voucher specimens were retained.

Statistical analysis. Predator and prey abundance data (N = 96) were analyzed using a repeated-measures analysis of variance model (RM-ANOVA), since abundances of predator and prey organisms could potentially be correlated over time. Two prey categories (gastropods and bivalves) and 2 predator categories (lobsters and molluscivorous fishes) were treated as individual dependent variables. Tests of significance of the main effects of location (Locations 1 and 2) and treatment (control, frame only, mesh-roof casita, full-roof casita) were based on a 2-way factorial design with 2 replicates (site[location × treatment]) repeated over time. Location and treatment were considered fixed effects and site as random and nested within the location × treatment combinations. Tests of both main effects and their interaction used the experimental error due to replicates rather than the overall experimental error. Time (6 sampling periods) and its interactions with the main effects were evaluated using the overall experimental error term. Samples collected during July 1993 were not included in these analyses since treatment effects were nonexistent at Time zero. Abundances were ln(x + 1)-transformed to normalize data and stabilize variances. Significant interactions and lower-level effects were examined using Student-Newman-Keuls (SNK) multiple comparisons test. Relationships between predator and prey abundances were tested with Pearson correlations.

Predator size may be an important factor in structuring prey populations. For example, rate of prey consumption and prey size preference may both be proportional to predator size. Therefore, mean predator size within the 2 predator categories was calculated for each sampling period, location, and site combination. Variation in mean size structure of predators over time and between locations for each predator group (spiny lobster and molluscivorous fishes) was examined using ANOVA.

Predators may also influence prey species diversity. Predators able to maintain prey populations at low abundance levels theoretically reduce competition between individuals, thus allowing more species to coexist in the community (Paine 1966). Local prey diversity, therefore, may be directly related to predation intensity. Gastropod and bivalve species richness (S) were analyzed using the repeated-measures analysis of variance described above to address the relationship between prey species richness and predator abundances.

RESULTS

Predator composition

During the experiment 870 crustacean and piscine predators representing 24 species were censused in structures included in this analysis (Table 1). Molluscivores were more prevalent (N = 664) than non-molluscivores (N = 206) and represented 76% of the total casita-associated fauna. *Panulirus argus* was the numerically dominant molluscivore, representing 86% of all molluscivores (N = 570), and occurred at 65% of sampled structures throughout the experiment (47 of 72 structures; controls and July 93 data excluded). Other molluscivores (Table 1) included various species of grunts (e.g. *Haemulon sciurus* and *Anisotremus virginicus*) and crabs (*Menippe mercenaria* and *Callinectes* spp.). Fishes were much more abundant than crabs, representing 90% of the molluscivores, exclusive of spiny lobsters. After *P. argus*, *H. sciurus* was the next most abundant molluscivore (N = 57), contributing 61% to the individual molluscivores. Non-molluscivores included predominately small grunts *H. aurolineatum* and *A. virginicus* and gray snapper *Lutjanus griseus*. These 3 species constituted 79% of the total casita-associated, non-molluscivore fauna. Other less abundant fishes in this predator category included *Equetus acuminatus* and *Diplectrum formosum*.

Five predator species were common to both locations and all 4 sites: *Panulirus argus*, *Anisotremus virginicus*, *Haemulon sciurus*, *H. aurolineatum*, and *Lutjanus griseus*. Five additional species were found in both locations but not at all sites: *Diplectrum formosum*, *Acanthurus coeruleus*, *H. macrostomum*, *Menippe mercenaria*, and an unidentified spider crab (possibly *Libinia dubia*). Three species were unique to Location 1 (observed at both sites): *Gerres cinereus*, *Sparisoma radians*, and *Hypoplectrus unicolor*, whereas only *Callinectes similis* was unique to Location 2.

