Influence of shelter availability on interactions between Caribbean spiny lobsters and moray eels: implications for artificial lobster enhancement

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ABSTRACT: The Caribbean spiny lobster *Panulirus argus* is a valuable fishing resource, but local populations may be limited by availability of crevice shelter on juvenile (seagrass) habitats. This has prompted research into the potential density enhancement of juvenile lobsters with 'casitas', large (1.1 m^2 surface area) but low-lying (3.8 cm entrance height) artificial shelters that exclude large predators. Moray eels (Muraenidae), however, fit into casitas and could therefore pose a threat to lobster enhancement. In a shelter-poor reef lagoon, we examined potential interactions between juvenile lobsters and the locally dominant morays *Gymnothorax vicinus* and *G. moringa* in the absence (four 1 ha control sites) and presence of casitas (five 1 ha 'casita sites', each with 10 casitas), before (6 surveys) and after (22 surveys) deployment. Morays and lobsters did not interact as predator–prey, as morays neither consumed nor intimidated co-occurring lobsters. Rather, the 2 taxa appeared to compete for limited shelter on the reef lagoon, as suggested by a significant increase in density and mean size of both taxa on casita sites after deployment. Casitas significantly increased cohabitation of morays and lobsters, yet they tended to co-occur less often than expected by chance, but this result likely reflects behavioral differences between the highly gregarious, more numerous lobsters and the typically solitary, cannibalistic morays. Our study exemplifies the influence of habitat complexity on the nature of interspecific interactions and shows that *G. vicinus* and *G. moringa* would not pose a threat to lobster enhancement with casitas.

KEY WORDS: Artificial shelters · Casitas · Competition · Environmental context · Interspecific interactions · Predation · Reef lagoon

INTRODUCTION

Communities are structured by interactions between coexisting species. Interactions are positive (e.g. mutualism) when one species improves another species' environment, or negative (e.g. predation or competition) when one species detracts from the environment of other species or has an impact on its components or fitness, such as survival, growth, or reproduction. However, interspecific interactions may be conditional, potentially shifting from negative, to neutral, to positive, depending on the environmental context (Stachowicz 2001, van Baalen & Jansen 2001, Hay et al. 2004). In particular, habitat complexity may have a profound influence on the nature and outcome of interactions between local species (Forrester & Steele 2004, Grabowski 2004, Hixon & Jones 2005) because high complexity habitats provide a greater spectrum of resources and more refuges that provide protection from predators than low complexity habitats (Sih 1984, Almany 2003, Lozano-Álvarez et al. 2007).

Moray eels (Pisces: Anguilliformes: Muraenidae) and spiny lobsters (Crustacea: Decapoda: Palinuridae) typically coexist in coral reef systems. Morays are generalist predators and are certainly able to consume spiny lobsters (Lipcius et al. 1998, Weiss et al. 2006), yet spiny lobsters are usually not present in stomach contents of morays (Hiatt & Strassburg 1960, Randall 1967, Chave & Randall 1971, Young & Winn 2003). If morays switch among prey species depending on their relative abundance as most generalist predators do (van Baalen et al. 2001, Rudolf 2008), these findings may simply reflect a lower local abundance of spiny lobsters relative to other types of prey. Alternatively, morays may affect lobsters indirectly (by intimidation) rather than by consumption (Preisser et al. 2005). However, morays and lobsters often share crevices without showing any obvious interactions (Berry 1971, Abrams et al. 1983, Lozano-Álvarez & Spanier 1997, Young & Winn 2003, Weiss et al. 2006). Berry (1971) considered this occurrence as a potential mutualism, wherein the lobster would be protected from other predators (e.g. octopuses) by the moray, and the moray would profit from consuming other predators attracted by the lobster.

However, because morays (Hixon & Beets 1989, 1993, Gilbert et al. 2005) and spiny lobsters (e.g. Butler & Herrnkind 1997, Briones-Fourzán et al. 2007) strongly depend on crevice shelter for protection against their predators, the 2 taxa might compete for limited shelter. For example, on soft-bottom seagrass habitats across the Puerto Morelos reef lagoon (Mexican Caribbean), crevice shelters (e.g. solution holes, small coral heads, and the bases of sponges and octocorals) are scarce and generally small (Briones-Fourzán & Lozano-Álvarez 2001). In this and other Caribbean reef lagoons, juvenile Caribbean spiny lobsters *Panulirus argus* (Latreille, 1804) coexist with purplemouth *Gymnothorax vicinus* (Castelnau, 1855) and spotted morays *G. moringa* (Cuvier, 1829) (Young & Winn 2003, Briones-Fourzán et al. 2007).

Panulirus argus is one of the most important fishery resources in the Caribbean region (Phillips & Melville-Smith 2006), but local populations of juvenile lobsters, which are more vulnerable to predation than adults, may be limited by availability of crevice shelters. These lobsters, however, are gregarious and their per capita survival tends to increase in large shelters that allow for cohabitation of multiple lobsters across a broad size range (Dolan & Butler 2006) because the larger lobsters collectively defend the shelter from approaching predators (the 'group defense' benefit, Childress & Herrnkind 1997) while the smaller lobsters may profit from a 'dilution effect' (Eggleston & Lipcius 1992, Briones-Fourzán & Lozano-Álvarez 2008). Also, lobsters seeking shelter home in on chemical cues released by sheltered conspecifics (Ratchford & Eggle-

ston 1998), thus reducing the time of exposure (the 'guide effect' benefit, Childress & Herrnkind 1997). However, if crevice shelter is limited, resident lobsters may behave aggressively towards other conspecifics attempting to share their shelter (Childress & Herrnkind 1997). Therefore, shelter limitation increases the risk of predation for those lobsters seeking shelter and also for those sheltering alone, potentially resulting in a local demographic bottleneck (Wahle 2003).

The dire consequences of shelter limitation for juvenile *Panulirus argus* lobsters have prompted research into their potential enhancement (increase in density and biomass) with artificial shelters (review in Briones-Fourzán et al. 2007). Although artificial shelters may also attract local predators, potentially increasing mortality of resident lobsters (Butler & Herrnkind 1997, Sosa-Cordero et al. 1998, Behringer & Butler 2006), it has been found that 'casitas' (large but low-lying artificial shelters) tend to increase survival and density of juvenile lobsters by excluding large predators while offering lobsters the potential for gregariousness (Eggleston et al. 1990, Eggleston & Lipcius 1992, Briones-Fourzán et al. 2007). But casitas do not exclude morays, which fit into narrow crevices given their snake-like bodies (Hixon & Beets 1989, 1993). Thus, morays have been considered as potential predators for lobsters in casitas (Eggleston et al. 1990, Sosa-Cordero et al. 1998).

