

SHELTER CHARACTERISTICS AND CARIBBEAN FISH ASSEMBLAGES: EXPERIMENTS WITH ARTIFICIAL REEFS

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ABSTRACT

It has long been assumed that structural shelter of the appropriate size is a primary limiting resource for coral-reef fishes. We tested two corollaries of this limited shelter hypothesis for fishes occupying 12 concrete-block reefs in a seagrass bed off St. Thomas, U.S. Virgin Islands. Each of three experiments involved six reefs (two replicates of each of three treatments) and lasted up to 27 months. The first corollary was that, holding reef size and hole size constant, reefs with more holes should support more fishes of that size than reefs with fewer holes. On reefs with 0, 12, and 24 large holes, the number of large resident fishes (squirrelfishes, groupers, and moray eels) increased directly with the abundance of holes. The availability of small shelters (gaps between blocks) was approximately constant on the reefs, so small resident fishes did not show the same pattern. When we subsequently reduced the small shelters on the reefs, the abundance of small fishes declined, especially on reefs where predatory fishes were most numerous, while the abundance of large fishes was unaffected. The second corollary was that, holding reef size and hole number constant, reefs with small holes (4×6 cm) should support more small fishes than reefs with large holes (12×14 cm), which should support more large fishes. This prediction was also verified. Beyond the effects of shelter variables, there was a statistically significant negative relationship between the number of resident piscivores and the maximum number of small fishes on any reef. This pattern suggested that piscivores set the upper limit to the number of small fishes on a reef. Overall, it appears that an indirect interaction exists between large shelters and small reef fishes: an increase in the abundance of large shelters causes an increase in the abundance of large piscivorous fishes, which in turn causes a decrease in the local abundance of small prey fishes. This phenomenon suggests that artificial reefs designed for persistent fisheries should include both small holes for small fishes (as refuges from predation) as well as large holes for predatory "target" species (as home sites).

The major factors determining the distribution and abundance of fishes on coral reefs are controversial. Some researchers maintain that post-recruitment interactions among established juveniles and adults are of primary importance, especially interspecific competition (Smith and Tyler, 1972; 1973; 1975; Gladfelter et al., 1980; Anderson et al., 1981; Gladfelter and Johnson, 1983) or predation (Shulman, 1985a; Shulman and Ogden, 1987). Others suggest that pre-recruitment factors, particularly mortality of larvae while in the plankton, may be the major determinants of adult population densities (Williams, 1980; Doherty, 1983; Victor, 1983; Sale et al., 1984; Wellington and Victor, 1985).

A potentially important habitat variable which can affect settlement, early survival, and post-recruitment interactions is structural shelter provided by reefs. That shelter is required by reef fishes is suggested by observations of resident species seldom wandering far from the reef framework, seeking shelter when approached by predators, and occupying shelter at dawn or dusk, presumably minimizing the risk of predation or surge-induced injury during inactive periods (Collette and Talbot, 1972; Hobson, 1972; Hobson and Chess, 1978).

Beyond these patterns, there is a long-standing *Limited Shelter Hypothesis* that structural shelter of the appropriate size is a primary limiting resource for reef fishes (Randall, 1963; Smith and Tyler, 1972; 1973; 1975; Sale and Dybdahl,

1975; Sale, 1977; 1978; 1984; Smith, 1978). To the extent that this hypothesis is true, competition for shelter contributes to structuring reef-fish communities. Of course, such competition may be induced by the threat of predation. Note also that shelter can potentially be limiting in quality as well as quantity. There is evidence that reef fishes prefer hole sizes near their body sizes (Randall, 1963; Robertson and Sheldon, 1979; Shulman, 1984). Thus, shelter on any given reef may potentially be limiting for one life-history stage or species and not for another.

Most evidence testing the limited shelter hypothesis has been circumstantial, being nonexperimental and/or not separating food from shelter effects. Such data largely support or are at least consistent with the hypothesis. First, fishes often defend shelter sites, suggesting that suitable holes are in short supply (Low, 1971; Hobson, 1972; Ebersole, 1977; Robertson and Sheldon, 1979; Shulman, 1985b). Second, settlement (by juveniles) and/or colonization (by adults) is more rapid to empty sites than to similar sites already occupied by fishes, which is consistent (but not sufficient) evidence of competition for shelter (Sale, 1976; Talbot et al., 1978; Sweatman, 1985). Third, fishes rapidly colonize artificial reefs or denuded natural reefs, suggesting that nearby natural reefs are crowded (Randall, 1963; Sale and Dybdahl, 1975; Molles, 1978; Talbot et al., 1978; Bohnsack and Talbot, 1980; Shulman et al., 1983; Walsh, 1985). Fourth, fish abundance has been correlated with structural complexity on some natural reefs (Luckhurst and Luckhurst, 1978), but not on others (Risk, 1972; Sale and Douglas, 1984).