In general, predator composition was more similar between sites within a location than between locations. Location 1 had a more diverse predator guild,

Table 1. Predator composition (fishes and crustaceans) observed at experimental sites during study (data collapsed across dates). Predator species (ranked by decreasing abundance) arranged by trophic category. Size ranges (based on estimated size of each organism during visual surveys) is total length for fishes, carapace length for spiny lobster, and carapace width for crabs. * = predator species observed at least once per site; ** = common (observed in ≥4 sampling periods or comprised at least 20% of predators observed per site). N: total abundance

Predator	N	Location 1			Location 2		
		ARB1	ARB2	Size range	PK	BK	Size range
Molluscivores							
Panulirus argus (≥25 mm)	570	**	**	25–95	**	**	25–90
Haemulon sciurus	57	**	**	40–150	*	*	30–150
Anisotremus virginicus (≥50 mm)	14	**	*	50–100	*	**	50–180
Gerres cinereus	6	*	*	50–100			
Menippe mercenaria	5	*	*	80–90	*		70–90
Callinectes similis	3				*	*	40–80
Haemulon carbonarium	2		*	80			
Haemulon sp.	2					*	40
Haemulon flavolineatum	1				*		40
Haemulon plumieri	1		*	ca. 80			
Lutjanus analis	1		*	60			
Callinectes sapidus	1					*	35
Unidentified puffer fish	1					*	30
Non-molluscivores							
Haemulon aurolineatum	83	**	*	30–60	**	**	20–70
Lutjanus griseus	58	**	*	60–300	*	**	50–150
Anisotremus virginicus (<50 mm)	21	*	*	20–40	*	*	20–30
Panulirus argus (≤20 mm)	9		*	20	*	*	15–20
Haemulon macrostomum	7		*	40–80		*	40
Equetus acuminatus	7	*		20–80			
Spider crab (*Libinia dubia*?)	6	*		80	*	*	20–70
Diplectrum formosum	5	*	*	60–150	*		80
Acanthurus coeruleus	2	*		100	*		80
Hypoplectrus unicolor	2	*	*	50–60			
Sparisoma radians?	2	*	*	80–150			
Ocyurus chrysurus	1	*		120			
Mithrax sp.	1		*	40			

with 15 species observed at each site over the course of the experiment; 10 species were common to both sites. Location 2 had 11 predator species associated with each site over the course of the experiment; 7 of these were common to both sites.

Predator abundance

Spiny lobster abundances did not differ significantly between locations (Table 2). In contrast, molluscivorous fish abundance was significantly greater at Location 1 than at Location 2 (Table 3).

Treatment was a significant predator-related factor (Tables 2 & 3). All forms of structure (i.e. casita frame, mesh-roof casita, and full-roof casita) attracted and aggregated a predator guild. Overall, predator abundance was manipulated as hypothesized; more complex structures accommodated more predators than simpler treatments. Additionally, treatments affected predator abundance similarly across sites and locations.

Also as predicted, patterns in casita occupancy differed between groups of predators (Figs. 2 & 3). Mean

lobster abundance at full-roof casitas was significantly greater than at mesh-roof casitas (SNK, p < 0.05; Fig. 2). Significantly more lobsters utilized these treatments than either the casita frames or controls (Fig. 2). Mean lobster abundance did not differ significantly

Table 2. *Panulirus argus.* Repeated-measures ANOVA for lobster abundance data, ln(x + 1)-transformed. Type III sums of squares are shown. Site(Location × Treatment) is error term used to test Location, Treatment, and Location × Treatment effects; all other factors tested with overall mean square error term. ***p < 0.0005

Source	df	SS	MS	*F*-value	p-value
Location (L)	1	0.2209	0.2209	0.54	0.4829
Treatment (Tr)	3	84.4811	28.1604	68.99	0.0001***
L × Tr	3	2.0257	0.6752	1.65	0.2528
Site (L × Tr)	8	3.2655	0.4082		
Time	5	7.1424	1.4285	1.82	0.1304
Time × L	5	5.0951	1.0190	1.30	0.2832
Time × Tr	15	9.7192	0.6479	0.83	0.6436
Time × Tr × L	15	11.3498	0.7567	0.97	0.5063
Error	40	31.3493	0.7837		
Total	95	154.6490			

Table 3. Repeated-measures ANOVA for molluscivorous fish abundance data, ln(x + 1)-transformed. Type III sums of squares are shown. Site(Location × Treatment) is error term used to test Location, Treatment, and Location × Treatment effects; all other factors tested with overall mean square error term. *p < 0.05; **p < 0.005; ***p < 0.0005

