REFUGE SPACING SIMILARLY AFFECTS REEF-ASSOCIATED SPECIES FROM THREE PHYLA

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ABSTRACT

Four reef-refuging, off-reef foraging species were censused monthly for 1 year on three artificial reef plots in the northeastern Gulf of Mexico. Reef plots differed in spacing of otherwise equivalent prefabricated concrete reef units. The plot with widely spaced reef units (uniform pattern, 60 m apart) consistently harbored more stone crabs (*Menippe* hybrids) and/or octopuses (*Octopus vulgaris*) than did plots with more aggregated reef units (i.e., a close uniform pattern, units 2 m apart, and a mixed pattern of clustered units, at least 60 m between clusters). Stone crab numbers declined markedly and approached zero as octopus occupancy reached maximum levels (61 animals per plot), suggestive of species interaction. Black sea bass (*Centropristis striata melana*) and gray triggerfish (*Balistes capriscus*) exhibited occupancy patterns qualitatively similar to stone crabs and octopuses. The widely spaced plot consistently harbored more sea bass (96–331 individuals) and triggerfish (2–39 individuals) than did the closely spaced plot (45–203 sea bass and 0–21 triggerfish per plot). Adult echinoderms and mollusks larger than 2.25 cm were quantitatively sampled at 1, 10, 20 and 30 m from widely spaced and closely spaced reef units. Mean abundances of these potential prey species, as a group, increased significantly with distance from refuge at both sites. The rate of increase was qualitatively greater for prey items around widely spaced reef units. Tagged stone crabs were resighted on widely spaced units more often than expected by chance (19% resightings vs. 6% on mixed and closely spaced reef plots). These results are consistent with our central hypothesis that widely spaced reef units (at this site and on the scale of our comparisons) provide a more favorable resource for mobile off-reef foragers by virtue of increased access to soft-bottom prey.

A myriad of reef-refuging species exploit adjacent sand and seagrass habitats to feed. Haemulid fishes, for example, restrict their diurnal activities to the immediate vicinity of Caribbean coral reefs, but often radiate several hundreds of meters away from reef structure to forage in seagrass beds at night (Ogden and Ehrlich, 1977; McFarland et al., 1979; Alevizon et al., 1985). Ogden et al. (1973) described regions of barren sand or "halos" around patch reefs created by nocturnally foraging sea urchins. Numerous consumers, across phyla and geographic regions, radiate away from shelter to forage, e.g., lobsters (Herrnkind et al., 1975; Cooper and Uzmann, 1980; Ennis, 1983; Jernakoff et al., 1987; Spanier et al., 1988), octopuses (Yarnall, 1969; Kayes, 1974; Ambrose, 1986) and fishes (Hobson, 1965; Starck and Davis, 1966; Ogden and Buckman, 1973; Parrish and Zimmerman, 1977). The value of reef structure to such animals likely varies with proximity of prey and their need for refuge.

Lindberg et al. (1990) manipulated the spacing of reef material and found that widely spaced reef patches, on the scale of their comparisons, harbored significantly more and larger stone crabs (genus *Menippe*) than did reef patches in more aggregated patterns. To explain these observations, the authors posited a resource mosaic hypothesis which, in part, states "as refuge dispersion [reef spacing] decreases, so too does access to prey on the soft-bottom that surrounds such refuge." The consequence of this functional relationship to stone crabs is a relative decline in the resource value of highly aggregated, but otherwise similar reef patches.

Our question here is whether the resource mosaic hypothesis is general across taxa? We expected other animals that exhibit the same behavior as stone crabs, i.e., reef refuging and off-reef foraging, to be affected by reef spacing in a similar manner. Specifically, we hypothesized that widely spaced reef patches would harbor more octopus (*Octopus vulgaris*), black sea bass (*Centropristis striata melana*) and gray triggerfish (*Balistes capriscus*) than would units in either a highly aggregated or mixed pattern.

In addition to patterns of occupancy, mechanisms inherent in the resource mosaic hypothesis allow for predictions of relative prey abundance and consumer residency times. For example, prey densities in or on the soft-bottom surrounding reef units are expected to increase with distance from refuge and the gradient or slope of that function should differ among reef units depending on their spatial configuration. In particular, the density of potential prey species should increase more rapidly with distance from widely spaced reef units than from closely spaced ones, where the greatest overlap in foraging activity is predicted to occur. Moreover, the greater abundance and accessibility of soft-bottom food resources around widely spaced patch reefs should also be reflected in greater residency times for the mobile, off-reef foragers.

By using a designed artificial reef system, on an appropriate spatial scale, we have begun to explore effectively the functional ecology of patch reefs. Our comparisons among species and tests of explicit hypotheses provide valuable insight into the relationship between hard and soft-bottom habitats and the effects of patch reef spacing on associated fauna.

NATURAL HISTORY

Stone crabs, octopuses, black sea bass and gray triggerfish were chosen as representatives of widely different taxa because they are numerically dominant among reef-refuging, off-reef foragers at our site.

