## Role of mangrove habitat as a nursery for juvenile spiny lobster, Panulirus argus, in Belize

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Abstract. The use of mangrove prop roots and associated coralline habitats by Caribbean spiny lobsters was investigated near two types of mangrove islands in Belize. Spiny lobsters sheltered among mangrove prop roots, in undercut peat banks and under corals near islands, and they ranged in size from newly recruited juveniles to subadults. Lobsters preferred to shelter under large stony corals, but their use of mangrove prop roots nd undercut peat banks increased when the density of corals was low. Den residence time and distance moved within a site were similar at islands isolated by deep water channels and islands separated by shallow seagrass beds, but as a consequence of high immigration rates, population sizes were highest near shallow islands. Predation on newly settled juveniles was greater in seagrass and coral crevices than in mangrove prop roots, whereas the survival of larger juveniles was higher in mangroves and coral patch reefs than in seagrass. These results suggest that mangrove habitats may function as a nursery for juvenile spiny lobsters but that the use of this habitat depends on shelter characteristics and the isolation of islands.

#### Introduction

The value of mangrove prop roots as a nursery habitat for marine and estuarine fauna is widely recognized (Odum et al. 1982; Robertson and Duke 1987; Vance et al. 1990; Laegdsgaa rd and Johnson 1995), but until recently, descriptions of mangrove habitat use by fish and invertebrates have been qualitative and often speculative. Recent quantitative studies have compared the community composition of fish and crustaceans in mangrove habitats with that in nearby vegetated and non-vegetated aquatic habitats in several tropical systems (Robertson and Duke 1987; Thayer et al. 1987; Chong et al. 1990; Vance et al. 1990; Sheridan 1992; Laegdsgaard and Johnson 1995). Mangroves serve either as nurseries for juveniles or as feeding areas for transient fish and crustaceans (Robertson and Duke 1990; Sheridan 1992). Several fish species shelter among red mangrove (Rhizophora mangle) prop roots in Florida during the day and feed in seagrass meadows at night, a behaviour that is similar to the dynamic use of seagrass meadows by some coral reef fish (Thayer et al. 1987). Postlarval penaeid shrimp settle in all types of aquatic vegetation in Australia and Malaysia, but the juveniles of some species are more abundant near fringing mangroves, indicating that they use this habitat as a nursery (Staples 1980a, 1980b; Robertson and Duke 1987; Chong et al. 1990; Vance et al. 1990). However, the degree to which mangrove habitat is used by mobile species may vary among systems in which shelter characteristics, food organisms and hydrography are distinctly different. Odum et al. (1982) noted such variation among mangrove habitats and described the faunal communities they observed in terms of Lugo and Snedaker's (1974) geological and hydrological classification of mangrove forests. Odum *et al.* (1982) concluded that the subtidal prop roots of fringing and overwash mangrove forests are important nurseries, presumably because they provide juveniles with abundant food and shelter from predators.

Mangrove prop root systems are presumed to be important nurseries for the Caribbean spiny lobster Panulirus argus, but little is known about the value of this habitat for postlarval settlers and juvenile lobsters. In Florida, the puerulus-stage postlarvae settle in nearshore vegetated habitats such as macroalgal beds and, perhaps, seagrass (Herrnkind et al. 1994). Juveniles appear to undergo ontogenetic shifts in habitat use and behaviour. Young juveniles (one to three months after settlement) live in vegetated habitats where they are solitary and cryptic, whereas older juveniles dwell gregariously in crevice shelters associated with hard-bottom communities (Marx and Herrnkind 1985; Herrnkind and Butler 1986; Childress and Herrnkind 1996). Yet, many regions in the Caribbean do not have extensive hard-bottom areas like those in Florida. Instead, Caribbean coasts typically have extensive seagrass beds with interspersed coral patch reefs and mangrovefringed shorelines. Mangrove prop roots may be continuously submerged because of the limited tidal range in the region and so may function as a nursery for lobsters. Because of differences in sizes of lobsters dwelling in mangrove and reef habitats in the US Virgin Islands, Olsen et al. (1975) suggested that mangroves serve as habitat for juveniles.