Source	df	SS	MS	F-value	p-value
Location (L)	1	1.5733	1.5733	6.70	0.0322*
Treatment (Tr)	3	4.9697	1.6566	7.05	0.0123*
L × Tr	3	1.0091	0.3364	1.43	0.3037
Site (L × Tr)	8	1.8796	0.2350		
Time	5	7.9816	1.5963	11.81	0.0001***
Time × L	5	4.9843	0.9969	7.37	0.0001***
Time × Tr	15	5.7965	0.3864	2.86	0.0041**
Time × Tr × L	15	4.8542	0.3236	2.39	0.0141*
Error	40	5.4070	0.1352		
Total	95	38.4553			
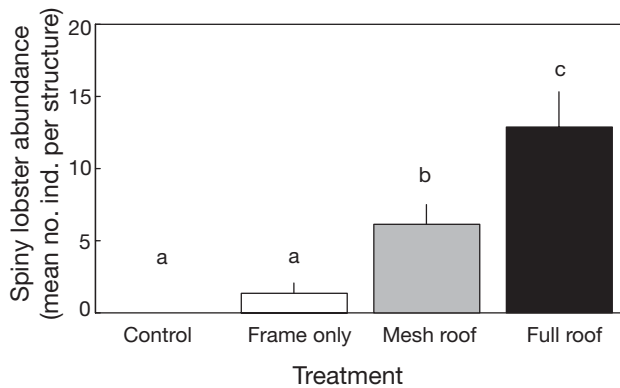
Fig. 2. *Panulirus argus*. Mean + 1 SE abundance of spiny lobsters associated with each type of experimental treatment over duration of experiment. Data from all sampling dates (exclusive of July 1993) were pooled. Treatments denoted with different letters are significantly different from each other (SNK test)
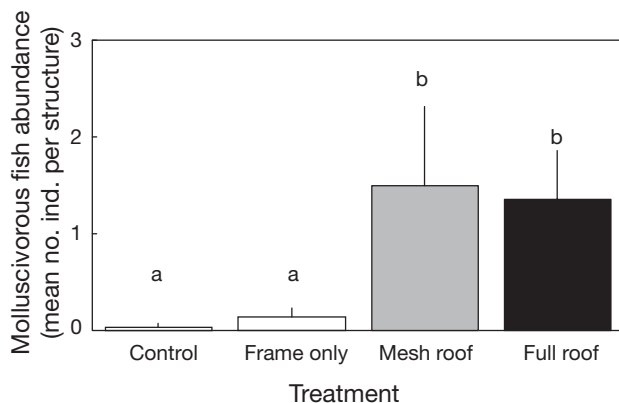

Fig. 3. Mean + 1 SE abundance of molluscivorous fishes associated with each type of experimental treatment over duration of experiment. Data from all sampling dates (exclusive of July 1993) were pooled. Treatments denoted with different letters are significantly different from each other (SNK test)

between these latter 2 treatments (SNK, p > 0.05). Thus, 3 functionally different treatments representing a decreasing gradient of spiny lobster abundance were recognized: full-roof, mesh-roof, casita frame (= control). In contrast, the mean abundance of molluscivorous fishes (Fig. 3) was highest at the mesh-roof casita, followed by the full-roof casita, casita frame and control. Full-roof and mesh-roof casitas, although not significantly different from each other with regard to their mean fish abundance (SNK, p > 0.05), were utilized by significantly more fishes than either the casita frame or control treatments (SNK, p < 0.05). The mean abundance of fishes did not differ significantly between these latter 2 treatments (SNK, p > 0.05).

Spiny lobster abundance did not differ significantly over time (Table 2). In contrast, the mean abundance of molluscivorous fishes differed significantly over the course of the experiment (Table 3). Significant differences in abundance over time were driven primarily by higher abundances during May 1994 and August 1995, in combination with significant treatment (more predators utilizing mesh- and full-roof casita treatments) and location (Location 1 > Location 2) effects.