Stone crabs in the region of our study are hybrids (*M. mercenaria* × *M. adina,* Williams and Felder, 1986; Bert and Harrison, 1988) mostly resembling *M. mercenaria* (Lindberg et al., 1990). These species may partially isolate by habitat (subtidal versus intertidal, Wilber, 1989), but readily occupy cavities in hard substrata or else burrow in consolidated sands or mud (Bert et al., 1978; Williams and Felder, 1986; pers. obs.). The veneer of sand/shell over limestone at our site is unsuitable for burrowing. Stone crabs take refuge by day and forage at night (Wilber and Herrnkind, 1986) on a variety of bivalves, gastropods, annelids and echinoderms (Bender, 1971; pers. obs.). These prey species are common inhabitants in and on the soft-bottom surrounding reef units at our study site.

Octopus vulgaris is common in the coastal waters of the northeastern Gulf of Mexico. As do other octopuses, *O. vulgaris* generally takes refuge in cavities of hard substrata by day and forages at night (Altman, 1967; Kayes, 1974; Mangold, 1983; Mather, 1988). The octopuses deposit prey remains (e.g., gastropod and bivalve shells) and hard materials in middens around den entrances. *Octopus vulgaris* is solitary and possibly territorial (Guerra, 1981), with semi-permanent dens (Woods, in Nixon, 1969) and variable residency times (Altman, 1967; Kayes, 1974). As opportunistic carnivores, octopuses radiate from dens to prey primarily on crustaceans, bivalves and gastropods, but will eat fish, polychaetes and even other cephalopods (Mangold, 1983 and references therein).

Black sea bass and gray triggerfish are common reef associated species which take refuge in reef cavities when disturbed. Both species are apparently visual, daytime feeders (Randall, 1968; Kendall, 1977, pers. obs.). Steimle and Ogren (1982) found most foods of black sea bass to be non-reef in origin. Black sea bass prey mainly on crustaceans, fish, mollusks and echinoderms, although the presence of barnacles, tunicates and other sessile invertebrates in their guts indi-

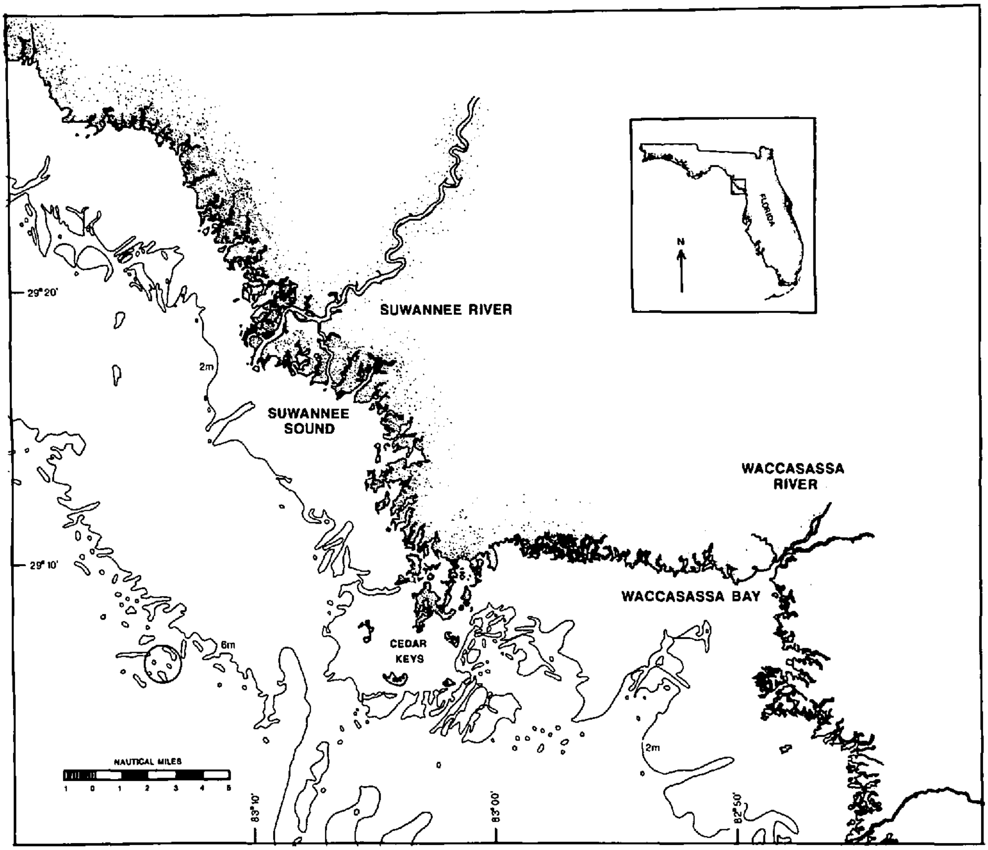

Figure 1. Artificial reef site (solid circle) is approximately 16km due west Cedar Key, along Florida's north central Gulf coast (see inset).

cates some grazing on fouling assemblages (Mercer, 1989). Gray triggerfish, like black sea bass, feed on a variety of sand dwelling invertebrates (e.g., mollusks, crustaceans and echinoderms), as well as sessile invertebrates associated with hard substrata (Nelson et al., 1986; Vose, 1990).

