

ONTOGENETIC DIET SHIFTS IN NASSAU GROUPER: TROPHIC LINKAGES AND PREDATORY IMPACT

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ABSTRACT

Understanding which fauna and flora from seagrass beds serve as primary food for reef-based commuturs is critical in defining trophic linkages between shallow-water habitats of tropical oceanic regions. Although numerous studies have documented the relative importance of crustaceans in the diet of reef fishes associated with tropical seagrass meadows, it is unknown if trophic importance corresponds to a significant effect on prey distribution and abundance patterns. We quantified size-specific diet of juvenile Nassau grouper (*Epinephelus striatus*) inhabiting natural and artificial patch reefs, and manipulated the density of artificial patch reefs (0, 8, and 16 patch reefs per ha) to examine the predatory impact of patch reef associates on nocturnally foraging crabs. Stomach content analysis indicated an ontogenetic shift in diet, where small grouper (<20 cm TL) consumed mainly brachyuran crabs and other small crustaceans, and large grouper (>30 cm TL) consumed primarily fish. Mid-size fish (20.0–29.9 cm TL) were transitional in diet, with crustaceans occurring more frequently than fish. Diet was least diverse for large fish, and nearly identical for mid-size and small fish. Similar numbers of prey taxa were ingested in natural and artificial patch reefs. Before patch reefs were deployed in the field, nighttime band censuses revealed a mean density of 3 crabs per 240 m² (ranges = 0–8 crabs/transect) in nearby seagrass beds. After patch reefs were deployed, crab densities dropped by one-half to 43-fold in sites with patch reefs compared to control sites (0 patch reefs). There was a negative and significant relationship between grouper density (no. ha⁻¹) and crab density (no. 240 m⁻²) at all sites and locations combined. These results suggest that patch reef associated predators have a significant predatory impact on nocturnally foraging crabs in adjacent seagrass meadows, and highlight an important trophic link between tropical patch reef and seagrass habitats.

Tropical seagrass meadows are often interspersed with patch coral reefs and unvegetated sand flats, creating a mosaic of shallow-water habitats. Important ecological linkages between these habitats include fluxes of energy or materials, and obligate use of a combination of habitats in the life history of animals (Myer et al., 1983; Parrish, 1989; Jones et al., 1991 and references therein). For example, the larval and postlarval stages of numerous species of reef fish and spiny lobster settle in seagrass or macroalgal habitats, with subsequent ontogenetic shifts to crevice and patch reef habitats (see reviews by Parrish, 1989; Herrnkind et al., 1994; Eggleston, 1995). Many of these species use patch reefs as a structural refuge from predation during the day, and are strongly dependent on food from adjacent seagrass and soft-bottom habitats taken during crepuscular and nighttime periods (Parrish, 1989; Jones et al., 1991, 1992). Understanding which fauna and flora from seagrass beds serve as primary food for reef-based commuturs is critical in defining trophic linkages between shallow-water habitats of tropical oceanic regions.

Benthic crustaceans (e.g., crabs, shrimps, stomatopods) are one of the most important components of the diets of fish foraging off-reef (Heck and Weinstein, 1989; Parrish, 1989 and references therein). For fishes residing in Panamanian seagrass (*Thalassia testudinum*) meadows, stomatopods, porcelain crabs, alpheid shrimp and spider crabs

were the dominant prey items (Heck and Weinstein, 1989). Results of that study were similar qualitatively to those from Randall's (1965) earlier analysis of stomach contents for fish collected from seagrass and patch reefs habitats in the U.S. Virgin Islands and Puerto Rico. For fish collected from seagrass (*Posidonia oceanica*) meadows in the Mediterranean, brachyuran crabs and caridean shrimps were the dominant food items for scorpaenids and serranids, respectively (Bell and Harmelin-Vivien, 1983). Similarly, crustaceans were the most important component of the diet of scorpaenids collected in seagrass (*Posidonia australis*) meadows in Australia (Burchmore et al., 1984). Although these and other studies have documented the relative importance of crustaceans in the diet of reef fishes associated with tropical seagrass meadows, it is unknown whether fish predation has a significant effect on prey distribution and abundance patterns.

From a predator-prey perspective, determining the relative importance of fish predators to mobile invertebrates such as benthic crustaceans, requires the joint assessment of (i) predator diet; (ii) the intensity of predation pressure via information on spatial and temporal patterns in predator abundance and foraging; and (iii) alteration of distribution and abundance of prey resulting from different levels of predation pressure, generated through controlled manipulations. The impact of fish predation on mobile crustaceans and molluscs has been examined using artificial reefs and predator exclusion cages (Reaka, 1985; Jones et al., 1992). Reaka (1985) used artificial reefs, in conjunction with fish exclusion cages and barriers to prey movement, to examine the effects of fish predation on stomatopods in St. Croix, U.S. Virgin Islands. She found that predation was important in shallow habitats only when barriers to stomatopod migration were present, with predation pressure increasing on deeper reefs (Reaka, 1985). Conversely, Jones et al. (1992) experimentally excluded reef fish predators from adjacent soft-sediment mollusc populations in One Tree lagoon, Great Barrier Reef, and found that only two of 10 species at one of three locations exhibited a significant predation effect. There was also no evidence that predation altered the size-structure of mollusc populations (Jones et al., 1992). Thus, general conclusions regarding the importance of reef-fish predation on mobile invertebrates remains equivocal (Jones et al., 1992).

Serranids such as Nassau grouper are considered to be among the most important carnivorous fishes in coral reef systems (Randall, 1965; Kingsford, 1992; Hixon and Beets, 1993; Eggleston, 1995; Eggleston et al., 1997), yet information on their trophic biology and impact on invertebrate distribution and abundance is scant, particularly young juvenile grouper inhabiting patch reef habitats. This study was part of a larger study aimed at identifying the predatory impact of juvenile Nassau grouper inhabiting patch reefs in the central Bahamas, on reef fish, spiny lobster and brachyuran crab prey. In this paper we focus on the diet of juvenile Nassau grouper and the impact of patch reef-associated predators on nocturnally foraging crabs. The specific objectives of this study were to: (1) identify size-specific differences in the diet of juvenile Nassau grouper inhabiting natural and artificial patch reefs; (2) determine the impact of patch reef-associated predators on nocturnally foraging crabs; and (3) determine the relationship between the density of Nassau grouper and nocturnally foraging crabs.