Prey composition

Prey abundance from a total of 112 suction samples (0.05 m^2 each) yielded 7480 total individuals, with density per sample ranging from 6 to 1027 (66.8 ± 10.6; $\bar{x}$ ± SE). Gastropod and bivalve molluscs were predominant and prevalent in the samples (gastropods, 98% of samples; bivalves, 94% of samples) both in abundance (gastropods, N = 884; bivalves, N = 3359) and diversity (75 gastropod and 25 bivalve taxa) and constituted 7 to 99% of organisms collected per sample ($\bar{x}$ = 43.5%). Density per sample ranged from 0 to 43 individuals (7.9 ± 0.7) for gastropods and 0 to 998 individuals (30.0 ± 10.3) for bivalves. Only 1 species showed a high degree of numerical dominance: *Brachidontes exustus* accounted for 87.6% of all bivalves collected. In contrast, the most abundant gastropod, *Nassarius albus*, accounted for only 20% of all gastropods collected. Four species of bivalves and 16 species of gastropods were represented by a single individual. In-depth analysis of the patterns of abundance and diversity of bivalve and gastropod molluscs has been reported elsewhere (Nizinski 1998).

Prey abundance

Location was a significant prey-related factor, with differences in mean density evident for both prey categories (Tables 4 & 5). Location 1 supported significantly

higher abundances of gastropods (Fig. 4), whereas Location 2 generally supported significantly higher abundances of bivalves (Fig. 5). The treatment effect was not significant for either prey category; casita complexity (i.e. treatment) had no direct effect on mean prey density (Tables 4 & 5).

Overall, seasonality did not play a major role in regulating gross trends in molluscan abundances at the study sites. Gastropod abundances remained relatively constant throughout the entire experimental period (time and its interactions were not significant; Table 4, Fig. 4). Bivalves, however, demonstrated seasonal trends most likely resulting from recruitment events of *Brachidontes exustus*. Bivalves were more abundant in winter/spring months (November 1993 and February, May 1994, February 1995) and least abundant during late summer (August 1994, 1995; Fig. 5).

Predator–prey abundance relationships

Predator and prey abundances were not significantly cross-correlated between any predator or prey groupings (Pearson correlations, $p > 0.05$). No linear or non-linear patterns were apparent; relationships between predator and prey abundances were similar between locations.

Predator size

Mean lobster size did not differ significantly between locations during the course of the study (2-way ANOVA, $F = 0.91$, df = 1, $p = 0.360$). However, significantly larger lobsters were observed during the August 1994 and August 1995 sampling periods (2-way ANOVA, $F = 8.64$, df = 5, $p = 0.001$; SNK, $p < 0.05$). This shift in the size structure in late summer indicates that a portion of the population of lobsters in Florida Bay is reaching maturity and presumably these individuals will soon migrate from the nursery/juvenile habitat in Florida Bay to adult habitats on ocean-side reefs. Small sample sizes and sporadic utilization of experimental structures by molluscivorous fishes precluded statistical analysis of size structure for this predator category. Qualitatively, the overall size structure of fishes utilizing experimental structures was not highly variable during the study period (Nizinski 1998).

Prey size — qualitative assessment

Collectively, the size of individuals within the gastropod assemblage remained relatively constant throughout the duration of the experiment; experimental loca-

Table 4. Repeated-measures ANOVA for gastropod abundance data, $\ln(x + 1)$-transformed. Type III sums of squares are shown. Site(Location × Treatment) is error term used to test Location, Treatment, and Location × Treatment effects; all other factors tested with overall mean square error term. **$p < 0.005$

Source	df	SS	MS	F-value	p-value
Location (L)	1	19.5846	19.5846	25.43	0.0010**
Treatment (Tr)	3	2.3194	0.7731	1.00	0.4396
L × Tr	3	3.3481	1.1160	1.45	0.2993
Site (L × Tr)	8	6.1612	0.7702		
Time	5	2.0215	0.4043	1.41	0.2402
Time × L	5	0.7961	0.1592	0.56	0.7324
Time × Tr	15	3.1404	0.2094	0.73	0.7384
Time × Tr × L	15	4.4168	0.2945	1.03	0.4472
Error	40	11.4405	0.2860		
Total	95	53.2285			