However, in a controlled experiment conducted in the Puerto Morelos reef lagoon, casitas significantly enhanced juvenile lobsters despite being also readily colonized by morays (Briones-Fourzán et al. 2007). This experiment thus provided an arena to test several hypotheses concerning potential interactions between morays and lobsters on shelter-poor (without casitas) and shelter-enhanced (with casitas) sites. If morays tend to consume co-occurring lobsters, this would be reflected in a meaningful contribution of lobsters to the diet of morays and in a negative relationship between the average numbers of morays and lobsters per casita. If morays affect lobsters indirectly (by intimidation), their presence would be expected to affect the distribution of lobsters among shelters, be they natural crevices (hereafter referred to as 'crevices') or casitas. If morays and lobsters potentially compete for limited, small shelters but can share large shelters, then morays — like lobsters — should undergo a significant enhancement with casitas, and both taxa would tend to cohabit more in casitas than in crevices. If cohabitation is beneficial to both taxa, then they should tend to co-occur in individual shelters more often than expected by chance. However, because social behavior may dictate the pattern of shelter occupancy, we compared the tendency of individuals of each taxon to dwell alone or aggregated.

MATERIALS AND METHODS

Field surveys. The shallow (≤5 m in depth) Puerto Morelos coastal reef lagoon (20° 40′ to 21° 12′ N and 86° 47′ to 86° 58′ W) is covered by extensive seagrass-macroalgal meadows and is delimited on the seaward side by a coral reef that runs at a distance of ~500 to 2000 m from the coast. Across the reef lagoon, 9 experimental plots were demarcated (Briones-Fourzán & Lozano-Álvarez 2001). Each plot measured 100 × 100 m (= 1 ha) and was separated from adjacent plots and from the reef tract by distances of 200 to 600 m. On 6 occasions between December 1997 and July 1998 (a period denoted as Before), we used SCUBA to survey the entire area of each plot for lobsters and all species of Anguilliformes to determine the dominant moray species. We also counted and measured all crevices on each site and arbitrarily categorized them into small (<25 cm across largest external diameter), medium (25 to 50 cm), and large (>50 cm) as a proxy for their potential refuge space (Childress & Herrnkind 1997, Briones-Fourzán & Lozano-Álvarez 2001). Out of 645 crevices observed, 61% were small, 24% medium, and 15% large, but crevices occurred on 4 plots (56 to 343 per plot) and were nearly non-existent on 5 plots (0 to 6 per plot). Given this pre-existing heterogeneity, 5 'casita sites' (with casitas) were randomly allocated to 2 plots with crevices and 3 plots without crevices, and 4 control sites (with no casitas) were randomly allocated to 2 plots with crevices and 2 plots without crevices. In late July 1998, we randomly deployed 10 casitas on each casita site (50 casitas in total). Adjacent casitas were separated by a distance of at least 20 m. Each casita consisted of a flat ferrocement slab 1.1 m^2 in surface area bolted to a double-stack frame built with PVC pipes 3.8 cm in diameter (entrance height), yielding an inner height of ~8 to 9 cm. Between September 1998 and November 2002 (a period denoted as After), we conducted 22 additional surveys and recorded the carapace length (CL, mm) of lobsters (Briones-Fourzán et al. 2007) and the total length (TL, cm) of spotted and purplemouth morays.

Effect of casitas on mean density and size of morays and lobsters. Mean densities (number of individuals ha^{-1}, or ind. ha^{-1}) of morays and lobsters were separately subjected to a Multiple Before–After Control-Impact (MBACI) analysis (Keough & Quinn 2000) to assess the effect of casitas by comparing the group of casita sites to the group of control sites. Briones-Fourzán et al. (2007) did an MBACI analysis for lobsters, but they used data from lobsters exclusively within the size range 15 to 50 mm CL and their Before period consisted of 13 surveys, whereas we included data from lobsters across the entire size range observed (6.2 to 87.2 mm CL) and our Before period con-

sisted of 6 surveys because prior to these surveys no data were collected for morays.

MBACI analyses were done with factorial ANOVAs. For these and all ANOVAs used in this study, the data were examined for compliance with ANOVA assumptions, which were met after appropriate transformations as evaluated with Levene's tests. For MBACI analyses, the data were transformed to log (x + 1) to remove multiplicative effects and homogenize variances. The main (fixed) factors were Treatment (Tr, with 2 levels, control and casita sites) and Before–After deployment of casitas (BA, 2 levels). Sites (S) were nested within Tr (with 4 and 5 levels, respectively), and Times (T) were nested within BA (with 6 and 22 levels, respectively). S and T were treated as random factors. The final models included the terms Tr, BA, Tr × BA, S(Tr) × BA, T(BA), and Tr × T(BA). The term of most interest was Tr × BA, which measures any change associated with the deployment of casitas. Prior to the MBACI analyses, we subjected each data set to a repeated-measures ANOVA to test for serial correlation of data and used the resulting Huynh-Feldt correction to adjust the degrees of freedom (df) of T and its Residuals in order to homogenize the variance-covariance matrix. These adjusted df were then used in the MBACI analyses to compute F-ratios for all terms involving T and its Residuals.

MBACI analyses do not detect trends through time, but an increase in density with casitas would be reflected as a significant divergence through time between casita sites and control sites. Therefore, for each taxon, we subtracted the mean densities of control sites from those of casita sites and subjected the differences in means to a correlation analysis to test for a linear trend through time (Keough & Quinn 2000, Briones-Fourzán et al. 2007). Trends were examined for the entire study period (Before + After) and for After alone.

Previous studies assessing density enhancement of target species with artificial structures have considered as indicative of enhancement a mean ratio (means averaged across After over means averaged across Before on treatment sites in MBACI designs, or means averaged for treatment sites over means averaged for control sites in the absence of a Before period) of >2 (Peterson et al. 2003) or ≥3 (Butler & Herrnkind 1997, Briones-Fourzán et al. 2007). However, Briones-Fourzán et al. (2007) found that mean After/Before ratios for lobsters on control sites could be as high as 2 due to natural variability. Therefore, for each taxon, we considered that enhancement occurred if both mean ratios (After/Before for casita sites, and casita sites/ control sites across After) were ≥3.

We also used ANOVAs to test the effect of casitas on the mean size of morays and lobsters After deploy-

ment. For morays, the final model included the terms Species (Sp, with 2 levels, *Gymnothorax moringa* and *G. vicinus*), Tr, S(Tr), and Sp × Tr, and for lobsters the final model included the terms Tr and S(Tr). Prior to ANOVAs, the size data were transformed to log (size + 1) to homogenize variances.