Materials and Methods

Our experimental reef is in the northeastern Gulf of Mexico, 16 km due west of Cedar Key, Florida, in approximately 7 m of water (Fig. 1). Construction and placement of reef materials was completed in the summer of 1987. Six reef plots, each containing 36 prefabricated concrete reef units (0.77 m × 0.58 m × 0.30 m), were interspersed in a 108-ha grid overlying a featureless sand bottom (Fig. 2). Within each reef plot, the 36 units were arranged in one of three spatial configurations: (1) a widely spaced pattern (Wide) in which reef units were regularly spaced at 60-m intervals, (2) a closely spaced pattern (Close) in which reef units were regularly spaced at 2-m intervals or (3) an intermediate, mixed pattern (Mixed) in which six patches of six closely spaced reef units (ca. 2 m edge to edge) were separated by at least 60 m. Lindberg et al. (1990) provide more detailed information on reef spacing and unit characteristics.

Monthly sampling for 1 year (August 1988 through July 1989) was concentrated on the three northeastern treatment plots. Paired SCUBA divers visually censused all adult stone crabs, octopuses, black sea bass and gray triggerfish associated with reef units at each of the three treatment plots. Data were collected during daylight hours and fishes were always counted before crabs and octopuses to minimize disturbance at any given site.

Reef units on the Wide treatment plot were censused sequentially. Both sea bass and triggerfish,

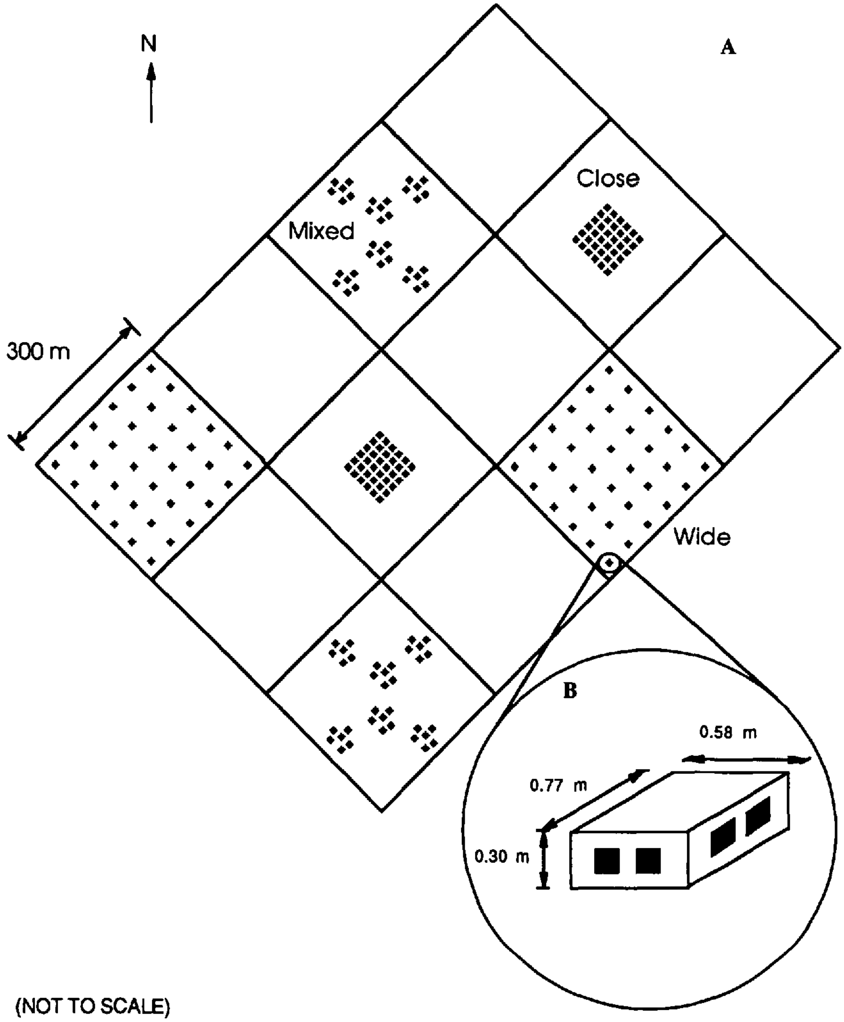

Figure 2. Schematic depiction of reef treatment plots interspersed in a 108 hectare grid. Each treatment plot contains 36 prefabricated concrete reef units (see inset) arranged in one of three spatial configurations.

when approached by divers, invariably sought refuge in or around the structure of a reef unit and their numbers were easily recorded. Each cavity in a reef unit was inspected visually or by touch as it potentially harbored one or more adult stone crabs or octopuses. The two species were never observed to occupy the same den simultaneously. Cavity locations of detected stone crabs and octopuses were recorded. In addition, stone crabs were removed from their dens and tagged with a color-coded rubber band (Ennis, 1984; Lindberg et al., 1990) placed over the merus of one claw. Crabs were sexed, measured with vernier calipers (carapace width, mm), phenotypically scored (Bert and Harrison, 1988) and returned to their original den. Crabs were not tagged or phenotypically scored on the mixed plot in either October or April due to time limitations.