Table 5. Repeated-measures ANOVA for bivalve abundance data, $\ln(x + 1)$-transformed. Type III sums of squares are shown. Site(Location × Treatment) is error term used to test Location, Treatment, and Location × Treatment effects; all other factors tested with overall mean square error term. *$p < 0.05$; ***$p < 0.0005$

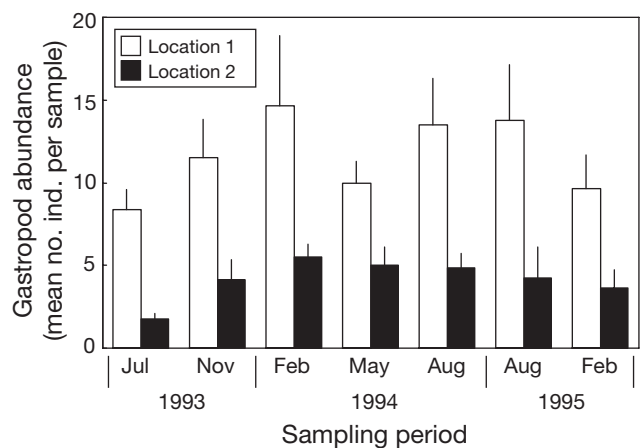| Source	df	SS	MS	F-value	p-value
Location (L)	1	26.0321	26.0321	8.62	0.0188*
Treatment (Tr)	3	8.2154	2.7385	0.91	0.4793
L × Tr	3	1.9687	0.6562	0.22	0.8817
Site (L × Tr)	8	24.1548	3.0194		
Time	5	31.6913	6.3383	8.08	0.0001***
Time × L	5	26.2385	5.2477	6.69	0.0001***
Time × Tr	15	12.6739	0.8449	1.08	0.4060
Time × Tr × L	15	10.7818	0.7188	0.92	0.5540
Error	40	31.3803	0.7845		
Total	95	173.1368			

Fig. 4. Mean + 1 SE abundances (number of individuals sample^{-1}) of gastropods collected in experimental locations during each sampling period
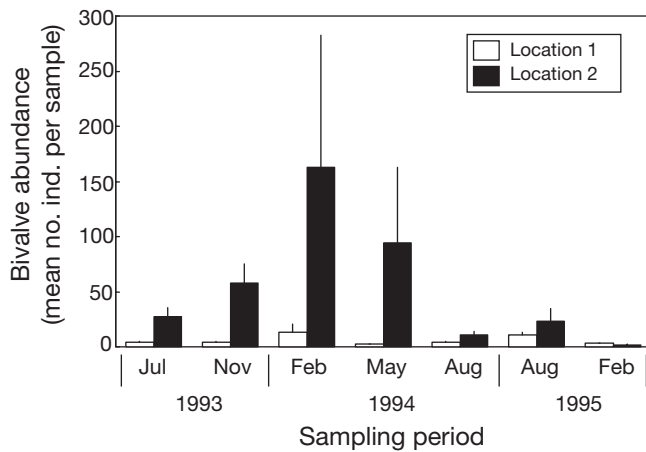
Fig. 5. Mean + 1 SE abundances (number of individuals sample^{-1}) of bivalves collected in experimental locations during each sampling period

Table 6. Repeated-measures ANOVA for gastropod species richness data. Type III sums of squares are shown. Site(Location × Treatment) is error term used to test Location, Treatment, and Location × Treatment effects; all other factors tested with overall mean square as the error term. **p < 0.005

Source	df	SS	MS	F-value	p-value
Location (L)	1	412.5104	412.5104	16.04	0.0039**
Treatment (Tr)	3	148.8646	49.6215	1.93	0.2034
L × Tr	3	114.5313	38.1771	1.48	0.2906
Site (L × Tr)	8	205.7500	25.7188		
Time	5	22.8021	4.5604	0.68	0.6384
Time × L	5	8.8021	1.7604	0.26	0.9301
Time × Tr	15	73.0729	4.8715	0.73	0.7399
Time × Tr × L	15	84.4063	5.6271	0.84	0.6264
Error	40	266.7500	6.6688		
Total	95	1337.4896			