Direct experimental verification has been limited. In the Caribbean, Shulman (1984) demonstrated by short-term manipulations of small shelters that increasing shelter availability increased settlement and survival rates of recently metamorphosed juveniles.

Evidence falsifying the limited shelter hypothesis has been derived largely from systems where the pool of available larvae appears to be very limited, thus precluding competition for shelter. Such recruitment-limited systems have been documented in the western Caribbean (Panama; Victor, 1983; 1986), the eastern Pacific (Panama; Wellington and Victor, 1985; 1988), and the Great Barrier Reef (One Tree Reef; Williams, 1980; 1983; Doherty, 1982; 1983). Experimental manipulations of natural shelters for a wrasse (Robertson and Sheldon, 1979) and a territorial damselfish (Robertson et al., 1981) indicated that shelter availability did not limit local populations on the Caribbean coast of Panama. Further, Sweatman (1985) found that increasing the abundance of conspecifics actually facilitated recruitment in social damselfishes occupying distinct coral heads on the Great Barrier Reef.

The goal of our study was to test experimentally the limited shelter hypothesis using artificial reefs. Artificial reefs have several advantages over natural reefs in testing hypotheses concerning structural shelter. Such reefs allow separation of food from shelter effects, control of both the structure and the history of a reef, and most importantly, controlled experimentation with true replication and randomized treatments.

Previous artificial-reef experiments that examined shelter characteristics did not test the limited shelter hypothesis because they confounded hole size and hole number (Molles, 1978; Talbot et al., 1978; Walsh, 1985). Constructing reefs with either many small holes or few large holes makes it impossible to separate the effects of these different variables; either hole size or hole number must be held constant while the other factor is varied. Moreover, including shelterless control reefs is essential to separate the effects of shelter characteristics from the simple attraction of fish to any structure (the so-called "FAD effect"). This was our basic experimental design.

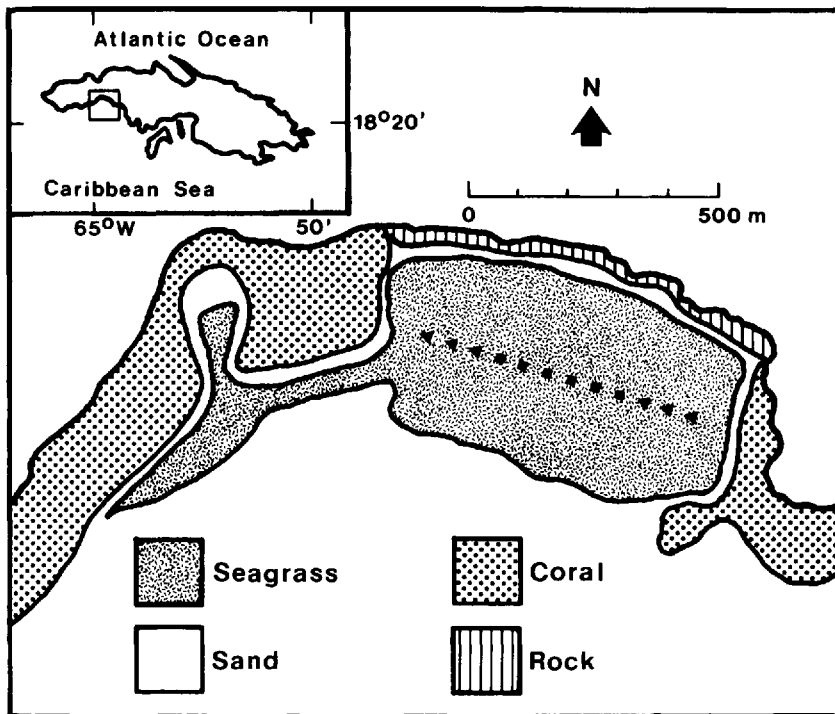


Figure 1. Map of the study site, Perseverance Bay, St. Thomas, U.S. Virgin Islands, showing the major benthic habitats and the locations of the 12 artificial reefs. The squares indicate the first set of reefs (constructed late June 1984); the triangles indicate the second set (constructed late July 1987). The reefs lie approximately along the 8 m depth contour.

We tested two explicit corollaries of the limited shelter hypothesis. If the hypothesis is true and reef size is held constant, then: (1) holding hole size constant, reefs with more holes should support more fishes of that size than reefs with fewer holes (*Corollary I*); and (2) holding hole number constant, reefs with small holes should support more juvenile and small adult fishes than reefs with large holes, which should support more large adults (*Corollary II*). Our preliminary experiments provide tentative support for these corollaries, as well as evidence for the importance of interactions between shelter size and predator-prey relations in determining the local abundances of reef fishes.