METHODS

FIELD SITE AND ARTIFICIAL PATCH REEFS.—Field observations and experiments were conducted at two locations, Sugar Cay Bay, near Great Exuma Island and Norman's Pond Cay, near Lee Stocking

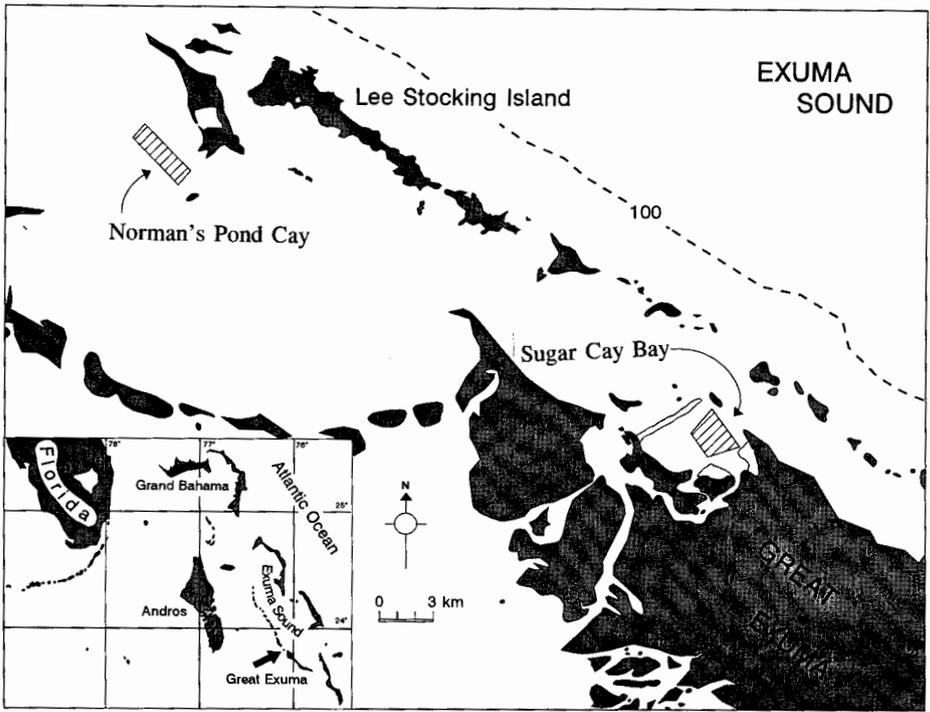


Figure 1. Two study locations, Norman's Pond Cay and Sugar Cay Bay, located near Lee Stocking Island, Bahamas.

Island (LSI), Exuma Cays, Bahamas ($23^{\circ}45'N$, $76^{\circ}10'W$) (Fig. 1). Grouper for diet analysis were collected from artificial and natural patch reefs at Sugar Cay Bay only. Sugar Cay Bay (20 km^2 in area) is composed of a shallow (2–3 m), relatively homogeneous seagrass meadow (*Thalassia testudinum*) of moderate density ($x = 396 \text{ shoots m}^{-2}$, $SD = 105$, $n = 12$ 1 m^2 quadrats) that extended onto a very shallow (0.5 m) sand shoal to the north, with patch coral heads in the center (Fig. 1). The western side of Norman's Pond Cay (Fig. 1) is characterized by a shallow (2–3 m) sand bank composed of sparse seagrass ($x = 62 \text{ shoots m}^{-2}$, $SD = 17$, $n = 12$ 1 m^2 quadrats). Patch reefs at both locations are typically dominated by the corals *Montastrea annularis* and *Porites astrooides*. The dominant macroinvertebrates at both locations are conch (*Strombus* spp.) and nocturnally foraging crabs (Majidae, Portunidae, Calappidae, Xanthidae) (see "Results: Distribution and abundance patterns of crabs and grouper").

Our design of artificial patch reefs was based on "casitas" (e.g., Eggleston et al. 1990, 1992, Eggleston and Lipcius 1992), which mimic rock and reef crevices (Fig. 2). Casitas were constructed with a reinforced concrete roof bolted to a supporting polyvinyl chloride (PVC) plastic pipe frame. Two casita sizes were used: small ($157.3 \text{ cm long} \times 105.1 \text{ cm wide} \times 3.8 \text{ cm height of opening}$) and large ($177 \times 118 \times 6 \text{ cm}$). The smaller casita opening height allowed easy entry of small fish and invertebrates (i.e., $<3.8\text{-cm}$ body height) and excluded most larger predators (Eggleston et al., 1997). Larger fish sometimes entered on their sides and resided beneath the roof, which was 6 and 12 cm above the seafloor in small and large casitas, respectively.

Impact of reef associates on nocturnally foraging crabs.—We examined the relationship between patch reef-associated predators and nocturnally foraging crab prey by manipulating casita density within sites at Sugar Cay Bay and Norman's Pond Cay. Within both locations, three 1-ha experimental sites located approximately 300 m apart were randomly assigned one of three shelter treat-

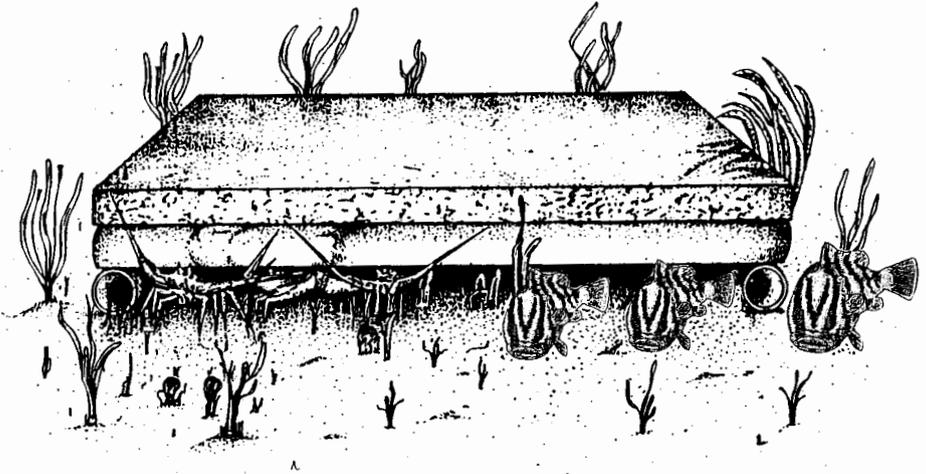


Figure 2. A large casita (artificial patch reef) constructed with a frame of PVC (polyvinyl chloride plastic) pipe and roof of reinforced concrete (177 cm length \times 118 cm width \times 6 cm height of opening).