Fish associated with each cluster on the Mixed plot were censused in a manner similar to those associated with single units on the Wide plot. Two total counts were made at each cluster and averaged. The sum of the six cluster averages was reported as the total count for the Mixed plot. Stone crabs and octopuses were censused as before.

Reef units on the Close plot were censused sequentially as on the Wide plot. Fish moving among reef units were noted and care was taken to avoid multiple counts of the same individuals. Two total

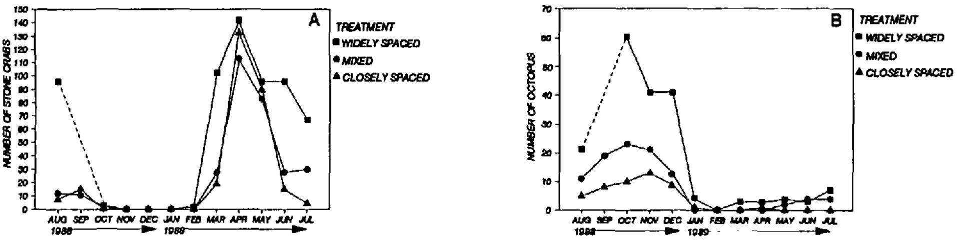

Figure 3. Total number of (A) stone crabs and (B) octopus on the different reef treatment plots during each of the 12-monthly-sampling periods. The Wide plot was not sampled in September.

counts were made and the average reported. Stone crabs and octopuses were censused as on the Wide and Mixed plots.

The sand bottom surrounding reef units was sampled for potential prey items during the week immediately following the last census, i.e., July 1989. Nine reef units were randomly selected from the Wide and Close plots and quadrats were sampled at each of four distances (1, 10, 20 and 30 m) away from individual reef units or in the case of the Close plot, away from the aggregation of reef units. Clearly, the inner units within the Close plot are not equivalent to those on the "fringe," while the latter more closely resemble those units at the Wide site. With this in mind, we note that the most interior reef units within the Close plot were not part of the random sample. Within a quadrat, i.e., a 1.5 m × 1.5 m frame placed on the sandy substratum, divers censused all macrofaunal invertebrates visible to the unaided eye. Each quatrat was raked to expose prey species buried up to eight cm in the sand, and prey were identified to the lowest possible taxon. Analyses were restricted to those benthic taxa which could be realistically assessed by this technique, i.e., adult echinoderms and mollusks greater than 2.25 cm (=least cross sectional measure).

An analysis of covariance (PROC GLM, SAS Institute, 1987) was used to define the relationship between distance and abundance of designated prey species around reef units at the Wide and Close reef plots. A square root transformation stabilized the variance of prey data. Counts of stone crabs and octopuses per reef unit allowed for tests of treatment effects on occupancy rates during each sampling period. Non-parametric procedures (PROC NPAR1WAY, SAS Institute, 1987) were employed as data could not be transformed to meet parametric assumptions. A consistent experimentwise error rate (alpha = 0.05) was maintained in all analysis. Total counts of black sea bass and gray triggerfish were compared qualitatively with occupancy patterns of stone crabs and octopuses. A G-test (Sokal and Rohlf, 1981) was used to determine if the observed numbers of resighted stone crabs differed from expected at the three reef plots.

RESULTS

Both stone crabs and octopuses occupied reef units during the first month of sampling (Fig. 3). Stone crabs, however, declined rapidly in the ensuing months and only five crabs occupied the reef plots by October. Octopuses increased concommitantly and exhibited peak occupancy when crab numbers were most depressed. By February 1989, octopuses no longer occupied reef units on any treatment plot and although they were observed during future sampling periods, their numbers remained low. Stone crabs recolonized reef units in March and maximum levels of occupancy were observed in late April. By July, occupancy levels and patterns of abundance among treatments were similar to August of the previous year.

As predicted, the widely spaced reef plot generally harbored more stone crabs or octopuses than did either the Mixed and Close plots. In addition, the Mixed plot consistently harbored more octopuses than did the Close plot during periods of peak occupancy. A similar pattern for stone crabs was less evident. Statistical analyses of occupancy rates (numbers per reef unit) confirmed these observations (Table 1).

Black sea bass and triggerfish exhibited qualitatively similar patterns in occupancy among the three treatment plots when compared with stone crabs and oc-

Table 1. Median number of stone crabs and octopus per reef unit on Wide, Mixed and Close treatment plots for each sampling month. Ranges are given in parentheses. *P*-values and rank-orderings reflect the significance level of Kruskal-Wallis tests and Wilcoxon pairwise follow-ups, respectively.