METHODS

Study Site.—Our experiments required a large and uniform study site with few natural shelters. These criteria were necessary for the artificial reefs to be isolated from each other, as well as from natural reefs, yet located in the same habitat. We chose the seagrass bed in Perseverance Bay, St. Thomas, U.S. Virgin Islands, because it meets these criteria, has no beach access, and is uncommonly visited by divers or fishermen.

The main part of the seagrass bed measures approximately 400 m by 700 m and ranges from 4 to 12 m in depth (Fig. 1). It is bordered to the east and west by fringing reefs, to the north by a rocky beach, and to the south by deep sand. Turtle grass (*Thalassia testudinum*) and manatee grass (*Syringodium filiforme*) dominate the sand bottom with scattered growths of various algae. Epiphytic animals and plants are common, and the dominant macroinvertebrates are conch (*Strombus* spp.) and occasional long-spined urchins (*Diadema antillarum*).

Such seagrass habitats are nursery grounds for small juvenile fishes before they settle permanently

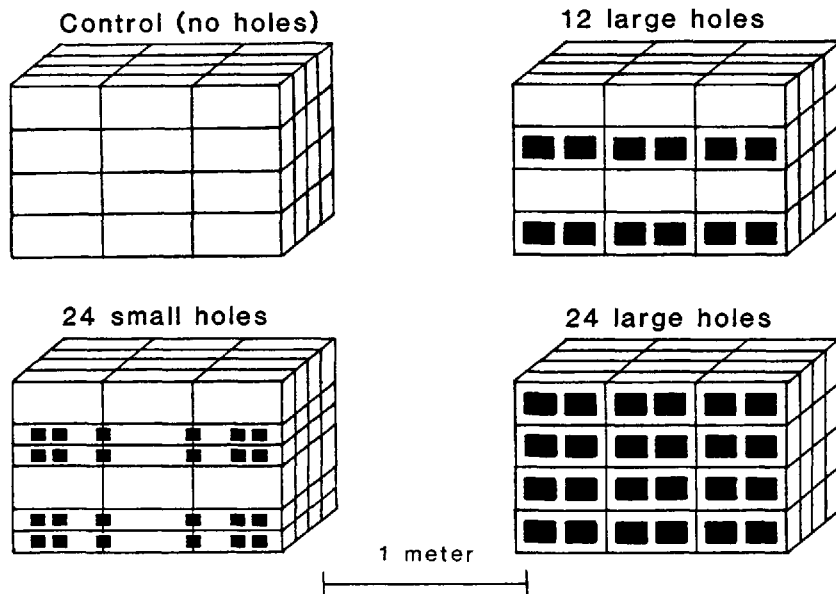


Figure 2. Designs of the concrete-block reefs. Experiments 1 and 2 involved two each of the control, 12 large-hole, and 24 large-hole structures. Experiment 3 involved two each of the control, 24 small-hole, and 24 large-hole structures.

on adjacent reefs (Shulman, 1985a). Thus, the potential sources of fishes colonizing our reefs were the plankton for settling larvae, the surrounding seagrass bed for small juveniles, and adjacent natural reefs for most adults.

Experimental Design.—Given limited funding, a trade-off existed between the size and number of reefs we could build. We chose the largest scale we could manage logistically and replicate: approximately 1 m³ per reef (Fig. 2). This rendered our experiments to the scale of small natural patch reefs: isolated large coral heads.

We built two sets of six concrete-block reefs, including four treatments (Fig. 2): (1) control reefs, providing no holes; (2) reefs with 12 large (12 cm high by 14 cm wide) holes; (3) reefs with 24 large holes; and (4) reefs with 24 small (4 cm high by 6 cm wide) holes.

Each of three experiments included six reefs, comprising two replicates of each of three treatments, distributed in a randomized block design with 50 m between reefs and each reef at least 100 m from the nearest natural reef (Fig. 1). At these distances, no reef was visible from any other reef. Each set of reefs used in each experiment was constructed within a 2-day period.

The first experiment was designed to test corollary (I) for large adults fishes, and ran from late June 1984, to early September 1986. This experiment compared control reefs to reefs with 12 and 24 large holes. Thus, if corollary (I) was true, then more large fishes would colonize the 24-hole reefs than the 12-hole reefs than the control reefs. We did not adequately reinforce this first set of reefs, so the blocks spread apart through time, providing abundant shelter for juveniles and small adults on all replicates. Therefore, this experiment was relevant only to resident fishes which were, first, too large to take advantage of (or did not utilize) the gaps between blocks, and second, small enough to fit into (and did utilize) the original holes within the blocks. In practice, these criteria included groupers and squirrelfishes 30 cm or greater in total length and moray eels 40 cm or greater in total length (species identified below). Thus, these fishes defined "large adults" and all other fishes were grouped as "juveniles and small adults."