Stomach content analyses for morays dwelling in casitas. Young & Winn (2003) analyzed stomach contents of spotted and purplemouth morays collected from natural crevices over a reef lagoon in Belize. We followed their sampling protocol to analyze stomach contents of morays collected exclusively from casitas. Morays were extracted from casitas by sedating them with quinaldine or by prodding them out of casitas and into a hand net, and anesthetized by introducing them in a container with seawater with 300 ppm tricaine methanesulphonate (MS-222). This procedure caused the morays to spontaneously regurgitate any food in their stomach. We preserved the stomach contents in 70% ethanol and returned the morays to the sea. Prey items were identified to the smallest possible taxonomic unit, but we pooled the items by gross prey categories (e.g. fishes, cephalopods, crustaceans) for statistical analyses. Crustaceans were subdivided into spiny lobsters and other crustaceans. For each moray, we weighed every prey category to the nearest 0.01 g and estimated its percent weight ($\%W$) relative to the weight of the entire stomach contents. The percent frequency ($\%F$) of each prey category was estimated relative to the total number of stomachs analyzed. With these data, we computed an Index of Relative Importance [IRI = $(\%F \times \%W)/100$] for each prey category. IRI values range from 0 to 100, with values >40 denoting preferred prey, values between 10 and 40 denoting secondary prey, and values <10 denoting occasional or accidental prey (Pinkas et al. 1971). To examine a potential overlap in diet between both species, we computed a Horn index of overlap (Horn 1966) using the $\%W$ of prey categories. The Horn index ranges from 0 (no overlap) to 1 (complete overlap). A value >0.6 is considered as indicative of a significant overlap.

Effect of morays on abundance and distribution of lobsters in shelters. The effect of morays on the abundance and distribution of lobsters was examined in the time period After. Casitas were individually marked, allowing for quantification of empty casitas and casitas occupied by either or both taxa as well as the number of occupants. We used a least-squares regression to examine the relationship between the mean number of morays and the mean number of lobsters (averaged across surveys) in each individual casita. A negative relationship would suggest that the abundance of predators (morays) controls the abundance of prey (lobsters) (Sih 1984, Hixon & Beets 1993, Eggleston et al. 1997). Then, to examine if the presence and the

number of resident morays affected the distribution of lobsters among casitas, we compared the frequencies of casitas harboring 0, 1, 2…>10 lobsters versus 0, 1, and ≥2 morays with a χ^2 contingency table (Zar 1999). Empty crevices were not quantified because crevices were not individually marked; therefore, we only compared the frequencies of crevices harboring solitary or aggregated (≥2) lobsters in the absence (0) or presence (≥1) of morays. Data from crevices on control sites and on casita sites were subjected to separate χ^2 analyses (Zar 1999).

Habitation patterns and co-occurrence of morays and spiny lobsters. To assess habitation patterns of morays and lobsters, we applied separate χ^2 analyses to the frequencies of shelters (crevices and casitas) harboring solitary versus aggregated (≥2) individuals of each taxon. For crevices, the analyses were separately done Before (all sites pooled) and After deployment (separating control sites and casita sites). Then, we separately compared the distribution of morays and lobsters among all occupied crevices (data pooled from all sites across the study period) and all occupied casitas (data pooled across After).

Co-occurrence of lobsters and morays in individual shelters was tested against a non-random pattern of species co-occurrence in a presence-absence matrix. A 'checkerboard distribution' would describe a pattern wherein only one of both taxa occurs in a given shelter, suggesting interactions leading to exclusion (Stone & Roberts 1990). The analyses were done using the software EcoSim 7.0 (Gotelli & Entsminger 2004), which compares the real data to a 'null model', i.e. a Monte-carlo randomization that produces the number of checkerboards expected in the absence of biological interactions (Gotelli 2000). The null model used was SIM2, in which row (taxon) sums are fixed (the number of occurrences of each taxon in the null communities is the same as in the original data base) and column (shelters) sums are equiprobable (each shelter has the same chance of being selected) (Lozano-Álvarez et al. 2007). We ran separate models for all occupied crevices on control sites and on casita sites Before and After, and for all occupied casitas. Each run generated 5000 random matrices and calculated a 'C-score', which measures the average number of checkerboard units between the 2 taxa, i.e. their tendency to not occur together. An observed C-score significantly larger than expected by chance (the average C-score of the 5000 simulations) would suggest interspecific exclusion, and one significantly lower than expected by chance would suggest a tendency of both taxa to co-occur.

Throughout the text, results are expressed as mean ± SE unless otherwise stated. Statistical results were considered as significant if p < 0.05.

Table 2. *Gymnothorax moringa*, *G. vicinus,* and *Panulirus argus.* Above: Multiple Before-After Control-Impact (MBACI) analyses to test for changes in density (log [ind. ha^{-1} + 1]) of moray eels and spiny lobsters following deployment of casitas on treatment sites. Below: correlations to test for trends through time. The df of Time (T), Residuals, and their interactions were adjusted with Huynh-Feldt estimators previously obtained through repeated-measures ANOVAs. Tr: Treatment, BA: Before/After (Before: December 1997–July 1998; After: September 1998–November 2002), S: Site

Effect	Moray eels				Spiny lobsters			
	df	MS	F	p	df	MS	F	p
Tr	1	2.192	2.363	0.168	1	9.992	2.618	0.150
BA	1	9.313	47.608	<0.001	1	17.591	27.751	<0.001
Tr × BA	1	5.013	53.059	<0.001	1	6.915	10.908	0.013
S (Tr)	7	0.928	9.818	0.004	7	3.817	6.021	0.015
T (BA)	16	0.196	3.567	0.008	7	0.392	2.466	0.128
S (Tr) × BA	7	0.095	1.629	0.134	7	0.165	3.837	0.002
Tr × T(BA)	16	0.055	0.946	0.520	7	0.159	0.962	0.469
Residual	114	0.058			47	0.165		
Trends through time								
Before + After								
r	0.734				0.845			
p	<0.001				<0.001			
Only through After								
r	0.272				0.133			
p	0.221				0.555			

RESULTS

Effect of casitas on mean density and size of morays and lobsters

Spotted and purplemouth morays constituted 98% of all Anguilliformes observed Before and 97% After casita deployment. The rest consisted of a few green morays *Gymnothorax funebris* and snake eels (Ophichthidae) (Table 1). The proportion of species did not differ significantly between periods or site groups (χ^2 = 2.550, df = 4, p = 0.636). Because spotted and purplemouth morays were by far the dominant species and their abundance ratio did not differ significantly from unity Before or After deployment (Table 1), we only considered these species in further analyses.

The MBACI analyses (Table 2) for the mean densities of morays (Fig. 1a) and lobsters (Fig. 1b) revealed that the term of most interest, the Tr × BA effect, was significant for both taxa (Table 2). The effect of Tr was not significant for either taxon, probably due to the large variability among sites [S(Tr)], and there was a significant effect of BA for both taxa, of time [T(BA)] for morays, and

of S(Tr) × BA for lobsters (Table 2). For both taxa, mean densities diverged significantly between control and casita sites across Before + After, but not through After alone (Table 2), reflecting a step change in densities on casita sites after deployment followed by fluctuations around a higher mean density relative to control sites.