Date	Crabs per reef unit					Octopus per reef unit				
	Wide	Mixed	Close	*P*-value[1]	Rank ordering[2]	Wide	Mixed	Close	*P*-value[1]	Rank ordering[2]
Aug 88	2 (0–8)	0 (0–2)	0 (0–2)	0.0001	W > M = C	1 (0–2)	0 (0–1)	0 (0–1)	0.0017	W = M > C
Sep 88[3]		0 (0–2)	0 (0–2)	NS	NS		0 (0–2)	0 (0–2)	0.0290	M > C
Oct 88[4]	0 (0–1)	0 (0–0)	0 (0–3)	NS	NS	2 (0–3)	1 (0–2)	0 (0–1)	0.0001	W > M > C
Nov 88	no crabs on reef plots					1 (0–4)	1 (0–2)	0 (0–2)	0.0001	W > M = C
Dec 88	no crabs on reef plots					1 (0–3)	0 (0–2)	0 (0–2)	0.0001	W > M = C
Jan 89[5]	no crabs on reef plots					0 (0–2)	0 (0–0)	0 (0–1)	NS	NS
Feb 89[4,5]	0 (0–1)	0 (0–0)	0 (0–0)	NS	NS	no octopus on reef plots				
Mar 89[5]	2 (0–9)	0 (0–7)	0 (0–3)	0.0001	W > M = C	0 (0–1)	0 (0–0)	0 (0–0)	NS	NS
Apr 89[5]	3 (0–11)	3 (0–9)	3 (0–8)	NS	NS	0 (0–1)	0 (0–0)	0 (0–1)	NS	NS
May 89[5]	3 (0–8)	2 (0–10)	2 (0–7)	NS	NS	0 (0–2)	0 (0–1)	0 (0–1)	NS	NS
Jun 89[5]	2 (0–6)	0 (0–5)	0 (0–3)	0.0001	W > M = C	0 (0–1)	0 (0–1)	0 (0–1)	NS	NS
Jul 89	2 (0–8)	0 (0–4)	0 (0–2)	0.0001	W > M > C	0 (0–1)	0 (0–1)	0 (0–0)	0.0245	W = M > C

[1] Kruskal-Wallis test with Chi-square approximation (two degrees of freedom).
[2] Wilcoxon pairwise comparisons (inequalities significant at $P < 0.017$).
[3] Wide reef plot not sampled in September.
[4] Less than five total stone crabs on reef plots.
[5] Less than seven total octopus on reef plots.

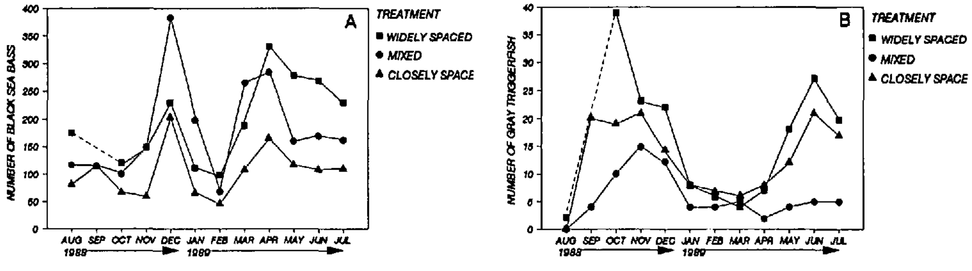

Figure 4. Total numbers of (A) black sea bass and (B) gray triggerfish on the different reef treatment plots during each of the 12-monthly-sampling periods. The Wide plot was not sampled in September.

topuses (Fig. 4). The Wide plot harbored more sea bass and triggerfish than did the Close plot during all sampling periods except during late winter months when triggerfish numbers were low and essentially equal among treatment plots.

Bottom temperature (°C) declined from August to February then increased steadily into the summer months (Fig. 5). Salinity (‰) remained relatively constant throughout the study.

Stone crabs differed in size (cw) among reef plots during April, May and July (Fig. 6). Crabs on the Wide plot were significantly larger than those on the Close plot (ANOVA, $F > 6.00$, $df = 2$ and $P < 0.005$ in all three cases). Individual octopuses, sea bass and triggerfish were not measured, but were not obviously different among treatment plots at any given sampling period.

The abundance of designated soft-bottom prey items, i.e., adult echinoderms and mollusks greater than 2.25 cm, (Fig. 7) increased significantly ($F = 82.8$, $df = 1$, $P < 0.001$) with distance from both the widely spaced and closely spaced reef units and were significantly ($F = 6.7$, $df = 1$, $P < 0.01$) more abundant around widely spaced reef units than closely spaced reef units at any given distance. There was no statistically significant interaction between distance and reef