The second experiment evolved from the first in an effort to control the abundance of small shelters on the reefs. In mid-September 1986, we reconstructed half of the six reefs, one of each treatment, on 3/4-in plywood foundations immediately adjacent to their original locations. We cemented the blocks with marine putty, effectively sealing the gaps between blocks. The resident fishes readily moved to the translocated blocks. This resulted in six unreplicated treatments: pairs of the original 0, 12, and 24 large-hole reefs, with one member of each pair having shelter for small fishes (unreconstructed)

and one lacking such shelters (reconstructed). If corollary (I) was true, then large fishes would not be affected by reconstruction, since their large shelters were unaffected. On the other hand, the abundance of small fishes would decrease substantially on the reconstructed reefs, which now lacked small shelters.

The third experiment was designed to test corollary (II) and began in mid-July 1987. This experiment compared control reefs to reefs with 24 small and 24 large holes. Thus, if corollary (II) was true, then more juveniles and small adults would colonize the small-hole reefs and more large adults would colonize the large-hole reefs. These reefs were cemented during construction to prevent gaps from developing between the blocks.

Fish Census Techniques.—We were able to census the reefs entirely, rather than relying on random sampling techniques and their potential biases. Two divers periodically censused six reefs during a single 90-min SCUBA dive. The divers observed a reef from opposite sides, slowly circling the reef while recording the number and sizes of each species on underwater slates (Sale and Douglas, 1981). From a distance of about 3 m, planktivores and other active species hovering above the reef were recorded. Then, from a distance of about 1 m, demersal and cryptic fishes (and large invertebrates) were enumerated. Finally, each hole was examined and occupants were recorded with a code for that hole. For each fish, the size class was estimated to the nearest 1 cm (below 10 cm total length) or to the nearest 5 cm (above 10 cm). The few cases with differences in census data between divers involved rare species (1 or 2 individuals) which one diver had overlooked.

Data Analyses.—The randomized-block design (Fisher, 1951) of our first and third experiments enabled us to test for significant treatment effects by two alternative one-way analyses of variance: one comparing the mean numbers of fish per reef over all censuses grouped by treatment; the other employing repeated-measure (i.e., repeated-census) analysis of numbers of fish per reef grouped by treatment (Winer, 1971). Note that both analyses incorporated the fact that repeated censusing of reefs increased the precision of estimates of fish population sizes per reef, but did not contribute to sample sizes for analysis. In other words, both analyses properly incorporated two replicates (reefs) per treatment. We ran these analyses using the SYSTAT microcomputer package following positive tests for normality (normal probability plots) and homogeneity of variances (Bartlett's tests). For our first experiment, we analysed the data gathered during our last four censuses (September 1984 to September 1986), which represented the period following the initial colonization of the reefs. For our third experiment, we analysed the data from our first three censuses (July 1987 to November 1987). Because these ANOVA's produced nearly identical patterns of significance, we report here the results of the more conservative analysis of mean census data.

As noted above, our second experiment did not involve replicated treatments, so inferential statistics were not appropriate. Instead, we simply compared mean differences between pairs of reefs of the same hole-number treatment before and after one member of each pair was reconstructed.

Tagging Study.—Crucial to the experiment design was the assumption that each reef was sufficiently isolated such that resident fishes did not move between reefs. We tested this assumption of independence during the first and second experiment by tagging and tracking resident adults. We captured fishes in situ by prodding a fish in a hole so that it swam into a holding bag covering the opposite opening. We tagged the fishes underwater with color-coded anchor tags inserted at the base of the dorsal fin.

RESULTS

Tagging Study.—Between March and June 1987, we tagged 15 adult fishes residing on the first set of reefs: 12 *Holocentrus ascensionis* squirrelfish (Holocentridae), 2 *Epinephelus striatus* groupers (Serranidae), and 1 *Acanthurus coeruleus* surgeonfish (Acanthuridae). Only two individuals were not seen after tagging (one squirrelfish and one grouper). Ten of the remaining 13 fish (all squirrelfish) were seen on all subsequent censuses at the reefs where they were tagged. The remaining grouper disappeared from its reef after at least 85 days in residence, the surgeonfish after 9 days, and one of the squirrelfish after 100 days. Most importantly, no tagged fish was seen at a reef other than where it was tagged. Although untagged, juveniles of grunts and other species known to migrate daily did not noticeably move between reefs. Therefore, our preliminary data suggest that the reefs were sufficiently isolated to constitute independent replicates.