ments: 16-casita site, 8-casita site, and a control site (0 casitas) (Fig. 3). This spacing provided a distance barrier to animal movements between sites. Each casita site contained an equal number of large and small casitas which were systematically interspersed and positioned approximately 35–40 m apart (Fig. 3). The large and small casitas were used to assess the interactive effects of shelter size and predation intensity on reef fish and spiny lobster prey (Eggleston et al., 1997).

Nighttime surveys were critical in characterizing the potential impact of predators associated with casitas on cryptic, nocturnally foraging crab prey species that were missed during daytime surveys for reef fish and Caribbean spiny lobster (Eggleston et al., 1997). Nighttime visual band censuses were conducted using SCUBA in August and October, 1990 at all three sites within each location before casita deployment, and on a monthly or quarterly basis after casita deployment in January, 1991. On each occasion, a nighttime census consisted of two parallel transects (ca. 120 m \times 2 m) across each site to observe potential prey (e.g., crabs) in seagrass beds. Transects were located approximately 30–40 m apart. We focused exclusively on crabs as potential prey since they were a dominant invertebrate component of grouper stomach contents (see "Results: Grouper diet"), and were the principal prey observed foraging in seagrass at night (pers. observ.). Band censuses were conducted 2 h after sunset. Crab carapace width (CW) was estimated to the nearest cm.

Although we conducted 78 individual nighttime band transects (13 mo \times 3 sites \times 2 transects per site), the proper experimental unit in this study was the Site (0-casita, 8-casita, 16-casita), with a total sample size of two (Sugar Cay Bay, Norman's Pond Cay). Thus, Site effects were identified with an unreplicated randomized complete block (RCB) ANOVA model with the difference between the mean number of crabs per 240 m² before versus after casita deployment (Fig. 5) as the response variable, Site (0-casita, 8-casita, 16-casita) as the treatment, and Location (Sugar Cay Bay, Norman's Pond Cay) as the blocking factor. Although this approach was somewhat conservative, the response variable was free from assumptions concerning statistical independence, normality and homogeneity of variances, and the model proved to be significant (see Results below). Differences between treatments (Sites) were revealed with a Ryan's *Q* multiple comparison test.

RELATIONSHIP BETWEEN GROUPER AND CRAB DENSITIES.—Casitas were censused visually by SCUBA for Nassau grouper each month, from initial placement in January 1991 through termination of the study 18 mo later in June, 1992. During our casita censuses, we recorded the number and sizes of all Nassau grouper. Total fish length (TL) was estimated using a ruler attached perpendicular to the

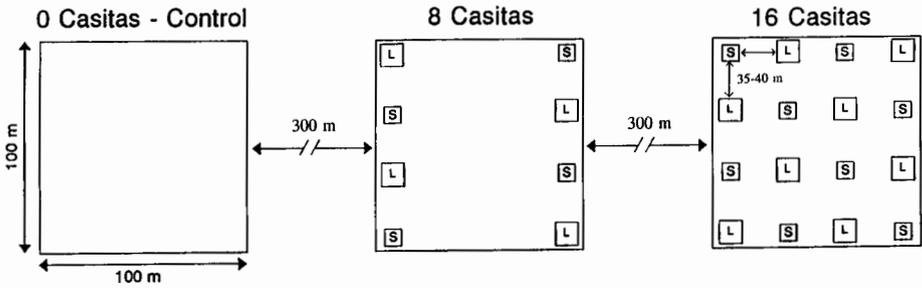


Figure 3. Schematic representation of experimental design. S = small and L = large.

far end of a 70-cm rod held out from a diver (see Bohnsack and Bannerot, 1986). This device increased the accuracy of visual estimations of body size. For a given location, we examined the relationship between mean crab density (no. 240 m^{-2}) and the total number of small- and mid-sized Nassau grouper ($<30\text{ cm TL}$) residing in casitas (i.e., number of grouper per hectare) with an AR1 time series regression model (SAS Procedure "Mixed"). We chose to focus on the potential impact of grouper $<30\text{ cm TL}$ because this size-class preys primarily on slow-moving crustaceans (see "Results: Grouper Diet"), and inclusion of large, piscivorous grouper may have diminished our ability to detect a grouper predator effect on crab prey. The AR1 time series model was chosen over a simple linear least-squares model because the casitas and sites were repeatedly sampled over time (i.e., errors were correlated). Data from Sugar Cay Bay and Norman's Pond Cay were pooled because the location blocking factor was non-significant (see "Results" below). Despite periodic removal of small numbers of Nassau grouper from certain casitas at Sugar Cay Bay for stomach content analysis ($\sim 5\%$ of the total no./ha), overall grouper abundance increased over time due to immigration (Eggleston et al., 1997). Any variation in crab prey abundances due to changing grouper abundance over time (either due to periodic removals or immigration) was accounted for in the regression approach described above.

GROUPE REMOVAL AND DIET.—During August 1991, 8 mo after initial casita deployment, we randomly selected equivalent numbers of small and large casitas at each site (8-casita, 16-casita) in Sugar Cay Bay to serve as permanent grouper Removal versus Control reefs (Eggleston, et al., 1997). Grouper were then removed from selected casitas 2 h after dawn by spearfishing. This procedure was repeated after casita censuses in September and December 1991, and March and April 1992. Nassau grouper were also removed from natural patch reefs in March and April, 1992 to compare diet between natural and artificial patch reefs.