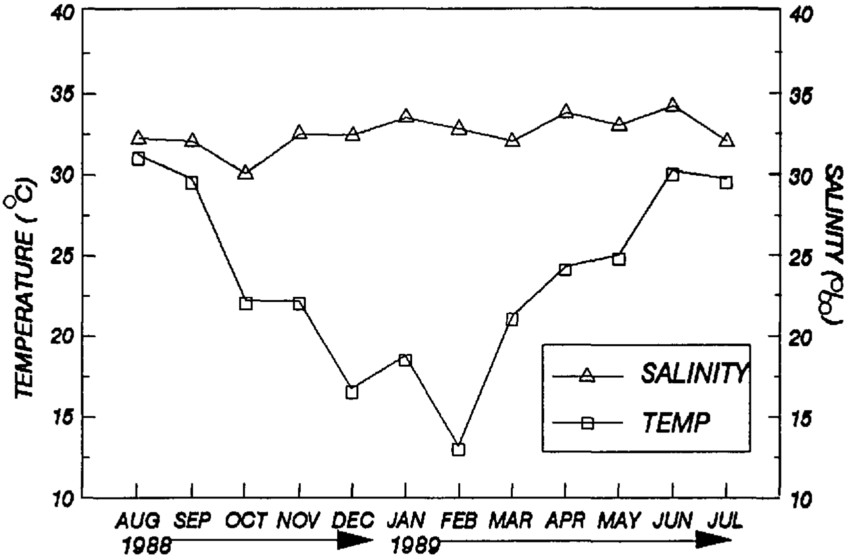

Figure 5. Bottom temperature (°C) and salinity (‰) at the study area for each of the 12-monthly-sampling periods.

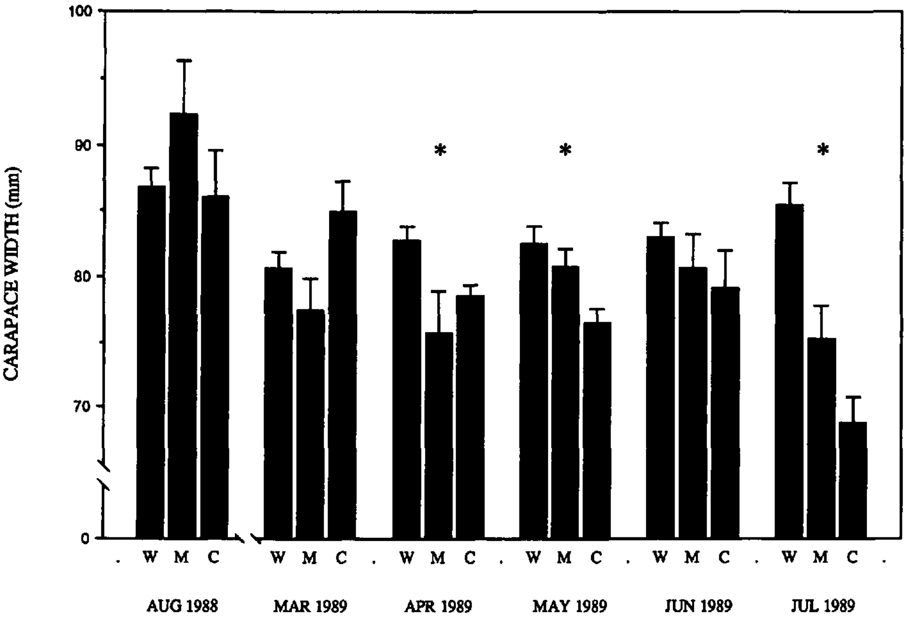

Figure 6. Mean size ± SE, i.e., carapace width (mm), of stone crabs on the three different reef treatment plots during those sampling periods amenable to statistical comparison. Asterisks (*) indicate significant differences at the $P < 0.05$ level.

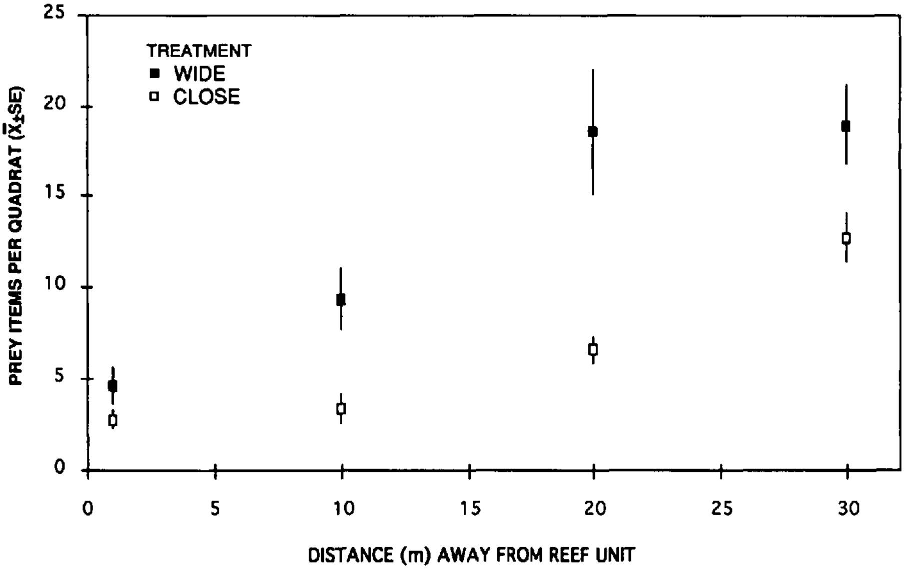

Figure 7. Mean number ± SE of adult echinoderms and mollusks greater than 2.25 cm in quadrat samples at 1, 10, 20 and 30 m from widely spaced and closely spaced reef units.