Table 7. Repeated-measures ANOVA for bivalve richness data. Type III sums of squares are shown. Site(Location × Treatment) is error term used to test Location, Treatment, and Location × Treatment effects; all other factors tested with overall mean square as error term. *p < 0.05; ***p < 0.0005

Source	df	SS	MS	F-value	p-value
Location (L)	1	4.5938	4.5938	1.22	0.3012
Treatment (Tr)	3	5.4479	1.8160	0.48	0.7033
L × Tr	3	3.7813	1.2604	0.34	0.8005
Site (L × Tr)	8	30.0833	3.7604		
Time	5	73.5521	14.7104	7.41	0.0001***
Time × L	5	38.2188	7.6438	3.85	0.0061*
Time × Tr	15	32.4896	2.1660	1.09	0.3944
Time × Tr × L	15	44.1563	2.9438	1.48	0.1584
Error	40	79.4167	1.9854		
Total	95	311.7396			

tions showed parallel trends. Individuals with shell height of 5 to 8 mm consistently constituted a high proportion of individuals collected in each location on each sampling date.

Overall, the size structure of the bivalve assemblage was also relatively stable over time and between locations, with very few large bivalves (>13.0 mm) collected throughout the experimental samplings. In contrast to the gastropod assemblage, bivalve size structure was influenced by at least 1 large recruitment event of *Branchidontes exustus*, which contributed extensively to the high frequency of 5 to 8 mm individuals collected in November 1993, February 1994, and May 1994, particularly at Location 2.

Prey species richness

Predation did not significantly influence gastropod species richness. The non-significant treatment effect (Table 6) implies that predators, which were successfully manipulated by treatment design (Tables 2 & 3), did not impact gastropod species richness. In contrast, location significantly influenced species richness, with Location 1 having more gastropod species (n = 70) than Location 2 (n = 37) (Table 6). Species richness did not change significantly over time throughout the duration of experiment (time and its interactions not significant; Table 6).

Bivalve species richness was also unaffected by predation, as indicated by the non-significant treatment effect (Table 7). Bivalve species richness did not differ significantly between locations, although the time × location interaction was significant (Table 7). Mean richness was significantly higher at Location 1 than Location 2 during the February 1994 and 1995 sampling periods (SNK, p < 0.05). Also, at Location 1, mean species richness was significantly greater in February 1994 and 1995 than in all other sampling periods. Mean species richness did not differ significantly over time at Location 2 (SNK, p > 0.05).

DISCUSSION

Predation has been shown to determine prey species composition and distribution in diverse marine communities (e.g. Paine 1966, Sih et al. 1985, Hixon 1991, Wilson 1991), yet the results presented herein indicate that the predator guild (spiny lobster and finfishes) associated with experimental structures in Florida Bay had minimal impact on the structure of the local molluscan prey assemblage. Neither prey density nor species richness was significantly impacted by predator density, which was significantly manipulated by the

experimental structures. Thus, even though predation pressure may be intense, it does not appear to be the primary structuring mechanism for the molluscan assemblage within this Florida Bay seagrass community.

Experiments conducted in other Florida seagrass beds and estuaries (Young et al. 1976, Young & Young 1978, Nelson 1981, Mahoney & Livingston 1982) also revealed inconclusive or minimal impacts from a variety of epibenthic predators. Furthermore, studies evaluating the importance of predation as a structuring mechanism in other subtropical and tropical marine communities also found little evidence to support the hypothesis that predation is a primary regulatory factor for benthic communities (Vargas 1988, Jones et al. 1992), or produced inconclusive and equivocal results regarding the significance of predation effects (Keller 1983, Jones et al. 1991). Based on available evidence then, predator–prey dynamics in tropical and subtropical soft-sediment systems affect these diverse systems similarly and suggest that predation provides little regulatory influence.