In order to better understand the role of mangrove habitat in lobster recruitment, we studied the population dynamics of juvenile Caribbean spiny lobsters in Belize around two types of mangrove islands that differ in geomorphology and the density of coral shelters on island margins. We surveyed juvenile spiny lobster populations, quantified their shelter preference, conducted mark-recapture experiments, and measured movement and den residence times at nine representative islands to test the null hypothesis that use of submerged mangrove habitat by lobsters is not affected by isolation of the island or availability of alternative shelters. To compare habitat-specific survival of different size classes of juveniles in potential nursery habitats, we measured relative predation rates on lobsters in mangrove prop roots, coral patch reefs and seagrass. Because predation pressure may influence the ontogenetic shift from vegetationdwelling to crevice-dwelling, we hypothesized that (1) survival of newly settled lobsters is similar in seagrass and mangrove prop roots but lower in crevice shelters on coral patch reefs, and (2) older juveniles survive better in coral crevice shelters than in mangrove prop roots or seagrass.

#### Materials and methods

#### Site description

The population dynamics of juvenile lobsters along the fringing mangrove habitat of nine islands off southern Belize were studied in March, August and December 1995 (Fig. 1). The islands lie approximately 5 km leeward of the Belize Barrier Reef and receive oceanic water from cuts in the main reef. They support both fringing and overwash red mangrove forests (Lugo and Snedaker 1974) and have a tidal range of 0.3-0.7 m. The mangrove trees at the nine islands have submerged prop root habitat 0.5 to 1 m deep at mean low tide. Four of the islands were typical of shallowwater mangrove islands, being surrounded by seagrass-covered margins 1-2 m deep that gradually increase in depth to about 5 m. One of these islands was located at Twin Cays and the three others in the Blue Ground Range (16°48.2'N,88°8.5'W). Five other islands were located at the Pelican Cays (Bird Cay, Cat Cay, Fisherman's Cay, Manatee Cay) and at Lagoon Cay (16°40.0'N,88°11.5'W). These isolated mangrove islands are part of an atoll-like formation surrounded by deep channels and flanked by a shallow shelf 1-2 m deep that drops off abruptly to 25-30 m.

#### Habitat characterization

The widths of the nine island margins range from 3 to 10 m, and the margins contain varying densities of stony corals, gorgonians and sponges that, in addition to mangrove prop roots, may serve as shelter for juvenile lobsters (Forcucci *et al.* 1994). To quantify differences among islands in habitat structure and density of shelters (dens) along island margins, substratum percentage cover and density of alternative shelters were measured along three replicate, randomly located transects on each island that were up to 15 m in length (depending on the width of island margins) and that were laid perpendicular to the mangrove line. Percentage cover of the seagrass *Thalassia testudinum*, the macroalgae *Laurencia* sp. and *Dictyota* sp., sand, or a heterogeneous mix of corals, sponges, algae and seagrass was recorded along each transect. The density of various potential shelters for lobsters (e.g. mound corals, fire coral, gorgonians) within 2 m of the transects was also recorded.

A multivariate analysis of variance (MANOVA) was performed to determine if there were differences in habitat structure among islands. Substratum percentage cover and shelter density were used in the analysis as the response variables and Pillai's trace was used as the MANOVA statistic since it is robust to departures from normality (Scheiner 1994). The univariate habitat variables were not distributed normally, so an angular transformation was used on the percentage cover data and a square-root



Fig. 1. Caribbean region (inset) and southern Belize, showing the locations of the shallow-water mangrove islands of the Blue Ground Range and Twin Cays and the isolated islands of the Pelican Cays and Lagoon Cay. Dotted lines indicate reef tracts, and water depths (in metres) are shown.

transformation on the shelter density data to improve normality. To test for homogeneity of variances and covariance matrices among dependent variables, correlation analyses were conducted on pairs of dependent variables, but no associations were found among island groups. The Ryan-Einot-Gabriel-Welch *F*-test (REGWF test) was used to determine which islands differed in habitat structure. All analyses were performed with the aid of the SAS computer package (Anon. 1989).

#### Habitat use

To determine spatial patterns in habitat utilization, five-day mark-recapture studies were conducted along 100 m of the margins of each of the nine mangrove islands. During each study, lobsters were captured, individually tagged underwater with colour-coded antenna tags, measured, sexed, and then returned to their original dens, which also were marked with unique tags. After the initial sampling, each island was revisited four times at daily intervals, unmarked lobsters were tagged, and the distance moved by each resignted lobster and the type of den it was using were recorded. Population size, loss by mortality/emigration, and immigration per site were estimated from the mark-recapture data with the aid of a Jolly-Scber model (Krebs 1989).