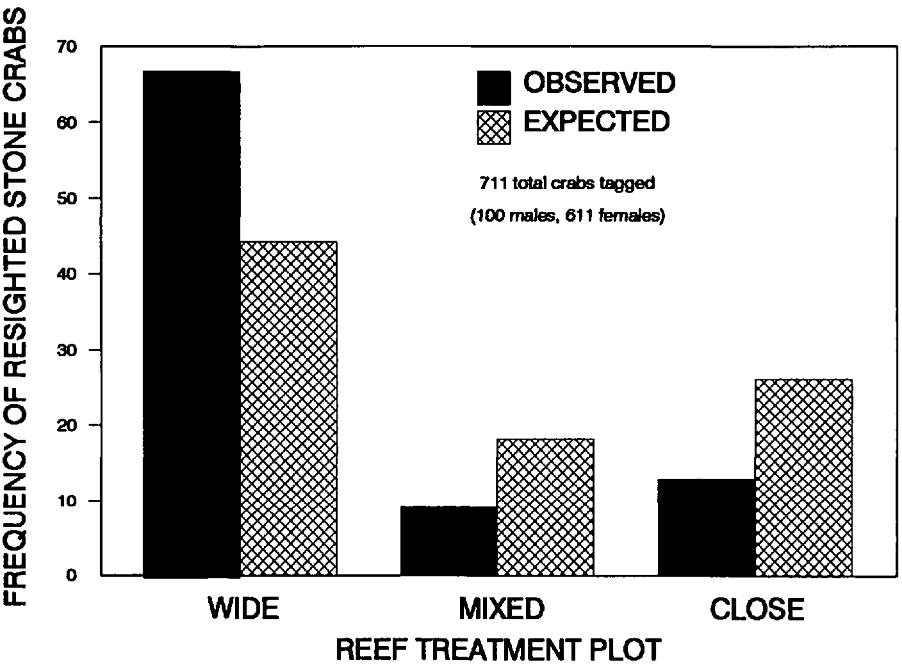

Figure 8. Expected and observed frequencies of resighted stone crabs on the three different reef treatment plots.

type ($P > 0.05$) so it cannot be concluded that the rate of increase of prey items differed quantitatively among plots.

Stone crabs were expected to reside longer on the Wide plot, assuming food was relatively more abundant near reef units at this site. Tag retention data is consistent with this prediction. A total of 833 stone crabs were tagged during the 12 months of study, but only the 711 crabs tagged after the 1988 exodus were used for analyses. Although 122 additional crabs were tagged in 1988, only one of them was observed after stone crabs recolonized the reef complex the following spring. Those tagged in July were not included in the analyses as there was no chance for those individuals to be resighted. Of the 352 crabs originally tagged on the Wide plot in 1989, sixty-seven (19.0%) were resighted (Fig. 8). Of those, sixty-two (92.5%) remained on the Wide plot, three (4.5%) had moved to the Mixed plot and two (3.0%) had moved to the Close plot. Of the 145 crabs tagged on the Mixed plot in 1989, only nine (6.2%) were resighted. Of those, six (66.7%) remained on the Mixed plot, two (22.2%) had moved to the Wide plot and one (11.1%) had moved to the Close plot. Of the 212 crabs tagged on the Close plot in 1989, thirteen (6.1%) were resighted. Of those, nine (69.2%) remained on the Close plot and the other four (31.8%) had moved to the Wide plot. Proportionately more crabs were resighted on the Wide plot than on the Mixed or Close plots ($G = 11.92$, $df = 2$, $P < 0.001$), reflecting a greater mean residency time at the widely spaced reef plot.

DISCUSSION

Our site with widely spaced reef units consistently harbored more stone crabs and/or octopuses than reef units in more aggregated spatial configurations. Black sea bass and gray triggerfish exhibited qualitatively similar patterns in occupancy suggestive of a general structuring process for these mobile, off-reef foragers. Findings here are consistent with those of Lindberg et al. (1990) and confirm additional predictions from the resource mosaic hypothesis. We restrict our conclusions, however, to this study site until replicated experiments on similar spatial scales are complete.

Temporal fluctuations in the total numbers of each species underscore the dynamic nature of reef systems, while at the same time providing insight into behavioral patterns and species interactions on ecologically relevant spatial scales. Stone crabs, for example, declined markedly with the invasion of octopuses. Direct predation does not explain the absence of crabs because no stone crab parts were ever observed in the dozens of middens we inspected. Induced emigration under the threat of predation seems more plausible. However, one testable alternative within the context of the resource mosaic hypothesis is that octopuses exploitatively outcompeted (in real time) stone crabs. Both species feed on many of the same sand-dwelling invertebrates and may have broad diet overlap. The octopuses, however, are larger, more mobile and presumably have higher metabolic requirements. The octopuses might quickly deplete prey available within the normal foraging radius of stone crabs, indirectly inducing crab departure from the reef site. Food supplementation experiments in the presence of both species could resolve the aforementioned alternatives. Daily movement patterns have not been described for stone crabs in the field, but would be central to such a test.