After/Before mean ratios (Table 3) showed that, after deployment, mean density of morays and lobsters increased on casita sites by a factor of 15.3 and 7.1, respectively, and on control sites by a factor of 1.7 and 2.1, respectively. The increase in mean density of both taxa on control sites after deployment likely reflects natural variability, given the longer duration of the After period (4 yr) compared to the Before period (8 mo). But even after this variability was taken into account, casitas significantly enhanced density of morays by a factor of 3.7 and density of lobsters by a factor of 4.2 (casita sites/ control sites mean ratios After, Table 3).

Mean size of spotted (n = 470, size range: 20 to 100 cm TL) and purplemouth morays (n = 487, 25 to 95 cm TL) was significantly larger on casita sites (57.5 ± 0.44 cm TL, n = 711) than on control sites (44.9 ± 0.85 cm TL, n = 175) ($F_{1, 6}$ = 34.023, p = 0.001) and was not significantly affected by Sp, S(Tr), or Sp × Tr (all p's > 0.1). Mean size of lobsters (n = 4612, size range: 6.2 to 87.2 mm CL) was also larger on casita sites (31.0 ± 0.22 mm CL, n = 3707) than on control sites (23.5 ± 0.37 mm CL, n = 905) ($F_{1, 5}$ = 8.246, p = 0.035) despite a significant effect of S(Tr) ($F_{5, 4605}$ = 46.315, p < 0.001).

Table 1. Anguilliformes. Species and total number (% in parentheses) of Anguilliformes (moray eels: Muraenidae; snake eels: Ophichthidae) observed on all sites (n = 9) during Before (December 1997–July 1998, 6 surveys), on control sites (n = 4) and casita sites (n = 5) during After (September 1998–November 2002, 22 surveys)

| Common name	Taxon	Before All sites	After Control sites	Casita sites
Muraenidae				
Spotted moray	*Gymnothorax moringa*	30 (56.6)	114 (50.7)	475 (47.1)
Purplemouth moray	*Gymnothorax vicinus*	22 (41.5)	105 (46.7)	505 (50.1)
Green moray	*Gymnothorax funebris*	0	1 (0.4)	1 (0.1)
Ophichtidae				
Snake eel	*Myrhicthys ocellatus*	1 (1.9)	4 (1.8)	25 (2.5)
Snake eel	*Myrhicthys breviceps*	0	1 (0.4)	2 (0.2)
Total		53 (100)	225 (100)	1008 (100)
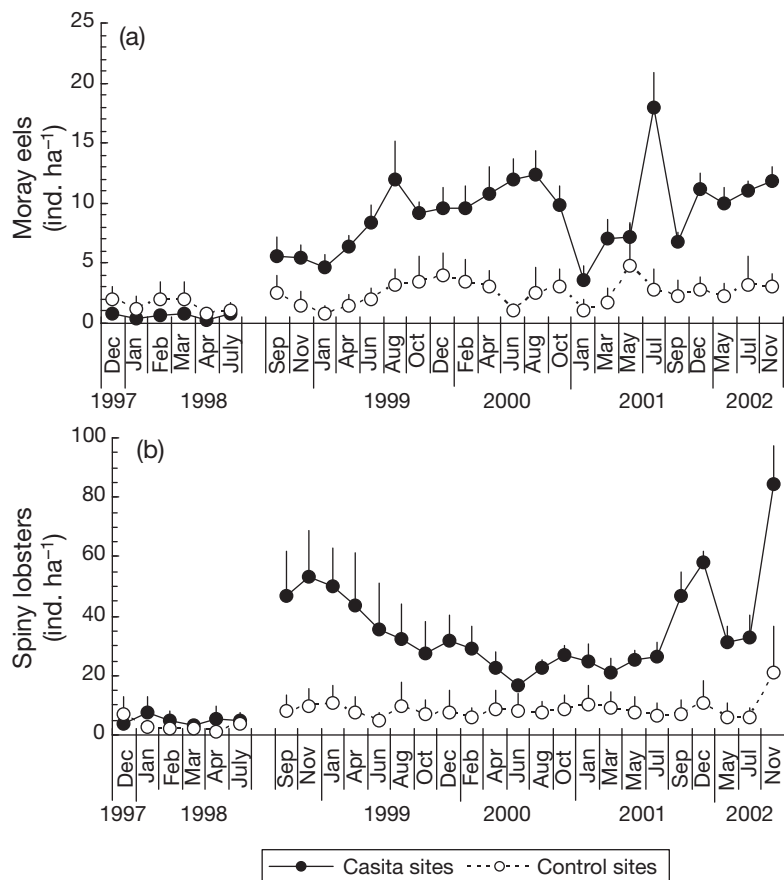
Fig. 1. *Gymnothorax moringa*, *G. vicinus,* and *Panulirus argus.* Mean (+SE) density (ind. ha^{-1}) of (a) moray eels and (b) spiny lobsters at control sites (n = 4, with no casitas) and casitas sites (n = 5, with 10 casitas site^{-1}) Before (December 1997–July 1998, 6 surveys) and After (September 1998–November 2002, 22 surveys) casita deployment. All sites measured 1 ha. Note that *y*-axes are different

Stomach contents analyses for morays

Most of the 91 purplemouth and 81 spotted morays collected from casitas had empty stomachs (76.9% and 63.0%, respectively), leaving a sample of 21 purplemouth and 30 spotted morays for stomach contents analyses. Both species had a broad diet spectrum composed of fishes (Anguilliformes, including Muraenidae and Ophichthidae, Haemulidae, Torpedinidae, Labridae and Diodontidae), octopuses (Octopodidae), crustaceans (Squillidae, Sicyoniidae, Palaemonidae, Diogenidae, Calappidae, and Palinuridae), and polychaetes (unidentified). The diet of both species showed some overlap (Horn's index = 0.572), reflecting their preference for fish prey (Table 4). However, purplemouth morays showed a greater preference for Anguilliformes (including conspecifics) and spotted morays for other fishes, especially for juvenile grunts (Haemulidae). Octopuses and crustaceans were occasional prey for both species (Table 4). In particular, lobsters were completely absent in the stomachs of purplemouth morays and only one spotted moray showed traces of lobster in its stomach (Table 4).

Effect of morays on abundance and distribution of lobsters

In casitas, the relationship between the average numbers of morays and lobsters (Fig. 2a) was weakly negative and non-significant (r^2 = 0.073, n = 50, p = 0.1), and the distribution of lobsters did not differ significantly in the absence or presence of either 1 or ≥2 resident morays (χ^2 = 17.911, df = 20, p = 0.593) (Fig. 2b). The distribution of lobsters among crevices also did not differ significantly in the absence or presence of resident morays on either control sites (χ^2 = 0.70, df = 1, p = 0.402) or casita sites (χ^2 = 0.030, df = 1, p = 0.852).