Grouper removed from reefs were placed immediately on ice and transported to the laboratory at LSI. No regurgitated prey were observed. For each specimen total body weight and length (TL) were recorded. The stomach was removed and preserved in 10% Formalin for 24 h, then switched to 50% ethanol for storage. Later, each stomach was opened, contents removed, and prey were identified to the lowest possible taxa, enumerated, blotted dry, and weighed to the nearest 0.01 g. Within a stomach, prey pieces within a taxon (e.g., legs, chelae) were counted as a single individual unless they clearly came from more than one individual. Stomach contents that were deemed incidental ingestions (i.e., coral rubble, algae, and turtle grass) were excluded from dietary analysis.

Although many prey items were identified to species, diet was analyzed at the family level in terms of numerical percentage composition (%N), gravimetric percentage composition (%Wt), and percent frequency of occurrence (%FO). These three analyses were combined to yield a more comprehensive assessment of prey importance, the index of relative importance (IRI) (Pinkas et al. 1971), defined as

$$\text{IRI} = (\%N + \%Wt) \times \%FO$$

A comparison of fish collected from three sites, 8-casita, 16-casita and natural patch reefs, revealed that fish lengths were not equivalent between sites (Kruskal-Wallis [K-W] one-way ANOVA, $P = 0.001$). As a result, the only unbiased between-site comparison involved mid-size fish, 20.0–29.9 cm TL. Fish lengths within this size class were equivalent across sites (K-W one-way ANOVA, $P = 0.11$). A comparison of the effect of fish size on diet used all fish, regardless of collection site, in three size classes: small (<20 cm), mid-size (20.0–29.9 cm), and large (>30 cm TL).

Diet overlap was calculated using an index of proportional similarity (PS) (Wallace 1981, Grover 1990) defined as

$$PS = 1 - 0.5 (\sum |P_{xi} - P_{yi}|)$$

where P_{xi} and P_{yi} are the proportions of prey category i in the diet at sites (or size classes) x and y , respectively. This index was chosen because it does not require resource-availability data (Wallace 1981), its value is independent of sample size (Kohn and Riggs, 1982), and it estimates overlap accurately for overlaps between 7% and 85% (Linton et al., 1981). The index ranges from 0.0 (indicating no overlap) to 1.0 (indicating complete overlap of diets). Values greater than 0.6 are generally considered to demonstrate significant overlap (Mathur, 1977, Wallace and Ramsey, 1983).

Diversity of diet was calculated for each size class and habitat using the Shannon-Wiener index, H , (Wilson and Bossert, 1971), defined as

$$H = -\sum P_i \log P_i$$

where P_i is the proportion of prey category i in the diet, by size class (or habitat).

RESULTS

DISTRIBUTION AND ABUNDANCE PATTERNS OF CRABS AND GROUPER.—In August and October 1990, before casita deployment in the field, an average density of 3 crabs per 240 m² (ranges = 0–8 crabs per transect) was observed during nighttime censuses in seagrass flats at all experimental sites in Sugar Cay Bay and Norman's Pond Cay (Fig. 4). Crabs ranged in size from 30–140 mm carapace width (CW), and were composed primarily of the families Calappidae, Majidae and Portunidae. No Nassau grouper were observed at any site during this time (Fig. 4). After casita deployment, crab densities dropped by one half to 43-fold in casita sites compared to control sites (Fig. 4), whereas grouper densities ranged from a few to 70 ha⁻¹ (Fig. 4).

IMPACT OF CASITA ASSOCIATES ON NOCTURNALLY FORAGING CRABS.—The difference between the mean number of crabs per 240 m² before versus after casita deployment (Fig. 5) varied significantly according to Site (RCB ANOVA; Site: $F = 19.57$, $df = 2,5$, $P < 0.05$); the blocking factor was non-significant ($F = 0.08$, $df = 1,5$, $P > 0.05$). There was no difference in mean crab densities in control sites before versus after casita deployment, whereas there was a significant decrease in crab densities after casita deployment at the 8- and 16-casitas sites (Ryan's Q test; Fig. 5).

GROUPER DIETS.—At all sites in Sugar Cay Bay, less than 40% of grouper collected had empty stomachs. Prey items were observed in the stomachs of 79% of grouper removed from casitas at the 8-casita site, in 61% of stomachs from the 16-casita site, and in 78% of stomachs from natural patch reefs. Grouper generally appeared to ingest their prey whole, with the exception of autotomized alpheid and brachyuran chelae. Although gut contents