This does not imply that predation does not occur or is not intense. In fact, predation was proposed as an important factor regulating prey species densities at seagrass/sand stations in Belize (Young & Young 1982), and abundances of macroinvertebrates in Florida seagrass beds (Young et al. 1976) and significant predation effects on motile epibenthic invertebrates (e.g. decapod crustaceans) in tropical and sub-tropical seagrass beds have been reported (Heck 1977, 1979, Heck & Wilson 1987). However, other factors such as habitat complexity (i.e. aboveground plant biomass, patch size, association with coral reef habitat) and species composition (i.e. cryptic and vagrant species) were also important in community organization within these systems (Heck 1977, 1979, Heck & Wilson 1987). These factors could also explain inconsistencies in results and the lack of significant differences in species density and richness between bare sand and seagrass samples in the other studies cited (Young et al. 1976, Young & Young 1982).

That activity of abundant and diverse predator guilds frequently cause minimal impacts on prey assemblages may seem counter-intuitive; however, Strong (1992) concluded that speciose systems in general are characterized by differentiated predation since consumption is dispersed and not directed towards a single prey species. Several factors, including those related to predator activity and to spatial and temporal dynamics within the benthic community, can act to suppress a trophic cascade (i.e. downward dominance through the food chain; Strong 1992). Many of these factors are evidenced in the Florida Bay ecosystem. For example, all predators observed at experimental sites

in this study are considered trophic generalists that include high taxonomic diversity in their diets (spiny lobsters: Herrnkind et al. 1975, Kanciruk 1980, Colinas-Sánchez & Briones Fourzán 1990; fishes: Carr & Adams 1973, Stoner 1980, Livingston 1982, Motta et al. 1995). With high incidence of trophic generalists in the predator guild, predation impacts appear to be more subtle; trophic levels tend not to be as discrete (Strong 1992). Additionally, where multiple species of prey are utilized by predators and several prey species function similarly within the community, fundamental structure and function of the community would not necessarily be affected by fluctuating abundances of one or a few prey species (Menge & Lubchenco 1981).

In addition, *Panulirus argus* undergoes dietary shifts relative to its ontogeny (Herrnkind et al. 1975, Kanciruk 1980) as do many piscine predators inhabiting seagrass beds (Carr & Adams 1973, Stoner 1980, Livingston 1982, Motta et al. 1995), including *Haemulon aurolineatum* (Sedberry 1985), *Anisotremus virginicus* (Randall 1967), and *Lutjanus griseus* (Hettler 1989) observed in the present study. The impact of a particular predator species, and the subsequent role that each species plays in community regulation, therefore, may change throughout the year due to ontogenetic changes in their diet (Nelson 1981). Also, many predator species that inhabit seagrass beds do so as juveniles, which have more generalized diets than older individuals (Livingston 1982). Ontogenetic and seasonal shifts, in concert with generalistic resource use among juvenile and adult stages of predators, would also tend to dilute major impacts by predators upon benthic prey.

The foraging behavior of the spiny lobster could possibly suppress a trophic cascade also. Spiny lobster foraging entails slow, undirected, meandering movements while probing the sediment in search of food (Herrnkind 1980, Kanciruk 1980). Finding suitable prey items, therefore, is unpredictable given the microhabitat preferences of individual prey species and the overall habitat heterogeneity within the seagrass bed. Molluscan prey in Florida Bay are not aggregated (Nizinski 1998); therefore, at each successful encounter, a predator feeding on these species finds only 1 to a few prey individuals each time, which may or may not be conspecifics, thus reducing the probability of defaunating the foraging grounds by eliminating a specific species. Lobsters may also feed on prey comprising a wide range of sizes. Various species of lobsters are capable of manipulating and ingesting large individual prey, but these species preferred prey smaller than the predicted, optimal prey size (Griffiths & Seiderer 1980, Tegner & Levin 1983, Edgar 1990a, Robles et al. 1990). Predators feeding on individuals throughout the observed size range further

randomize prey size-frequency distributions by distributing predation pressure over the entire, available prey population.