General Patterns.—We observed 79 fish species from 24 families on the reefs. The occurrence of 20 species at any given time on a single reef was common. We

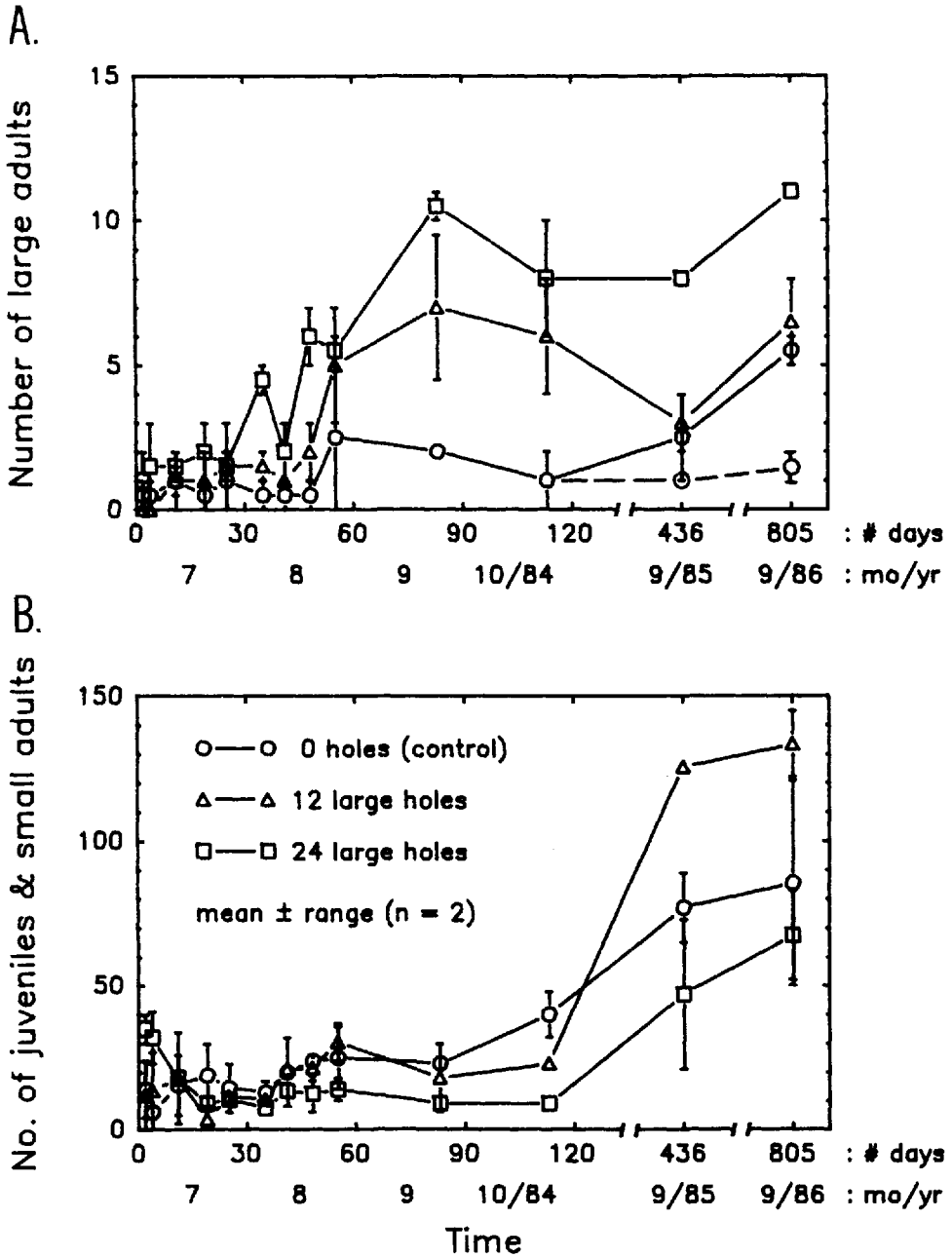


Figure 3. Experiment 1: Number of resident fish occupying six artificial reefs over 27 months (2 replicates per treatment). A, large adults which utilized only the large holes. The dashed curve excludes groupers that burrowed under the control reefs. B, juveniles and small adults which utilized gaps between blocks on all reefs.