We postulated that movement of lobsters would increase with size, so we initially analysed mean daily distance moved and mean den residency times by analysis of covariance (ANCOVA), with size of individual lobsters as the covariate. However, size of individuals was not associated with the univariate response variables, so a MANOVA was used to test for differences in the individual lobster variables (i.e. lobster size, distance moved and den residence time) among islands. Roy's Greatest Characteristic Root (GCR) was used as the test statistic, and we used a canonical correlation analysis to inspect the relationship among response variables. Because the univariate variables were distributed normally, we used the Box test to check for equality of variances and covariance matrices. The analysis testing for differences in habitat structure among islands revealed that islands could be placed in two groups: Pelican Caystype islands (Bird Cay, Cat Cay, Fisherman's Cay, Manatee Cay), and Blue Ground Range-type islands (Blue 1, Blue 2, Blue 3, Twin Cays, Lagoon Cay) (see Results). We applied a multivariate pairwise orthogonal contrast to these two groups of islands, again using the Greatest Characteristic Root criterion (Harris 1985). The same analyses were performed separately on the Jolly–Seber population variables (i.e. standing population size, loss by mortality/emigration, and immigration), and a similar *post hoc* orthogonal contrast was run on the two island groups.

To estimate shelter preference by juvenile lobsters, we used Johnson's rank preference test (Johnson 1980) and computed the rank order of shelter use by lobsters and shelter density per island to determine if there were differences in shelter preference among lobsters on the different island types.

#### Habitat-specific predation

The relative value of potential nursery habitats in terms of shelter from predators was assessed by tethering two size classes—new settlers of 8–15 mm carapace length (CL), and older juveniles of 20–45 mm CL—in three habitats: among red mangrove prop roots, in crevices on coral patch reefs, and in seagrass. Lobsters were tethered on a 0.5-m length of 10-kg-test monofilament line secured to the carapace by gel cyanoacrylate glue and were placed at random distances at least 1 m apart along unmarked transects. Experiments were conducted for 24 h from dusk to dusk in water depths of about 1 m. Juvenile lobsters tethered among mangrove prop roots or in rock crevices remained quiescent, and those placed at the base of seagrass blades retreated to the ends of their tethers and then also became quiescent. Results were scored either as alive or as eaten with evidence of predation (fragments of carapace on the tether).

Tethering has been widely used in predation research despite debate over possible experimental treatment bias (e.g. Peterson and Black 1994; Aronson and Heck 1995). Our observations of tethered lobsters suggest that tethering artefacts due to behavioural differences among habitat treatments are minimal because the tethered lobsters did not behave in a manner that would attract predators. Data were analysed with the aid of a log-linear model and the likelihood ratio  $G^2$  test (Stokes *et al.* 1995). No significant treatment interactions were found, so the model was reduced to test for differences in predation by habitat and lobster size class.

#### Results

Multivariate analyses of island margin habitats show that there are distinct differences in habitat characteristics between the two geomorphologically different island types (i.e. shallow-water versus deep-water islands). *Post hoc* REGWF tests show that the four islands at the Pelican Cays (Bird Cay, Cat Cay, Fisherman's Cay, Manatee Cay) differed from the five islands at Blue Ground Range (Blue 1, Blue 2, Blue 3, Twin Cays and Lagoon Cay) in substratum percentage cover and density of alternative shelters (Table 1). Substratum cover at Blue Ground Range was dominated by the seagrass *Thalassia testudinum* (Fig. 2A, 'seagrass'), whereas the substratum at the Pelican Cays consisted of a heterogeneous mix of zoanthid and stony corals, gorgonians, sponges, macroalgae and sparse seagrass (Fig. 2A, 'coral mix').

Although all types of alternative shelters were found on most islands, densities were significantly higher at the Pelican Cays (Fig. 2B). Mound corals such as Montastrea and Diploria (Fig. 2B, 'mound corals') as well as smaller stony corals such as Agaricia, Acropora and Porites (Fig. 2B, 'other corals'), gorgonians, and sponges were more abundant in the Pelican Cays; the abundance of the fire coral Millepora was not significantly different between islands. Lagoon Cay is similar in geomorphology to the Pelican Cays in its isolation by deep water, but its habitat characteristics were similar to those of the Blue Ground Range (Fig. 2, Table 1). Because of possible confounding effects and lack of replication for Lagoon Cay, this site was not included in the post hoc orthogonal contrasts of habitat use by lobsters. Orthogonal contrasts were conducted on lobsters occupying the Pelican Cays (Bird Cay, Cat Cay, Fisherman's Cay, Manatee Cay) versus the Blue Ground Range (Blue 1, Blue 2, Blue 3, Twin Cays).