Habitation patterns of morays and lobsters

Irrespective of period, site group, or shelter type, significantly more shelters occupied by morays harbored solitary than aggregated morays (Table 5). For lobsters, the pattern was more variable. Before deployment, similar proportions of crevices harbored solitary versus aggregated lobsters, but After deployment significantly more crevices harbored solitary versus aggregated lobsters, and significantly more casitas harbored aggregated

Table 3. *Gymnothorax moringa*, *G. vicinus,* and *Panulirus argus.* Mean ± SE densities (ind. ha^{-1}) of moray eels and spiny lobsters on casita sites (n = 5) and control sites (n = 4) averaged across Before (December 1997–July 1998, 6 surveys) and After (September 1998–November 2002, 22 surveys) casita deployment

| | ——— Moray eels ——— | | ——— Spiny lobsters ——— | |
	Casita sites	Control sites	Casita sites	Control sites
Before	0.6 ± 0.10	1.5 ± 0.23	4.8 ± 0.63	4.1 ± 0.86
After	9.2 ± 0.70	2.5 ± 0.27	35.9 ± 3.34	8.5 ± 1.13
Mean ratios After/Before	15.3	1.7	7.5	2.1
Mean ratios Casita/ Control sites After	3.7		4.2	

Table 4. *Gymnothorax moringa* and *G. vicinus*. Summary of stomach content analyses for spotted morays (n = 30) and purplemouth morays (n = 21) sharing casitas with spiny lobsters *Panulirus argus*. %*W*: percent weight; %*F*: percent frequency; IRI: Index of Relative Importance

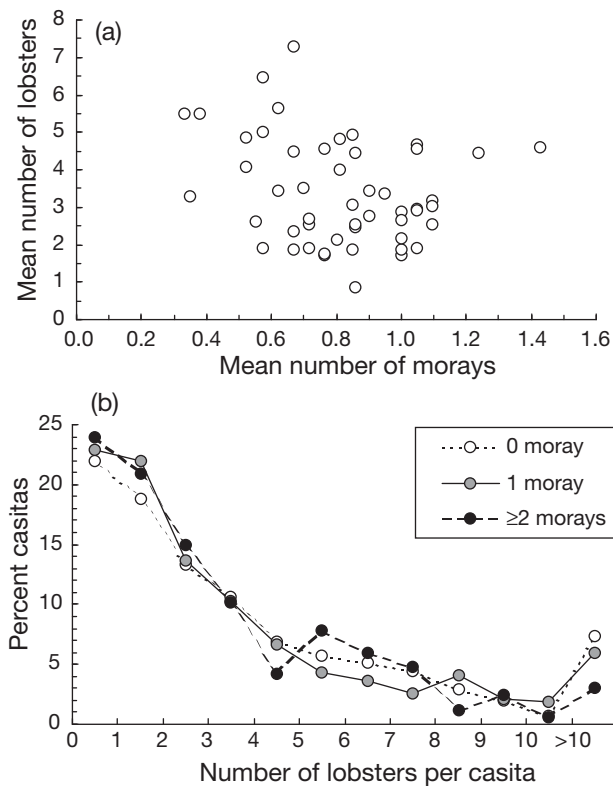| Prey category	*Gymnothorax moringa*			*Gymnothorax vicinus*		
	%*W*	%*F*	IRI	%*W*	%*F*	IRI
All fishes	57.7	77.8	46.45	92.7	84.7	78.52
Anguilliformes	4.6	11.1	0.51	73.6	30.8	22.65
Other fishes[a]	53.1	66.7	35.42	19.1	53.9	10.27
All crustaceans	14.7	19.4	3.65	3.1	7.7	0.24
Spiny lobsters	1.4	3.3	0.04	0	0	0
Other crustaceans	13.3	16.1	2.87	3.1	7.7	0.24
Octopuses	27.3	13.9	3.79	4.1	3.9	0.16
Other taxa	0.15	5.55	<0.01	0.01	3.9	<0.01

[a]Mostly juvenile grunts (Haemulidae)

Fig. 2. *Gymnothorax moringa*, *G. vicinus*, and *Panulirus argus*. (a) Mean numbers of moray eels and spiny lobsters averaged across 22 surveys After deployment (September 1998–November 2002), per casita (n = 50). (b) Lobster distribution in casitas with 0 morays (n = 405), 1 moray (n = 468) and ≥2 morays (n = 167)

versus solitary lobsters (Table 5). Across After alone, the distribution of morays among occupied shelters differed significantly with shelter type (χ^2 = 22.281, df = 3, p < 0.001) (Fig. 3a). More casitas (25.9%, n = 635 casitas) than crevices (11.5%, n = 254 crevices on all sites) harbored aggregated morays, with most aggregations

consisting of 2 morays (Fig. 3a). However, 58.7% of aggregations in casitas and 57.1% in crevices consisted of heterospecific morays. Conspecific aggregations were more common for purplemouth morays (20.9% of aggregations in casitas, 32.1% in crevices) than for spotted morays (11.0% and 7.1%, respectively). The distribution of lobsters also differed significantly with shelter type (χ^2 = 90.550, df = 3, p < 0.001) because most crevices occupied by lobsters harbored a single lobster (64%, n = 482 crevices) and most casitas (73.3%, n = 843) harbored aggregated lobsters, in particular ≥4 ind. (42.0% of casitas) (Fig. 3b).

Co-occurrence of morays and lobsters in individual shelters

Both Before and After casita deployment, more crevices harbored lobsters than morays and few (usually the largest) harbored both taxa (Table 6). Consequently, observed C-scores for crevices were significantly higher than expected C-scores (Table 6). Because the occupancy pattern of crevices did not differ significantly between periods and site groups (χ^2 = 5.323, df = 4, p = 0.256), we pooled the data from all crevices for comparison with casitas. The difference was significant (χ^2 = 396.50, df = 2, p < 0.001). More casitas (34.3%) harbored lobsters than morays (12.3%) yet 53.4% were shared by both taxa compared to 8.0% of all occupied crevices (Table 6). Regardless, the observed C-score for casitas was significantly higher than the expected C-score (Table 6), indicating that morays and lobsters also tended to co-occur in casitas less often than expected by chance.