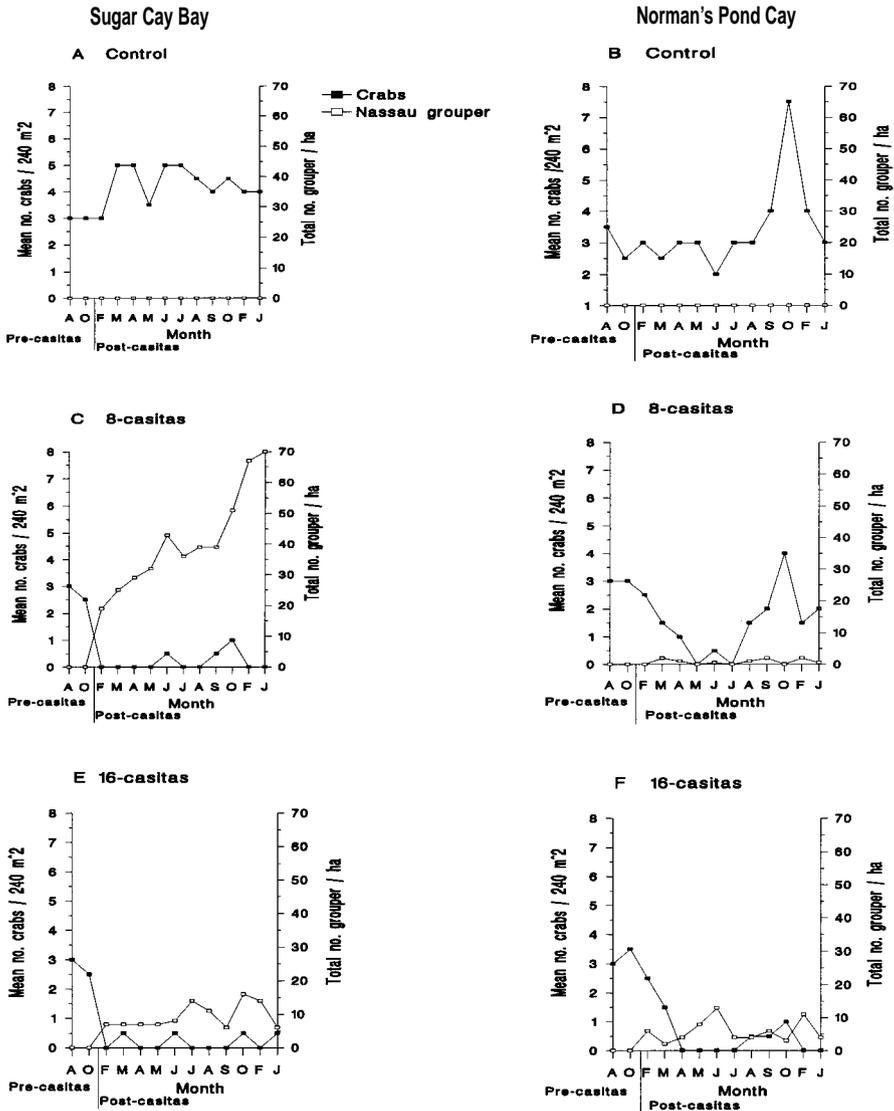


Figure 4. Changes in the density of nocturnally foraging crabs, quantified during nighttime band censuses, and Nassau grouper (<30 cm TL) residing in casitas or seagrass from August 1990 to June 1992. "Pre-casitas" denotes period before casitas were deployed; "post-casitas" denotes period after casita deployment.

were analyzed at the familial level, many prey were identified to genus or species (Table 1), and some differences in prey composition were seen between casita sites and natural patch reefs at the generic level.

The relative importance of crustaceans versus fish, and species abundance and diversity in the diet varied with grouper size. Small grouper ate greater numbers of prey than large grouper, but the individual prey items ingested by large grouper generally weighed more. The dominant small prey ingested by small grouper were stomatopods and

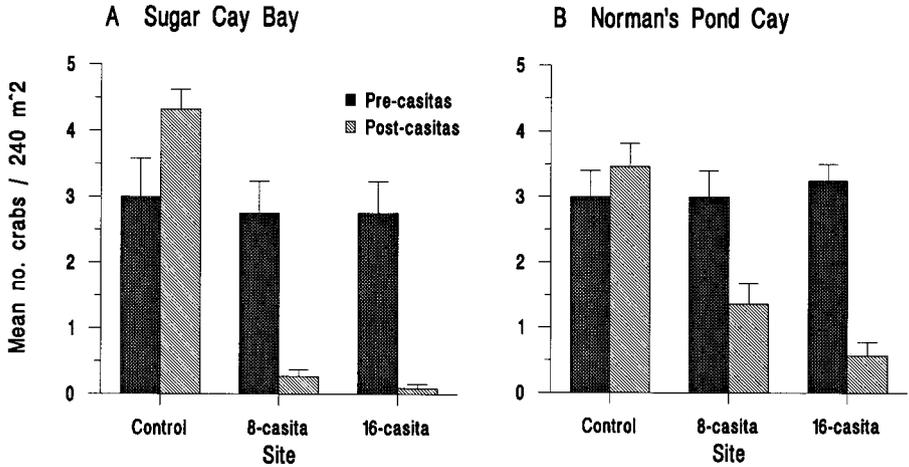


Figure 5. The effects of Site (Control, 8-casita, 16-casita) and Casita deployment (pre-casita vs post-casita) on the mean number of nocturnally foraging crabs per 240 m² at (A) Sugar Cay Bay and (B) Norman's Pond Cay. Values are means + 1 SE. Sample sizes for the pre-casita means are four (2 transects per month \times 2 mo), whereas sample sizes for the post-casita means are 22 (2 transects per month \times 11 mo). The difference between the mean number of crabs before versus after casita deployment at Sugar Cay Bay was 1.32, -2.48, and -2.67 at 0-, 8-, and 16-casita sites, respectively. The difference between the mean number of crabs before versus after casita deployment at Norman's Pond Cay was 0.46, -1.64, and -2.68 at 0-, 8-, and 16-casita sites, respectively. See text for significance levels in the analyses of mean differences.

palaemonid shrimp, both of which were of minor importance in the diet of mid-size grouper and absent from the diet of large grouper (Table 2). Crabs, especially majids and portunids, were very important in the diet of small- and mid-size grouper. Spider crabs (majids) were the dominant prey for mid-size grouper at all sites (Table 3), although fish were nearly as important in the diet on natural patch reefs, and xanthid and portunid crabs were nearly as important in the diet at the 8-casita site. Majid crabs of the genus *Pitho* were the single most numerically abundant prey item. Fish were the most important prey for large grouper, and also made a large contribution to the diet of mid-size grouper (Tables 2,3). Majid crabs were the only other prey of note in the diet of large grouper. For grouper from all sites at Sugar Cay Bay (Tables 2,4), diet was least diverse for large fish ($H = 0.5903$) and nearly identical for mid-size ($H = 1.0667$) and small ($H = 0.9017$) fish. A number of prey taxa were represented by only one or two prey items: Gastropoda, Pelecypoda, Cephalopoda, Pycnogonida, Isopoda, Penaeidae, Paguridae, Porcellanidae, and Calappidae. While most of these taxa contributed little to the diet, a lone octopus ingested by a mid-size grouper from the 16-casita site was quite large, so its contribution to the diet was noticeable in terms of prey weight (Tables 2,3). In comparing the diet of mid-size grouper across sites (8-casita, 16-casita, natural patch reefs), diet was least varied in terms of the number of prey taxa at the 8-casita site, compared to other sites (Table 3). Similar numbers of prey taxa were ingested at the 16-casita site and natural patch reefs (Table 3). At the 16-casita site, more taxa of crabs were ingested than at the other sites. Diversity index values for mid-size grouper reflected these patterns: $H = 0.8771$ at the 8-casita site, $H = 1.0293$ at the 16-casita site, and $H = 1.0075$ at natural patch reefs (Table 4).