Fig. 2. Habitat characterization of two types of mangrove islands: shallow-water islands (Blue Ground Range, including Twin Cays and Lagoon Cay) and isolated islands (Pelican Cays). This grouping of islands is based on island geomorphology and habitat structure. (A) Substratum percentage cover; (B) density of alternative shelters. \*, difference between island types significant at an  $\alpha$  level of 0.05; ns, difference not significant. Histograms are means, and error bars are  $\pm 1$  s.e.

# Table 1. Results of MANOVA testing whether (A) substratum percentage cover or (B) density of alternative shelters differs among islands

Shown are the results for the MANOVA using Pillai's trace for significance tests, the standardized coefficients for the first two canonical variates from a canonical analysis, and the results of *post hoc* REGWF tests for determining significant differences among island groups (i.e. the Pelican Cays and the Blue Ground Range; island groups sharing a dashed line do not differ significantly for that dependent variable)

(A) MANOVA on substratum percentage cover

Source	Pillai's trace	F	Num DF	Den DF	Pr > <i>F</i>
Island	2.2723	2.9	32	72	0.0001

Standardized canonical coefficients			REG	WF tests
Percentage cover Canl Can2		Pelican Cays	Blue Ground Range	
Seagrass	1.6824	1.0229		
Coral mix	-1.6107	0.6752		
Macroalgae	0.4249	1.5001		
Sand	-0.2877	-0.0419	***********	

#### (B) MANOVA on density of alternative shelters

Source	Pillai's trace	F	Num DF	Den DF	$\Pr > F$
Island	2.4832	1.6	48	108	0.02

Standardized canonical coefficients			REC	SWF tests
Shelter density	Can 1	Can2	Pelican Cays	Blue Ground Range
Mound coral	1.2375	2.0558		
Fire coral	0.4542	-0.6511		
Other coral	1.5135	-0.9777		
Gorgonians	0.9836	-0.5245		
Sponges	1.0040	-0.0740		

Spiny lobsters sheltering in mangrove habitat ranged in size from 10 to 65 mm CL (mean  $\pm$  s.e.:  $35.15 \pm 1.22$  mm CL), and the male:female ratio was approximately 1:1. Lobsters showed a marked preference for stony coral shelters, but their use of mangrove prop roots and undercut peat banks increased when the abundance of alternative shelters decreased on the island margins (i.e. at the Blue Ground Range, Twin Cays and Lagoon Cay; Johnson's rank preference test: F = 65.4, d.f. = 111, P < 0.001).

During the five-day censuses of the 100-m transects on the nine mangrove islands, 112 lobsters were captured (Table 2A). The number of lobsters tagged in the Pelican Cays was 37, with 63% resignted on at least one additional day, and 62 lobsters were tagged in the Blue Ground Range, with 62% resignted. The individual variables of lobster size, den residence time, and distance moved differed significantly among islands, as indicated by the MANOVA results (Table 2B). However, the orthogonal contrast between the Pelican Cays and the Blue Ground Range was not significant, suggesting that the single Lagoon Cay site had the greatest effect in the MANOVA response variables. The canonical analysis revealed that individual lobster size and distance moved were associated and were inversely related to den residence time. The first canonical variate indicates that den residence time accounted for most of the differences among island types (canonical  $r^2 = 0.22$ , or 51% of the explainable variation). Den residence time was greatest on Lagoon Cay, where most lobsters, regardless of size, remained on the site. Individual size, den residence time, and distance moved within sites were similar at the Pelican Cays and the Blue Ground Range despite differences in habitat structure.