Table 1. Experiment 1: Tests for significant effects of the number of large holes on the number of large adult resident fish per reef (A) including and (B) excluding fish that burrowed under the control reefs. Analysis of variance: ns = not significant ($P > 0.05$), * = significant ($P < 0.05$). Student-Newman-Keuls (SNK) multiple comparisons: underlined means are not significantly different

A. Including burrowers: Analysis of variance:					
Source	SS	df	MS	F	P
Among treatments	44.0	2	22.0	8.2	0.06 ns
Within treatments	8.0	3	2.7		
SNK multiple comparisons:					
Treatment:		0 holes	12 holes		24 holes
Mean number of fish:		<u>2.8</u>	<u>5.8</u>		<u>9.4</u>
B. Excluding burrowers: Analysis of variance:					
Source	SS	df	MS	F	P
Among treatments	64.2	2	32.1	13.4	0.03*
Within treatments	7.2	3	2.4		
SNK multiple comparisons:					
Treatment:		0 holes	12 holes		24 holes
Mean number of fish:		<u>1.4</u>	<u>5.8</u>		<u>9.4</u>

excluded from analysis seven species of lizardfishes (Synodontidae), trumpetfishes (Aulostomidae), jack (Carangidae), and goatfishes (Mullidae), which visited the reefs sporadically as transients. We considered the remaining species to be "residents," which consistently remained near the reefs and sought shelter in the reefs when divers approached. Consistently the most abundant residents were juvenile and adult squirrelfishes (Holocentridae) and juvenile grunts (Haemulidae = Pomadasyidae). Numerically common were groupers and their relatives (Serranidae), cardinalfishes (Apogonidae), juvenile snappers (Lutjanidae), wrasses (Labridae), and gobies (Gobiidae). Uncommon yet persistent were moray eels (Muraenidae), angelfishes (Pomacanthidae), butterflyfishes (Chaetodontidae), damselfishes (Pomacentridae), parrotfishes (Scaridae), surgeonfishes (Acanthuridae), and puffers (Tetraodontidae).

Except for obvious differences concerning adult fish sizes, there were no major differences between treatments in terms of species composition. Therefore, we present our results as the number of fish of a given size class per reef.

Corollary I: Experiment 1. — The first experiment involved 13 censuses taken over 27 months. Six species met our criteria for "large adult residents" defined above, which colonized the reefs as adults: three moray eels (*Gymnothorax funebris*, *G. moringa*, and *G. vicinus*), longjaw squirrelfish (*Holocentrus ascensionis*), red hind (*Epinephelus guttatus*, a small grouper), and Nassau grouper (*E. striatus*).

Within 1 month of reef construction, the abundance of large adult residents was greatest on the high-shelter (24-hole) reefs, intermediate on the low-shelter (12-hole) reefs, and lowest on the shelterless control reefs (Fig. 3A). These differences between treatments persisted and, in the case of the high-shelter reefs, increased in magnitude throughout the experiment. However, during the last two censuses (1985 and 1986) there were no pronounced differences between the low-shelter and control reefs. This was due to some of the groupers creating shelter by burrowing holes beneath the control reefs, which rendered the overall pattern

Table 2. Experiment 1: Tests for significant treatment effects of the number of large holes on the number of juvenile and small adult resident fish per reef. Analysis of variance: * = significant ($P < 0.05$). Student-Newman-Keuls (SNK) multiple comparisons: underlined means are not significantly different

Analysis of variance:					
Source	SS	df	MS	F	P
Among treatments	1,760.6	2	880.3	11.8	0.04*
Within treatments	223.9	3	74.6		
SNK multiple comparisons:					
Treatment:	24 holes		0 holes		12 holes
Mean number of fish:	<u>33.1</u>		<u>56.4</u>		75.0

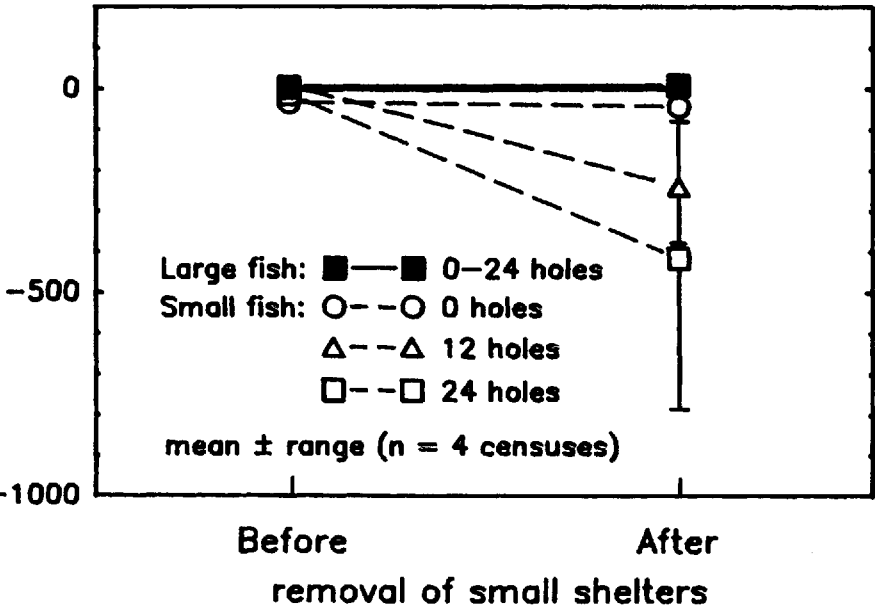
only marginally significant (Table 1A). However, excluding the burrowers from analysis (Fig. 3A) resulted in a significant trend overall (Table 1B), thus supporting corollary (I).