DISCUSSION

Our results indicate that purplemouth and spotted morays do not interact with juvenile *Panulirus argus* lobsters as predator–prey. Morays using casitas did not appear to control the abundance of co-occurring lobsters and lobsters were virtually absent in stomach contents of morays. These morays have been observed feeding on lobsters previously killed by other predators (Weiss et al. 2006), but morays in general tend to respond quickly to chemical cues from dead or injured animals irrespective of their size (Bardach et al. 1959, Miller 1989). In contrast, *Gymnothorax* morays use visual cues to select live animals that they can swallow

Table 5. *Gymnothorax moringa*, *G. vicinus,* and *Panulirus argus.* Percentages of natural crevices and casitas on all sites (n = 9) Before casitas deployment (December 1997–July 1998, 6 surveys), and on control sites (n = 4) and casita sites (n = 5) After deployment (September 1998–November 2002, 22 surveys) harboring solitary vs. aggregated (≥2) ind. of moray eels or spiny lobsters. Where results were significant, bold numbers indicate the prevalent occupancy pattern. [ns] p > 0.05, ***p < 0.001

| Taxon	Period	Site group	Shelter type	n total	% with solitary ind.	% with aggregated ind.	χ^2
Morays	Before	All sites	Crevices	44	**97.7**	2.3	40.1***
	After	Control sites	Crevices	179	**86.6**	13.4	95.9***
	After	Casita sites	Crevices	75	**90.7**	9.3	49.6***
	After	Casita sites	Casitas	635	**73.7**	26.3	142.7***
Lobsters	Before	All sites	Crevices	64	57.8	42.2	1.6[ns]
	After	Control sites	Crevices	359	**63.0**	37.0	24.1***
	After	Casita sites	Crevices	123	**66.7**	33.3	13.7***
	After	Casita sites	Casitas	843	26.7	**73.3**	183.2***
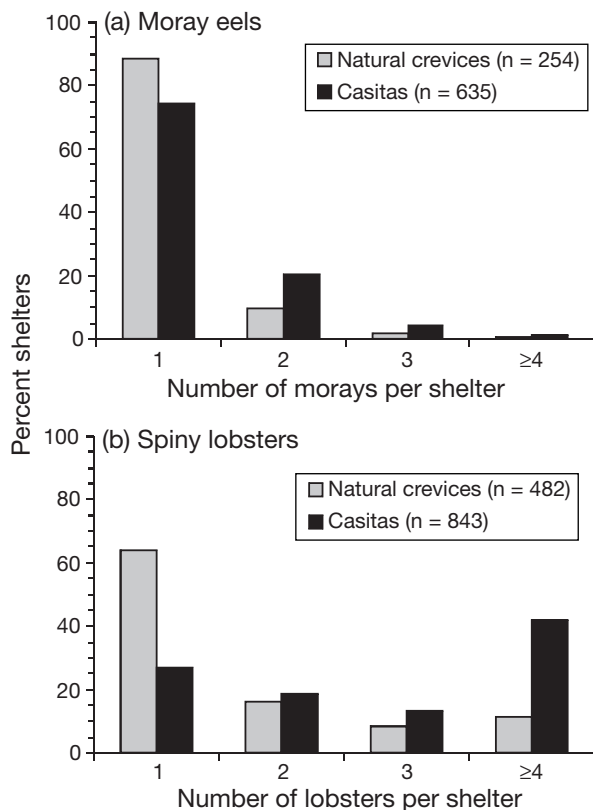
Fig. 3. *Gymnothorax moringa*, *G. vicinus,* and *Panulirus argus.* Distribution of (a) moray eels, and (b) spiny lobsters among occupied natural crevices (data pooled from all 9 sites for entire study period) and among occupied casitas on casita sites (n = 5) across 22 surveys After deployment (September 1998–November 2002)

whole (Miller 1989, Fishelson 1997, Metha & Wainwright 2007). Lipcius et al. (1998) and Weiss et al. (2006) observed green and purplemouth morays, respectively, attacking live *P. argus* lobsters in the field. However, these attacks may have been an artifact of tethering (Lipcius et al. 1998) or captivity (Weiss et al. 2006).

The most abundant potential prey for morays residing in our casitas were juvenile *Panulirus argus* lobsters, juvenile grunts (Haemulidae) and Anguilliformes (Briones-Fourzán et al. 2007). The morays preyed more heavily on fish prey, but purplemouth morays preferred Anguilliformes, and spotted morays preferred juvenile grunts (Haemulidae). These findings support Young & Winn's (2003) contention that these coexisting moray species tend to minimize competition for food by feeding preferentially on different types of available prey, and may also explain the prevalence of heterospecific over conspecific moray aggregations that we observed. However, our most important finding was that neither moray species capitalized on the readily available juvenile lobsters. We found traces of lobster in the stomach of only 1 spotted moray, and Young & Winn (2003) found lobster remains in the stomach of only one purplemouth moray. Whether these lobsters were consumed dead or alive is unknown, but these findings indicate that purplemouth and spotted morays would not tend to consume *P. argus* lobsters in casitas.

Visual or chemical cues indicative of the risk of predation have been shown to intimidate *Panulirus argus* lobsters. For example, these lobsters tend to avoid chemical cues from octopuses (Berger & Butler 2001) as well as chemical cues emanating from injured conspecifics or from injured individuals of a sympatric congener, *P. guttatus* (Briones-Fourzán et al. 2008). *P. argus* lobsters also rapidly flee their shelters upon the approach of an octopus (Weiss et al. 2008), but not upon the approach of purplemouth or spotted morays, with which they were recorded sharing crevices for up to 1 h at a time by fixed video cameras (Weiss et al. 2006). In a different field experiment, *P. argus* lobsters were observed feeding side by side with morays (Lozano-Álvarez & Spanier 1997) and, in our study, the presence of resident morays did not affect the distribution of lobsters among shelters. In conjunction, these findings indicate that spotted and purplemouth morays do not typically intimidate juvenile *P. argus* lobsters.

On 7 different occasions we observed a transient barracuda *Sphyraena barracuda* rapidly snatching exposed morays, showing that morays depend on crevice shelter for survival as strongly as lobsters do. Thus, in the absence of casitas, the low densities, small mean sizes, and low level of cohabitation of morays and lobsters suggest that these taxa potentially compete for

Table 6. *Gymnothorax moringa*, *G. vicinus*, and *Panulirus argus.* Numbers (% in parentheses) of natural crevices and casitas on experimental sites (Before and After deployment of casitas) that harbored only *G. moringa* and/or *G. vicinus* morays, only spiny lobsters, or co-occurring morays and lobsters. Before: December 1997–July 1998; After: September 1998–November 2002. The C-score ('checkerboard index') measures the tendency of morays and lobsters to not co-occur. An observed C-score significantly larger than the expected C-score indicates that co-occurrence is lower than expected by chance

Shelter occupants	Before All sites Crevices	After		
		Control sites Crevices	Casita sites Crevices	Casitas
Morays only	36 (37.5)	128 (26.9)	59 (31.7)	119 (12.3)
Lobsters only	52 (54.2)	308 (64.7)	114 (61.3)	331 (34.3)
Morays and lobsters	8 (8.3)	40 (8.4)	13 (7.0)	516 (53.4)
Total	96 (100)	476 (100)	186 (100)	966 (100)
Observed C-score	1872	39424	6726	39389
Expected C-score	543	10194	1789	22709
p	<0.001	<0.001	<0.001	<0.001

limited crevice shelter in the reef lagoon. Morays and lobsters did share some large crevices: up to 7 lobsters were observed cohabiting with 1 moray of either species and up to 3 lobsters with 2 heterospecific morays. Smaller crevices, by contrast, usually harbored either 1 or more lobsters or 1 moray, suggesting that the occupancy of these crevices was probably dictated by the animal that established prior residency (the 'priority effect', Almany 2003, Hixon & Jones 2005). But after deployment, the increase in shelter availability and refuge area provided by casitas reduced competition for shelter between morays and lobsters and increased their potential for cohabitation, resulting in enhancement of both taxa on casita sites.