Table 1. The occurrence of prey items in the diet of Nassau grouper by habitat (SC8: 8-casita site; SC16: 16-casita site; Patch: natural patch reefs). (Provisional identifications in parentheses).

Prey taxa		SC8	SC16	Patch
Gastropoda				X
	(<i>Cerithium</i> sp.)			X
Pelecypoda				X
Cephalopoda	<i>Octopus</i> sp.		X	
Pycnogonida			X	
Stomatopoda		X		
	<i>Alima</i> (<i>hyalina</i>)	X		
	<i>Squilla</i> sp.	X		
	<i>Pseudosquilla</i> sp.	X	X	X
Isopoda	<i>Rocinela</i> (<i>signata</i>)			X
Decapoda		X	X	X
Penaeidae				X
Caridea		X	X	X
Palameonidae	<i>Periclimenes</i> sp.	X	X	X
	<i>P. americanus</i>			
	<i>P. patae</i>			
Alpheidae		X	X	X
	<i>Alpheus</i> sp.	X		X
	<i>Synalpheus</i> sp.	X	X	
Hippolytidae	<i>Thor</i> sp.	X		
	<i>Trachycaris restricta</i>	X		
Paguridae				X
Porcellanidae	<i>Petrolisthes</i> sp.			X
Calappidae	<i>Calappa gallus</i>		X	
Majidae	<i>Macrocoeloma diplacanthum</i>	X		
	<i>Mithrax</i> sp.	X		X
	<i>M. coryphe</i>			
	<i>M. forceps</i>			
	<i>M. spinosissimus</i>			
	<i>Pitho</i> sp.	X	X	X
	<i>P. aculeata</i>			
Portunidae		X	X	
	<i>Cronius tumidulus</i>	X		X
	<i>Portunus</i> sp.	X	X	
	<i>P. bahamensis</i>			
	<i>P. ordwayi</i>			
Xanthidae		X		
	<i>Micropanope</i> sp.	X	X	
	(<i>M. pusilla</i>)			
	<i>Panopeus</i> sp.	X		
Goneplacidae			X	
	<i>Euryplax nitida</i>	X	X	X
Pisces		X	X	X
Lutjanidae		X		
Scaridae		X	X	
	<i>Scarus</i> sp.			X
Gobiidae	<i>Corhoterus</i> sp.			X

Table 2. Composition of the diet of Nassau grouper as a percentage, in terms of weight (%Wt), number (%N), frequency of occurrence (%FO), and index of relative importance (%IRI), where $IRI = (\%N + \%Wt) \times \%FO$. Results are separated by size class, with small <20 cm, mid-size 20.0–29.9 cm, and large ≥ 30 cm TL.

Prey items	Size Class											
	Small				Mid-size				Large			
	N=12		N=40		N=40		N=6		N=6		N=6	
	%Wt	%N	%FO	%IRI	%Wt	%N	%FO	%IRI	%Wt	%N	%FO	%IRI
Gastropoda					0.11	1.63	2.50	0.10				
Pelecypoda					0.03	0.81	2.50	0.05				
Cephalopoda					20.37	0.81	2.50	1.17				
Pycnogonida					0.03	0.81	2.50	0.05				
Stomatopoda	38.12	10.64	33.33	25.18	4.27	2.44	7.50	1.11				
Isopoda					0.32	0.81	2.50	0.06				
Decapoda	4.94	6.38	16.67	2.93	1.62	6.50	20.00	3.60	10.04	10.00	16.67	3.22
Penaeidae					0.41	1.63	5.00	0.22				
Caridea	0.96	6.38	25.00	2.84	1.11	9.76	22.50	5.41				
Palaemonidae	3.35	19.15	41.67	14.52	0.89	10.57	17.50	4.44				
Alpheidae	4.47	10.64	25.00	5.85	4.57	7.32	22.50	5.92	0.18	10.00	16.67	1.64
Hippolytidae					0.76	2.44	5.00	0.35				
Paguridae									1.16	10.00	16.67	1.79
Porcellanidae					0.27	0.81	2.50	0.06				
Calappidae					2.86	0.81	2.50	0.20				
Majidae	12.44	19.15	41.67	20.39	19.54	23.58	40.00	38.17	33.05	20.00	16.67	8.52
Portunidae	30.46	19.15	33.33	25.62	14.91	7.32	20.00	9.84				
Xanthidae	2.55	4.26	16.67	1.76	5.43	8.13	22.50	6.75				
Goneplacidae	2.55	2.13	8.33	0.60	0.84	2.44	7.50	0.54				
Pisces	0.16	2.13	8.33	0.30	21.67	11.38	30.00	21.95	55.58	50.00	83.33	84.83

Considering diet overlap as measured by the index of proportional similarity (Table 5), significant overlap (i.e., $PS > 0.6$) was not seen between any of the size classes or between any of the sites in terms of prey weight. However, in terms of the number of prey, the diet of all small and mid-size grouper demonstrated significant overlap, as did the diet of mid-size grouper at the 8-casita site and natural patch reefs (Table 5). Although several cross-over comparisons (size class versus habitat) showed a high degree of overlap, both in terms of prey weight and numbers of prey, the validity of these comparisons is questionable because 75% of small grouper came from the 8-casita site, 83% of large grouper came from natural patch reefs, and all of the site data are based on mid-size grouper.

RELATIONSHIP BETWEEN DENSITIES OF GROUPER AND CRABS.—There was a negative and significant relationship between the density (no./ha) of medium- and small-sized Nassau grouper (<30 cm TL) observed during monthly daytime censuses at all sites, and the density of nocturnally foraging crab prey (Fig. 6).

DISCUSSION

The use of artificial reefs as analogs for natural reefs must be interpreted cautiously (e.g., Jones et al. 1991). The responses of predator and prey to novel substrata and shelter placed in their habitat may differ from that exhibited under totally natural circumstances.