Corollary I: Experiment 2. — As described above, gaps between the concrete blocks provided abundant shelter for resident juveniles and small adults on all reefs during the first experiment. Consequently, the small fish did not exhibit the trend shown by the large adults; through most of the first experiment there were no appreciable differences between treatments (Fig. 3B). There was a tendency during the last two censuses for the high-shelter reefs to support the fewest and the low-shelter reefs to support the most small fishes, nearly opposite the pattern for large fishes. This trend resulted in a barely significant pattern overall, although neither hole treatment was significantly different from the holeless controls (Table 2).

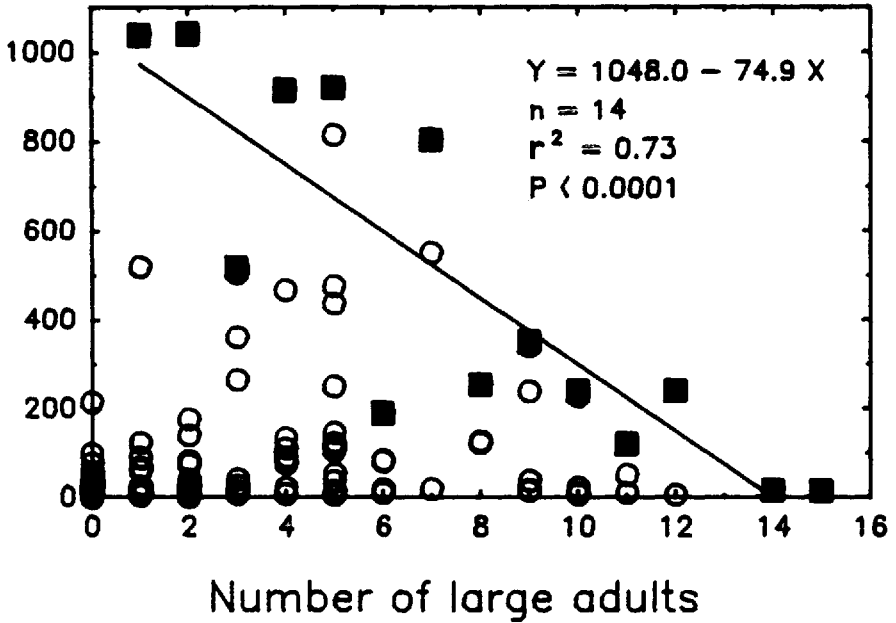
To determine whether gaps between the blocks had indeed caused the abundances of small fishes to be similar between treatments, we terminated the first experiment and reconstructed one set of replicates (three reefs) to remove the gaps. We censused the reefs nine times after reconstruction. However, to create equal samples, we compared the first four “after-reconstruction” censuses with the four “before-reconstruction” censuses occurring after the reefs became fully colonized (i.e., the last four censuses in Fig. 3). We examined the mean differences between pairs of reefs in the same hole-number category before and after one member of each pair was reconstructed. Figure 4 shows that this difference virtually did not change for large adult residents, yet decreased progressively from 0 to 12 to 24-hole reefs for small fishes after reconstruction. However, the 0-hole reef showed virtually no decline in small fish after reconstruction. Thus, in two of three cases these results supported the prediction that decreasing the abundance of small shelters should decrease the abundance of small fishes.

Interactions between Large and Small Fishes. — The first two experiments suggested an inverse relationship between the densities of large and small fishes. In the first experiment, there appeared to be nearly opposite patterns of abundance between the two size classes. For example, large fishes were consistently most abundant and small fishes were consistently least abundant on the 24-hole reefs (Fig. 3). In the second experiment, during which the number of small fishes declined where small shelters were removed (on the reconstructed reefs), the extent of the decline increased with the number of large holes on the reef (Fig. 4), and thus with the number of resident large fishes (Fig. 3). If only shelter characteristics

Difference in no. of fish between reefs of same hole category (rebuilt - control)



No. of juveniles & small adults



determined the abundance of small fishes, then the decline in the number of small fishes should have been approximately equal between reconstructed reefs.