It is unlikely that a temperature decline at the reef site triggered the stone crabs departure as these animals have been observed to overwinter at these same reef sites during previous years (Lindberg et al., unpubl. data). Low temperatures, on the other hand, may be directly related to the 1989 decline in octopus numbers as well as pulses of increased black sea bass abundance at our reef site. Musick and Mercer (1977) noted that temperatures below 14°C may initiate movement of black sea bass out of mid-Atlantic estuaries and Reid (1954) found no juveniles in Cedar Key estuaries during an unseasonably cold December. A sharp decline in temperature during December of this study (to 16°C offshore and 12.4°C in nearby estuarine areas, Florida Department of Natural Resources, unpubl. data) most likely triggered a directed offshore movement of juvenile black sea bass. We assume that many of these fish encountered reef units at our experimental site, thus explaining their high numbers on all three treatment plots.

Juvenile black sea bass are gregarious. Large groups encountering isolated reef units on the Wide plot may have found the refuge less favorable, perhaps even unsuitable, when compared with that provided by clusters of reef units on the Mixed plot. This could explain the higher numbers of black sea bass on the Mixed plot during December and an apparent inconsistency in the more generally observed pattern, i.e., widely spaced reef units harbor greater numbers of individuals. Furthermore, the large influx of juveniles may have masked a characteristic pattern of occupancy exhibited by adults.

Low numbers of gray triggerfish on the Mixed plot relative to the Wide and Close plots is possibly a reflection of plasticity in their social organization. For example, Fricke (1980) showed the mating system of the damselfish, *Dascyllus marginatus,* to be affected by patch reef size. Solitary male damsels successfully defended small patches with one or more females. On larger patches, however, multi-male groups were common. At our study site, triggerfish were observed singly or in pairs on reef patches within the Wide plot. On the Mixed plot, no more than five triggerfish were ever observed on a cluster of six closely spaced units, and in 90% of the observations, two or fewer triggerfish were counted.

Triggerfish on the Close plot did not appear to occupy defended areas and, in fact, often formed some semblance of an aggregation during periods of high occupancy. Individual or paired gray triggerfish might defend an area the size of one of our clusters, but not the size of the Close plot. Consequently the number of triggerfish on the Mixed plot could be lower than on the Wide plot, because they reside on six patches of refuge rather than 36. Little work has been published on this aspect of gray triggerfish ecology and a more detailed behavioral study is necessary to test this hypothesis.

Stone crabs on the Wide plot were larger than those on the Close plot during late spring and summer when patterns in occupancy were most pronounced. Differences in crab sizes and increased residency times at this site coupled with observations of increased prey items support our contention that food resources were more favorable around widely spaced reef units. We suggest that reef occupants, through their own feeding activities, can create relative differences in the availability and accessibility of soft-bottom food resources around reef units with different spatial configurations with consequent effects for their own local populations. This feedback mechanism is in accordance with the observed temporal changes in abundance of stone crabs, as well as, octopus.

We expected prey densities to increase at a faster rate with distance from reef units on the Wide plot, but our data only qualitatively suggest this. The sigmoidal nature of the relationship between prey abundance and distance from widely spaced reef units may reflect a decrease in the foraging radii of reef-refuging consumers which might have masked the significance of a steeper gradient at shorter distances, e.g., 1 to 20 m. Large epifaunal invertebrates, mainly echinoids, dominated our samples. Sand dollars are commonly eaten by triggerfish in the region of our study (Frazer et al., 1991) and stone crabs, too, have been observed with sand dollars in their chelipeds. Kurz (1992) investigated, in more detail, the interaction between gray triggerfish and a guild of sand dollars and suggested a mean maximal foraging radius of 20 m from refuge. Kurz's findings lend credence to the ideas presented above.

Our sampling procedure did not allow us to collect data on small soft-bottom infauna. Ambrose and Anderson (1990), however, found the overall effect of an artificial reef on surrounding infauna was limited to a small area around reef material and suggest that physical factors may be more important than predation in determining their observed patterns of infaunal abundance. Scouring around reef units at our study site is restricted to the immediate vicinity (<1 m) of refuge and is not likely to account for the patterns of abundance for adult echinoderms and mollusks reported here.

We suggest that hard-bottom refuge and soft-bottom food resources are inextricably linked in this community; the size and relative locations of reef patches affect access to prey and thereby influence the structure of the reef-associated faunal assemblage. Our comparisons across broad taxa over time and our tests of explicit hypotheses corroborate this claim. Data presented here carry potentially significant management implications and are deserving of further inquiry.

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