Table 3. The composition of the diet of mid-size (20.0–29.9 cm TL) Nassau grouper, by habitat, as a percentage, in terms of weight, number, frequency of occurrence, and index of relative importance, as defined in Table 2. SC8 = 8-casita site at Sugar Cay Bay; SC16 = 16-casita site at Sugar Cay Bay; and Patch = natural patch reefs in Sugar Cay Bay.

Prey items	Habitat											
	SC8				SC16				Patch			
	N=17				N=12				N=11			
	%Wt	%N	%FO	%IRI	%Wt	%N	%FO	%IRI	%Wt	%N	%FO	%IRI
Gastropoda									0.41	5.71	9.09	1.15
Pelecypoda									0.10	2.86	9.09	0.55
Cephalopoda					42.22	2.78	8.33	9.12				
Pycnogonida					0.06	2.78	8.33	0.57				
Stomatopoda					6.83	5.56	16.67	5.02	3.66	2.86	9.09	1.22
Isopoda									1.22	2.86	9.09	0.76
Decapoda	1.61	1.92	11.76	0.61	1.68	13.89	33.33	12.62	1.52	5.71	18.18	2.71
Penaeidae									1.52	5.71	18.18	2.71
Caridea	1.50	9.62	29.41	4.76	0.22	5.56	16.67	2.34	2.34	14.29	18.18	6.23
Palaemonidae	0.86	7.69	17.65	2.20	0.90	16.67	16.67	7.12	0.91	8.57	18.18	3.56
Alpheidae	8.70	9.62	29.41	7.84	1.12	5.56	16.67	2.71	6.91	5.71	18.18	4.73
Hippolytidae	3.01	5.77	11.76	1.50								
Paguridae												
Porcellanidae									1.02	2.86	9.09	0.73
Calappidae					5.94	2.78	8.33	1.77				
Majidae	24.92	26.92	47.06	35.51	15.90	13.89	33.33	24.15	21.04	28.57	36.36	37.20
Portunidae	28.25	9.62	23.53	12.97	15.34	8.33	25.00	14.40	1.52	2.86	9.09	0.82
Xanthidae	17.51	17.31	47.06	23.84	2.13	2.78	8.33	0.99				
Goneplacidae					1.34	5.56	16.67	2.80	0.71	2.86	9.09	0.67
Pisces	13.64	11.54	29.41	10.78	6.33	13.89	33.33	16.39	57.11	8.57	27.27	36.94

Natural reefs in the vicinity of Lee Stocking Island range from small (1 m²), isolated patches to nearly contiguous reefs that extend hundreds of meters (D. Eggleston, pers. obs.). Thus, we feel that the density and dispersion of casitas in this study is somewhat representative of natural patch reefs. Moreover, the density and species diversity of reef fish inhabiting casitas is similar to natural patch reefs in the Bahamas and Caribbean (Eggleston et al., 1997). Thus, we conclude that our patch reef manipulation was ecologically realistic and representative of natural systems.

The results of this study suggest that patch reef associated predators have a significant predatory impact on nocturnally foraging crabs in adjacent seagrass meadows. Moreover, these results highlight an important trophic link between tropical patch reef and seagrass habitats. Crab densities at experimental and control (no casitas) sites were similar before reef deployment, but densities at experimental sites were reduced by one-half to 43-fold after reef deployment. Crabs were rarely observed residing beneath artificial patch reefs, and probably reside buried in sand habitats during the day, emerging to feed at night. Stomach content analysis of Nassau grouper removed from casitas indicated an ontogenetic shift in diet, whereby small grouper (<20 cm TL) consumed mainly small crustaceans, and large grouper (>30 cm TL) consumed primarily fish. Mid-size fish (20.0–29.9 cm TL) were transitional in diet, with crustaceans occurring more frequently than fish. Mid-size fish also possessed the most taxonomically diverse diet. For mid-size grouper,

Table 4. Index of diversity ($H = -\sum P_i \log P_i$), for diet of mid-size Nassau grouper by habitat, and for grouper from all habitats by size class. Size classes in cm TL.

Size class	Habitat	H
20.0–29.9	SC8	0.8771
20.0–29.9	SC16	1.0293
20.0–29.9	Patch	1.0075
<20.0	all	0.9017
20.0–29.9	all	1.0667
>29.9	all	0.5903

the diversity (H') of diet for fish collected from natural patch reefs was intermediate between the 8- and 16-casita sites, and the total numbers of prey items were similar between fish collected from natural patch reefs and the 16-casita site. Thus, the diet of Nassau grouper was generally similar between natural and artificial patch reefs. Finally, there was a negative and significant relationship between the density of small- to mid-sized Nassau grouper observed during daytime casita surveys, and the density of nocturnally foraging crabs.

ONTOGENETIC SHIFTS IN GROUPER DIET.—The shift in grouper diet from primarily crustaceans at small sizes (<20.0 cm TL) to mainly fish at large sizes (>30.0 cm TL), was similar to ontogenetic shifts in trophic habits of *E. striatus* collected from natural reef systems in the Virgin Islands and Puerto Rico (Randall 1965). Similarly, stomach contents of juvenile *E. striatus* (5–19 cm TL) collected from seagrass beds near Panama contained primarily porcellanid and xanthid crabs with minor amounts of fish (Heck and Weinstein, 1989). Moreover, stomach content analysis of a congeneric species collected from Campeche Bank, Yucatán, Mexico, revealed that the juvenile red grouper (*E. morio*) also preys heavily on demersal crustaceans such as brachyuran crabs and stomatopods (Brule and Rodriguez, 1993). Thus, the collective evidence from stomach content analy-

Table 5. Index of proportional similarity (PS) for diet of Nassau grouper, in terms of prey weight and number of prey, by habitat and size class. Size classes in cm TL. Values below the diagonal are based on prey weight. Values above the diagonal are based on number of prey.