Multivariate analysis also indicated that island types differed significantly with respect to population size, loss by

Table 2. (A) Mean values  $\pm$  s.e., and results of MANOVA testing whether (B) individual lobster variables (i.e. individual size, den residence time, distance moved) or (C) population parameters (i.e. population size, loss by mortality/emigration, immigration) differ among islands

Shown are the results for the MANOVA using GCR for significance tests, the orthogonal contrasts for island groups (PC, Pelican Cays; BGR, Blue Ground Range), and the standardized coefficients for the first two canonical variates from a canonical correlation analysis

Island	Ind. size	Residence	Movement	Pop. size	Loss	Immigration
Twin	36.0 (2.5)	2.0 (0.46)	15.4 (8.4)	13.5 (1.0)	0.8 (0.14)	1.43 (0.0)
Blue 1	40.4 (5.8)	2.08 (0.42)	24.5 (5.7)	14.8 (8.2)	0.58 (0.4)	2.2 (0.3)
Blue 2	30.0 (2.1)	3.6 (0.36)	18.4 (7.9)	15.3 (2.1)	0.92 (0.2)	1.7 (0.8)
Blue 3	39.3 (4.2)	2.1 (0.71)	20.8 (6.2)	15.4 (1.9)	0.89 (0.11)	3.9 (0.0)
Bird	40.9 (5.2)	2.75 (0.62)	16.6 (12.2)	4.3 (1.0)	0.87 (0.07)	0.55 (0.7)
Fisherman's	43.8 (5.9)	2.2 (0.32)	15.7 (10.7)	4.7 (1.2)	0.83 (0.12)	1.63 (0.1)
Cat	36.4 (4.0)	3.0 (0.63)	16.9 (12.2)	4.8 (0.7)	1.0 (0.0)	0.7 (0.0)
Manatee	27.6 (2.1)	2.58 (0.42)	18.2 (11.1)	6.2 (1.7)	0.77 (0.51)	1.1 (0.3)
Lagoon	38.1 (2.8)	4.38 (0.42)	5.4 (1.4)	11.9 (1.3)	0.95 (0.05)	1.9 (0.2)

(A) Mean  $(\pm s.e.)$ 

(B) MANOVA on individual variables (n.s., not significant)

Source	GCR	F	Num DF	Den DF	Pr > <i>F</i>
Island	0.2863	3.61	8	101	0.001
Contrast: BGR v. PC	0.0389	1.28	3	99	n.s.

Standardized canonical coefficients for individual variables

Variable	Canl	Can2
Individual size	-0.6104	0.7690
Residence time	0.9181	0.4525
Movement	-0.0838	-0.6757

(C) MANOVA on population variables

Source	GCR	F	Num DF	Den DF	$\Pr > F$
Island	7.0781	15.93	8	18	0.0001
Contrast: BGR v. PC	3.8608	20.59	3	16	0.0001

Standardized canonical coefficients for population variables

Variable	Can l	Can2	
Population size	2.0854	1.3910	
Immigration	0.8952	-1.4933	
Mortality/emigration	-1.1142	-0.1357	

mortality/emigration, and immigration (Table 2C). In this case, the orthogonal contrast revealed a significant difference between the Pelican Cays and the Blue Ground Range: the latter had larger populations and greater

immigration rates. Canonical analysis indicated that population size and immigration were positively correlated and were inversely related to mortality/emigration, with changes in population size accounting for most of the variation (canonical  $r^2 = 0.87$ , or 68% of the explainable variation). This suggests that the Blue Ground Range has larger populations of lobsters resulting from immigration, perhaps from the surrounding seagrass meadows or nearby islands. Fewer lobsters immigrated to the more isolated Pelican Cays.

Small juveniles (8–15 mm CL) had significantly higher survival in mangrove prop root habitat than in seagrass or coral shelter on patch reefs ( $G^2 = 29.6$ , d.f. = 2, P < 0.0001; Fig. 3). Larger juveniles (20–45 mm CL) had similar survival in mangroves and coral crevices ( $G^2 = 1.81$ , d.f. = 2, P > 0.05) and lower survival in seagrass. Predation on small juveniles was higher than that on larger lobsters in all habitats.



Fig. 3. Survival of two size classes of spiny lobster tethered in three types of shelter. Survival of small lobsters <15 mm CL was significantly higher in mangrove prop roots and survival of large lobsters >20 mm CL was significantly higher in mangrove prop roots and coral crevices. The number of lobsters tethered in each habitat is shown above each histogram.