Spatial and temporal heterogeneity within both predator and prey assemblages also prevent intense consumption from becoming a runaway cascade (Strong 1992). Predator abundances in Florida Bay were variable and unpredictable at individual experimental structures between sampling periods. Ontogenetic shifts in habitat use would add further to variability in predator abundance. Since Florida Bay is an important nursery habitat for many species of finfishes and crustaceans, long-term residency in the seagrass bed would not be expected for all predatory species. Predator species composition and abundance would fluctuate as juveniles and subadults living in the seagrass bed matured and subsequently moved to adult habitats. This behavior is characteristic of spiny lobsters (e.g. Herrnkind 1980), gray snapper (Rutherford et al. 1989) and other species of reef fishes utilizing seagrass beds as nursery habitat (e.g. Heck & Weinstein 1989, Peters et al. 1994).

Variations in abundance and spatial distribution of prey populations in Florida Bay also contributed to the overall spatial and temporal heterogeneity of the system. Significant location differences were apparent in gastropod and bivalve abundances as well as gastropod species richness. In general, within a location, the prey assemblage consisted of randomly distributed, speciose assemblages, with species represented only by a single or a few individuals per sample. Observed patterns in the benthos could be an artifact of the sampling regime (both in timing and frequency of sampling periods and sieve size utilized); however, similar patterns of variability in local spatial and temporal distributions of mollusc populations have been independently documented in Jamaica (Jackson 1972) and Australia (Edgar 1990a, Jones et al. 1990).

The results presented here provide evidence that the seagrass/macroalgal community of Florida Bay does not appear to be regulated primarily by predation activities of the Caribbean spiny lobster and various finfishes; rather, localized impacts of predation upon benthic community structure are minimal. Interconnections between consumers and their prey appear to be reticulated; there seems to be high connectivity within the trophic web. Consumers are resource generalists often preying upon individuals from multiple trophic levels. Considering the overall habitat heterogeneity exhibited by this system, in concert with spatial and temporal variability within predator and prey abundances and distributions, and ontogenetic shifts in diets and habitat use by predators, consumption can only be described as diffuse in time and space within the Florida Bay seagrass habitat. Sih et al. (1985)

hypothesized that predation impacts would be less in more complex systems with high structural heterogeneity compared to simpler rocky intertidal and lake communities. Alternatively, predation effects may be concealed by other factors and thus not observable or measurable without more extensive sampling efforts. The patterns of prey abundance, size, and diversity observed throughout this experiment could have been produced historically by predation of spiny lobsters and finfishes. Possibly, mollusc populations are now maintained at relatively constant levels through a variety of mechanisms. Direct and indirect effects are difficult to observe and quantify in some habitats or communities. However, similarities in the low predation impacts found between the present study and those conducted in other subtropical and tropical systems suggest that predator–prey dynamics operate in a similar fashion in these regions and that these communities are not regulated from the top down.

As has been suggested by others (e.g. Dayton 1984, Alongi 1989, Wilson 1991), soft-sediment systems seem to abide by different rules and probably need their own paradigms. Many benthic ecology concepts formulated from temperate work are not readily applicable to tropical benthic ecosystems (Alongi 1989). Alongi (1990) hypothesized that the tropics are not the stable, environmentally constant habitats once thought. Therefore, benthic community structure must be examined in the light of many potential regulatory factors that constantly change both temporally and spatially (Alongi 1989). As was the case in the rocky intertidal (Menge & Sutherland 1987), the most realistic view of subtropical and tropical soft-bottom benthic community structure will probably involve the interplay between several regulatory factors. Which factor(s) dominate, therefore, will be dependent on, and vary with, environmental conditions and types of organisms found within these communities. Mollusc populations within Florida Bay are undoubtedly influenced by a variety of mechanisms including predation, recruitment, and physical factors. Why *Panulirus argus* does not function as a dominant predator in the seagrass meadows of Florida Bay may be a function of the ecology of this system. Experimental locations were representative of distinct sub-environments in Florida Bay (Nizinski 1998). Thus, regional differences in macrophyte biomass, sediment composition and water quality (Nizinski 1998), which are complementary to the hydrology of the ecosystem, may be of primary importance in structuring prey communities within Florida Bay.

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