Co-occurrence of morays and lobsters in casitas, however, was still lower than expected by chance but this result, rather than reflecting a potential negative interaction, more likely reflects differences in social behavior and movement ranges between both taxa. Morays are typically solitary and tend to be cannibalistic (Hixon & Beets 1989, 1993, Fishelson 1997, Young & Winn 2003, this study), traits that are common to many predators (Rudolf 2008). In contrast, *Panulirus argus* lobsters are highly gregarious and display cooperative defense. Juveniles of *P. argus* may move overnight between shelters separated by <1 m to a few tens of meters (Butler & Herrnkind 1997) but tend to persist longer where available shelters allow for gregariousness (Briones-Fourzán et al. 2007). In contrast, morays may move overnight between shelters within distances of 25 to 100 m but tend to shift sites after a few weeks (Abrams & Schein 1986, Chapman & Kramer 2000, Young & Winn 2003). Therefore, lobsters were overall more numerous than morays across the reef lagoon, and individual casitas typically harbored more (aggregated) lobsters than (solitary) morays.

The increase in cohabitation of morays and lobsters with casitas may reflect a mere 'alignment of interests', i.e. an increase in fitness of both taxa with the increase in refuge (van Baalen & Jansen 2001), but this does not exclude the possibility of a conditional mutualism. For example, octopuses, which are predators of juveniles of *Panulirus argus* in the Puerto Morelos reef lagoon (Weiss et al. 2006, 2008) and also use crevice shelters for protection, were also found on our experimental sites, but typically in a shelter by themselves rather than sharing shelters with morays and/or lobsters. Thus, the lobsters may indeed profit from cohabiting with a moray if the latter intimidates predators such as octopuses (the principle of 'the enemy of my enemy is my friend'; van Baalen et al. 2001, Hay et al. 2004). The moray may also profit from consuming predators — including octopuses — attracted to the lobsters but, as shown in this and other studies (Hiatt & Strassburg 1960, Randall 1967, Young & Winn 2003), morays tend to feed rather infrequently. They also tend to remain inactive in their shelters for days at a time and, if satiated, do not tend to respond to stimuli from potential prey or to become involved in aggressive interactions (Abrams et al. 1983, Fishelson 1997). These traits of morays may underlie their 'tolerance' to other animals, including potential prey, in or near their shelters (Abrams & Schein 1986, Miller 1989). Therefore, further investigation is required into the potential establishment of a conditional mutualism between co-occurring morays and lobsters.

In summary, over the Puerto Morelos reef lagoon, spotted and purplemouth morays did not interact as predator–prey with juvenile *Panulirus argus* lobsters but rather as competitors for limited crevice shelter. Deployment of casitas reduced this competitive interaction and increased the potential for cohabitation, resulting in enhancement of both taxa. These results show that interactions between morays and lobsters may vary with habitat complexity and, more importantly, that spotted and purplemouth morays do not pose a threat to the artificial enhancement of *P. argus* with casitas.

LITERATURE CITED

Abrams RW, Schein MW (1986) Individual movements and population density estimates for moray eels on a Caribbean coral reef. Coral Reefs 5:161–163

Abrams RW, Abrams MD, Schein MW (1983) Diurnal observations on the behavioral ecology of *Gymnothorax moringa* (Cuvier) and *Muraena miliaris* (Kaup) on a Caribbean coral reef. Coral Reefs 1:185–192

Almany GR (2003) Priority effects in coral reef fish communities. Ecology 84:1920–1935

Bardach JE, Winn HE, Mensel DW (1959) The role of the senses in the feeding of the nocturnal reef predators *Gymnothorax moringa* and *G. vicinus.* Copeia 1:570–574

Behringer DC, Butler MJ (2006) Density-dependence population dynamics in juvenile *Panulirus argus* (Latreille): the impact of artificial density enhancement. J Exp Mar Biol Ecol 334:84–95

Berger DK, Butler MJ (2001) Octopuses influence den selection by juvenile Caribbean spiny lobster. Mar Freshw Res 52:1049–1053

Berry PF (1971) The spiny lobsters (Palinuridae) of the eastern coast of Southern Africa: distribution and ecological notes. S Afr Mar Biol Res Invest Rep 27:1–23

Briones-Fourzán P, Lozano-Álvarez E (2001) Effects of artificial shelters (Casitas) on the abundance and biomass of juvenile spiny lobsters *Panulirus argus* in a habitat-limited tropical reef lagoon. Mar Ecol Prog Ser 221: 221–232

Briones-Fourzán P, Lozano-Álvarez E (2008) Coexistence of congeneric spiny lobsters on coral reefs: differences in conspecific aggregation patterns and their potential antipredator benefits. Coral Reefs 27:275–287

Briones-Fourzán P, Lozano-Álvarez E, Negrete-Soto F, Barradas-Ortiz C (2007) Enhancement of juvenile Caribbean spiny lobsters: an evaluation of changes in multiple response variables with the addition of large artificial shelters. Oecologia 151:401–416

Briones-Fourzán P, Ramírez-Zaldívar E, Lozano-Álvarez E (2008) Influence of conspecific and heterospecific aggregation cues and alarm odors on shelter choice by syntopic spiny lobsters. Biol Bull 215:182–190

Butler MJ, Herrnkind WF (1997) A test of recruitment limitation and the potential for artificial enhancement of spiny lobster (*Panulirus argus*) populations in Florida. Can J Fish Aquat Sci 54:452–463

Chapman MR, Kramer DL (2000) Movements of fishes within and among fringing coral reefs in Barbados. Environ Biol Fishes 57:11–24

Chave RE, Randall HA (1971) Feeding ecology of the moray eel, *Gymnothorax pictus.* Copeia 1971:570–574

Childress MJ, Herrnkind WF (1997) Den sharing by juvenile Caribbean spiny lobsters (*Panulirus argus*) in a nursery habitat: cooperation or coincidence? Mar Freshw Res 48: 751–758

Dolan TW, Butler MJ (2006) The adaptive value of aggregation among juvenile Caribbean spiny lobster: an evaluation using individual-based modeling. J Crustac Biol 26: 565–578