Habitat Size Class	NUMBER OF PREY----->					
	SC8 20–29.9	SC16 20–29.9	Patch 20–29.9	All <20	All 20–29.9	All >29.9
SC8 20–29.9	*	0.57	0.63	0.61	0.79	0.43
SC16 20–29.9	0.44	*	0.56	0.69	0.71	0.43
Patch 20–29.9	0.47	0.32	*	0.56	0.75	0.40
All <20	0.51	0.42	0.26	*	0.68	0.38
All 20–29.9	0.62	0.71	0.56	0.43	*	0.45
All >29.9	0.40	0.24	0.78	0.18	0.43	*

<-----PREY WEIGHT

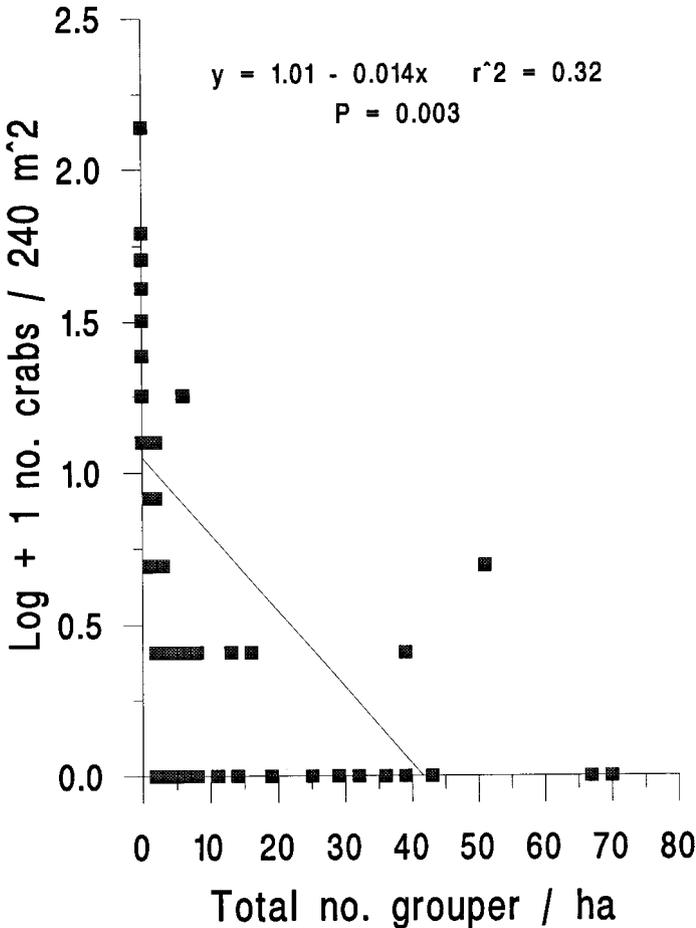


Figure 6. The relationship between grouper density (no. ha⁻¹), quantified during daytime casita censuses, and crab density (no. 240 m⁻²), quantified during nighttime band transects, at all Sites and Locations combined. The figure represents 78 individual data points (2 locations × mean of 2 transects per site × 3 sites × 13 mo); however, many of the x and y values are the same, which mask numerous points. Y -values were log + 1 transformed to help linearize the relationship.

sis of Nassau grouper in this study and others (Randall, 1965; Heck and Weinstein, 1989), combined with our observations of reduced densities of nocturnally foraging crabs where grouper densities were enhanced, suggests that small Nassau grouper forage off-reef during crepuscular or nighttime periods on slow moving crustaceans. Juvenile Nassau grouper residing on patch reefs are capable of short bursts of speed that allow them to ambush crabs located up to 7 m away from a patch reef, and return to a reef within 5 s (D. Eggleston, pers. observ.).

Benthic crustaceans, particularly crabs, generally appear to be an important prey item for reef fish (see reviews by Parrish, 1989; Jones et al., 1991). For example, benthic crustaceans accounted for 76% of the food in the diets of reef fish in the northern Hawaiian Islands (Parrish et al. 1985). Stomach contents of fish collected in their study contained mainly crabs, with shrimps, stomatopods, and amphipods also present in appre-

ciable numbers (Parrish et al., 1985). Crustaceans were also reported to be extremely important components of the diet for reef fish in the Great Barrier Reef, Australia (Williams and Hatcher, 1983).

The propensity for large grouper to consume primarily fish (Randall, 1965; this study) may be due to increased visual perception and swimming burst speed with increasing body size (e.g., Kao et al., 1985; Ryer, 1988). Large grouper are probably foraging on reef fish prey that are either associated with a reef (Eggleston et al., 1997) or in adjacent seagrass meadows. In our companion study (Eggleston et al., 1997), the total abundance and species richness of medium reef fish prey (4–10 cm TL) was significantly higher in small shelters from which grouper were removed. When we compared species' relative abundances on casitas with low versus high numbers of Nassau grouper, grouper appeared to reduce reef fish prey in a generalized, non-selective pattern, with no difference in the number of rare versus common prey species that were extirpated (Eggleston et al., 1997).

In terms of habitat-specific differences in diet, there was a slight trend towards greater numbers of fish in the diet of medium-sized grouper taken from natural patch reefs compared to casitas. However, in general, the stomach contents of grouper collected from natural patch reefs was similar to that observed for grouper collected from casitas. Given that Nassau grouper forage in areas surrounding reefs, the type of shelter, either natural or artificial, may have little effect on diet.

TROPHIC LINKAGES AND PREDATORY IMPACT.—The results from this study suggest that the high biomass of Nassau grouper observed on patch reefs (1–22 fish per casita) is supported, at least in part, by brachyuran crabs foraging in adjacent seagrass beds. Thus, important trophic linkages exist between small (<20 cm TL) and medium (20–29.9 cm TL) Nassau grouper inhabiting patch reefs, and adjacent seagrass beds. The negative impact of reef associates on nocturnally foraging crabs was probably due to a suite of potential reef-associated predators. Other potential predators included apogonids, balistids, haemulids, holocentrids, labrids, lutjanids and sparids, as well as the Caribbean spiny lobster, *Panulirus argus* (Eggleston et al., 1997). However, with the exception of *P. argus*, which were relatively abundant, *E. striatus* were, on average, five to seven times more abundant than all of the remaining potential predators combined. Size-specific predation by *P. argus* on brachyuran crabs is unexplored, and predation by lobster may have a significant impact on local crab populations. Nevertheless, our results suggest that the trophic importance of brachyuran crabs to juvenile Nassau grouper equates with a significant predatory effect on crab distribution and abundance patterns in seagrass beds within our experimental sites.

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