#### Discussion

Geomorphology and habitat structure along island margins differ remarkably among mangrove islands in Belize. The Blue Ground Range and Twin Cays are typical of islands fringed by shallow-water mangroves, having gently sloping margins with a seagrass substratum and with low densities of corals and other shelter for juvenile spiny lobsters. The Pelican Cays, however, have high densities of alternative shelters on their margins, are flanked by steep rubble slopes, and are isolated from each other by deep channels. Species diversity on these islands appears to be unusually high (e.g. ascidians; Goodbody 1995). Lagoon Cay possesses characteristics of both island groups, being isolated by deep water and having a seagrass-dominated margin with sparse alternative shelters. All sites are near oceanic water and are relatively silt-free, representing adequate habitat for juvenile lobsters, which have a low tolerance for silty environments (Herrnkind *et al.* 1988). Spiny lobsters preferred the crevice shelter of stony corals, but their use of mangrove prop roots or undercut peat banks increased wherever coral cover was sparse on island margins.

The size and sex ratio of juvenile lobsters found on the two types of islands were similar, but lobster abundances were different. The shallow-water islands of the Blue Ground Range had higher densities of juveniles, which appears to be a consequence of higher rates of migration among islands. At Lagoon Cay, all lobsters moved little, which extended their mean residence time per den. The isolation of this island and the low density of alternative shelters structures may explain this pattern of habitat use, but this type of island was unreplicated in the present study. Since movement to and from the isolated islands at the Pelican Cays was minimal, population sizes there may reflect actual levels of postlarval recruitment and survival in the absence of migration of juveniles among islands.

Loss by mortality/emigration was not different among islands, and the Jolly-Seber mark-recapture method does not discriminate between these two sources of loss. However, measurement of predation on lobsters tethered in different shelter types gives a relative estimate of shelter effects on mortality for different size classes. Small juveniles (recent settlers) had highest survival in mangrove prop root habitat, whereas larger juveniles survived equally well in mangrove prop roots and coral patch reefs but had low survival in seagrass. Although these field surveys indicate that large juvenile lobsters preferred to shelter under corals and in other crevice shelters along island margins, they readily fled to the fringing mangrove prop roots to escape capture. Thus, their proximity to this additional shelter may decrease successful predatory attacks. Mangroves may be especially important for sheltering small juveniles in regions where other densely vegetated habitat for settlers may be scarce.

Postlarvae of *P. argus* arriving from the oceanic plankton settle in macroalgae in southern Florida, where there are extensive areas of macroalgae-dominated hard bottom (Marx and Herrnkind 1985; Herrnkind and Butler 1986; Herrnkind *et al.* 1994). After a few months, the juvenile lobsters take up residence in large sponges, gorgonians and solution holes in hard-bottom areas that serve as nursery habitat (Forcucci *et al.* 1994; Herrnkind *et al.* 1994; Butler and Herrnkind, 1997). This type of habitat is rare in Belize and other Caribbean regions. In the Caribbean, fringing mangroves with associated margins of seagrass, macroalgae and crevice shelters function as nursery habitat for juvenile spiny lobsters. Nearshore coral patch reefs can also shelter large juveniles, but smaller lobsters experience high mortality in these habitats. Although postlarvae may settle in vegetation, the survival of larger juveniles may depend on their proximity to fringing mangroves and adjacent coral crevice shelters. The relative role of mangrove prop root habitats as a nursery for Caribbean spiny lobster probably depends on habitat quality, areal extent of submerged mangrove prop roots, and proximity of mangrove habitat to oceanic currents that supply lobster postlarvae. Mangroves not only provide food and shelter for a host of fish and benthic organisms but also function in stabilizing sediments and reducing siltation (Odum et al. 1982). Therefore, the availability and protection of fringing mangrove forests may be essential to maintaining lobster populations in Caribbean regions, because destruction of mangroves will decrease nursery habitat area and may increase siltation in nearby habitats.

#### Acknowledgments

This research was supported by a grant from the Smithsonian Institution's Caribbean Coral Reef Ecosystems Program. Additional financial support to C.A.A. was provided by the PADI Foundation. We are grateful to Klaus Ruetzler for his generous support, Mike Carpenter for his assistance at the Carrie Bow Cay Marine Field Station, and Denice Robertson for her help in the field. We thank Michael Childress, William Herrnkind and Alistair MacDiarmid for their insightful critiques of the manuscript. This is Contribution No. 504, Caribbean Coral Reef Ecosystems Program, Smithsonian Institution.

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