Eggleston DB, Lipcius RN (1992) Shelter selection by spiny lobster under variable predation risk, social conditions, and shelter size. Ecology 73:992–1011

Eggleston DB, Lipcius RN, Miller DL, Cobá-Cetina L (1990) Shelter scaling regulates survival of juvenile Caribbean spiny lobster *Panulirus argus.* Mar Ecol Prog Ser 62: 79–88

Eggleston DB, Lipcius RN, Grover JJ (1997) Predator and shelter-size effects of coral reef fish and spiny lobster prey. Mar Ecol Prog Ser 149:43–59

Fishelson L (1997) Olfaction and visual detection of food and relevant morphometric characters in some species of moray eels (Muraenidae). Isr J Zool 43:367–375

Forrester GE, Steele MA (2004) Predators, prey refuges, and the spatial scaling of density-dependent prey mortality. Ecology 85:1332–1342

Gilbert M, Rasmussen JB, Kramer DL (2005) Estimating the density and biomass of moray eels (Muraenidae) using a modified visual census method for hole-dwelling fauna. Environ Biol Fishes 73:415–426

Gotelli NJ (2000) Null model analysis of species co-occurrence patterns. Ecology 81:2606–2621

Gotelli NJ, Entsminger GL (2004) EcoSim: null models software for ecology, version 7. Acquired Intelligence Inc. & Kesey-Bear, Jericho, VT; available at: http://garyentsminger.com/ecosim/index.htm

Grabowski JH (2004) Habitat complexity disrupts predator-prey interactions but not the trophic cascade on oyster reefs. Ecology 85:995–1004

Hay ME, Parker JD, Burkepile DE, Caudill CC, Wilson AE, Hallinan ZP, Chequer AD (2004) Mutualisms and aquatic community structure: the enemy of my enemy is my friend. Annu Rev Ecol Evol Syst 35:175–197

Hiatt RW, Strassburg DW (1960) Ecological relationships of the fish fauna on coral reefs of the Marshall Islands. Ecol Monogr 30:65–127

Hixon MA, Beets JP (1989) Shelter characteristics and Caribbean fish assemblages: experiments with artificial reefs. Bull Mar Sci 44:666–680

Hixon MA, Beets JP (1993) Predation, prey refuges, and the structure of coral reef fish assemblages. Ecol Monogr 63: 77–101

Hixon MA, Jones GP (2005) Competition, predation, and density-dependent mortality in demersal marine fishes. Ecology 86:2847–2859

Horn HS (1966) Measurement of 'overlap' in comparative ecological studies. Am Nat 100:419–424

Keough MJ, Quinn GP (2000) Legislative vs. practical protection of an intertidal shoreline in southeastern Australia. Ecol Appl 10:871–881

Lipcius RN, Eggleston DB, Miller DL, Luhrs TC (1998) The habitat-survival function for Caribbean spiny lobster: an inverted size effect and non-linearity in mixed algal and seagrass habitats. Mar Freshw Res 49:807–816

Lozano-Álvarez E, Spanier E (1997) Behaviour and growth of captive spiny lobsters (*Panulirus argus*) under the risk of predation. Mar Freshw Res 48:707–713

Lozano-Álvarez E, Briones-Fourzán P, Osorio-Arciniegas A, Negrete-Soto F, Barradas-Ortíz C (2007) Coexistence of congeneric spiny lobsters on coral reefs: differential use of shelter resources and vulnerability to predators. Coral Reefs 26:361–373

Mehta RS, Wainwright PC (2007) Raptorial jaws in the throat help moray eels swallow large prey. Nature 449:79–82

Miller TJ (1989) Feeding behavior of *Echidna nebulosa, Enchelycore pardalis*, and *Gymnomuraena zebra* (Teleostei: Muraenidae). Copeia 1989:662–672

Peterson CH, Grabowski JH, Powers SP (2003) Estimated enhancement of fish production resulting from restoring oyster reef habitat: quantitative valuation. Mar Ecol Prog Ser 264:249–264

Phillips BF, Melville-Smith R (2006) *Panulirus* species. In: Phillips BF (ed) Lobsters: biology, management, aquaculture and fisheries. Blackwell, Oxford, p 359–384

Pinkas L, Oliphant MS, Iverson ILK (1971) Food habits of albacore, bluefin tuna and bonito in California waters. Calif Dep Fish Game Fish Bull 152

Preisser EL, Bolnick DL, Bernard MF (2005) Scared to death? The effects of intimidation and consumption in predator-prey interactions. Ecology 86:501–509

Randall JE (1967) Food habits of reef fishes of the West Indies. Stud Trop Oceanogr 5:655–847

Ratchford SG, Eggleston DB (1998) Size- and scale-dependent chemical attraction contributes to an ontogenetic shift in sociality. Anim Behav 56:1027–1034

Rudolf VHW (2008) Impact of cannibalism on predator-prey dynamics: size-structured interactions and apparent mutualism. Ecology 89:1650–1660

Sih A (1984) The behavioral response race between predator and prey. Am Nat 123:143–150

Sosa-Cordero E, Arce AM, Aguilar-Dávila W, Ramírez-González A (1998) Artificial shelters for spiny lobster *Panulirus argus* (Latreille): an evaluation of occupancy in different benthic habitats. J Exp Mar Biol Ecol 229:1–18

Stachowicz JJ (2001) Mutualism, facilitation, and the structure of ecological communities. Bioscience 51:235–246

Stone L, Roberts A (1990) The checkerboard score and species distributions. Oecologia 85:74–79

van Baalen M, Jansen VAA (2001) Dangerous liaisons: the ecology of private interest and common good. Oikos 95: 211–224

van Baalen M, Krivan V, van Rijn PCJ, Sabelis MW (2001) Alternative food, switching predators, and the persistence of predator-prey systems. Am Nat 157:512–524

Wahle R (2003) Revealing stock-recruitment relationships in lobsters and crabs: Is experimental ecology the key? Fish Res 65:3–32

Weiss HM, Lozano-Álvarez E, Briones-Fourzán P, Negrete-Soto F (2006) Using red light with fixed-site video cameras to study the behavior of the spiny lobster, *Panulirus argus*, and associated animals at night and inside their shelters. Mar Technol Soc J 40:86–95

Weiss HM, Lozano-Álvarez E, Briones-Fourzán P (2008) Circadian shelter occupancy patterns and predator-prey interactions of juvenile Caribbean spiny lobsters in a reef lagoon. Mar Biol 153:953–963

Young RF, Winn HE (2003) Activity patterns, diet, and shelter site use for two species of moray eels, *Gymnothorax moringa* and *Gymnothorax vicinus*, in Belize. Copeia 2003:44–55

Zar JH (1999) Biostatistical analysis, 4th edn. Prentice-Hall, Upper Saddle River, NJ