All of the large adult resident species on our reefs are known to consume small fishes (Randall, 1967; Gladfelter and Johnson, 1983; Beets, unpublished). Thus, a significant inverse relationship between the abundances of the two size classes would suggest that predation by large fishes may have partially determined the abundance of small fishes.

In fact, a highly significant negative relationship existed between the abundance of large fishes and the maximum number of small fishes (mostly juvenile grunts) observed across all reefs and censuses made through November 1987 ($P < 0.0001$, $r^2 = 0.73$, $df = 12$, Fig. 5). The maximum number of small fishes at each nonzero large-fish density occurred after the reefs were saturated, a year after the experiments began (the 1985 census and beyond). (This period included a large recruitment of grunts late in 1986.) This pattern suggests the hypothesis that resident piscivores set the upper limit to the abundance of small fishes on the reefs.

Corollary II: Experiment 3.—Data from the first 4 months of this experiment (three censuses) support the corollary. Large nonburrowing adults (moray eels and groupers) colonized the large-shelter reefs more extensively than the control and small-shelter reefs (Fig. 6A). Conversely, juveniles and small adults were most abundant on the small-shelter reefs (Fig. 6B). Overall, these initial trends are significant for small fishes, but not for large adults (Table 3). Thus, these data tentatively support the underlying assumption of the limited shelter hypothesis that fishes select hole sizes similar to their body sizes.

DISCUSSION

Shelter Characteristics and Fish Abundance.—Our preliminary experiments supported two corollaries of the limited shelter hypothesis. Corollary (I) states that, if reef size and shelter size are held constant, then reefs with more shelters should support more fishes of that size than reefs with fewer shelters. Our first experiment involved shelters of two sizes: large holes in concrete blocks (which varied in abundance between treatments) and small gaps between the blocks (which were abundant and roughly constant between treatments). In support of corollary (I), the abundance of large fishes increased with the abundance of large shelters, and the abundance of small fishes did not (Fig. 3). These results suggest that large fishes require large shelters as home sites and that such shelters were limiting on our reefs.

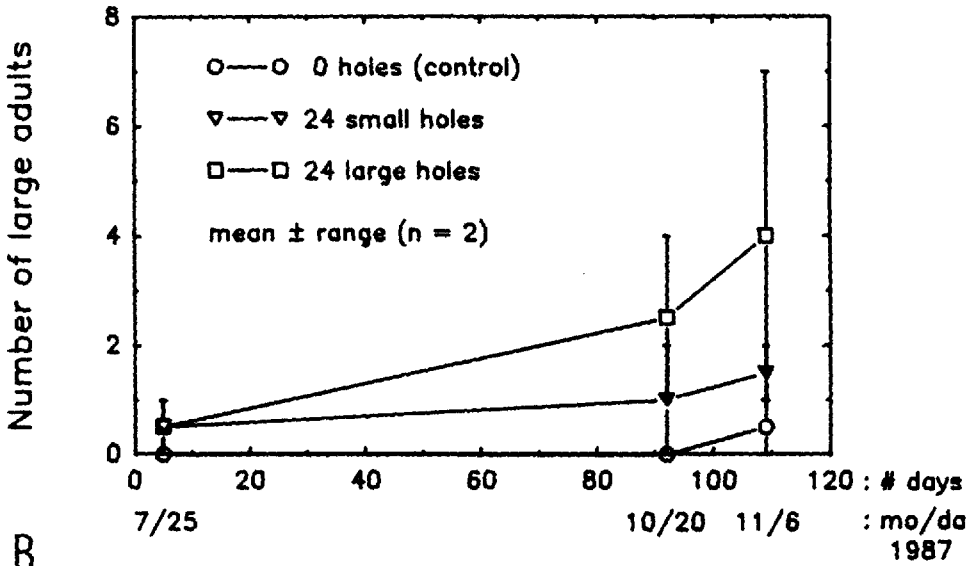
In our second experiment, we eliminated the small shelters. In further support of corollary (I), this manipulation decreased the abundance of small fishes and had no effect on large fishes (Fig. 4). However, the decline in the abundance of small fishes increased with the number of large holes and thus large fishes on the

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Figure 4. Experiment 2: Differences in fish abundances between reefs of the same hole-number category from experiment 1, before and after one reef of each pair was rebuilt, removing small shelters. The negative differences for small fish after reconstruction indicate that the abundances of small fish decreased on reconstructed reefs relative to reefs that were not rebuilt.

Figure 5. The number of juvenile and small adult fish as a function of the number of large adult fish on each of six reefs over 22 censuses (July 1984 to November 1987, $N = 132$ points). All points near the origin occurred early during initial colonization. The solid-square points represent the maximum number of small fish in the presence of large fish after the reefs were fully colonized. The regression through the square points is highly significant.

A.



B.

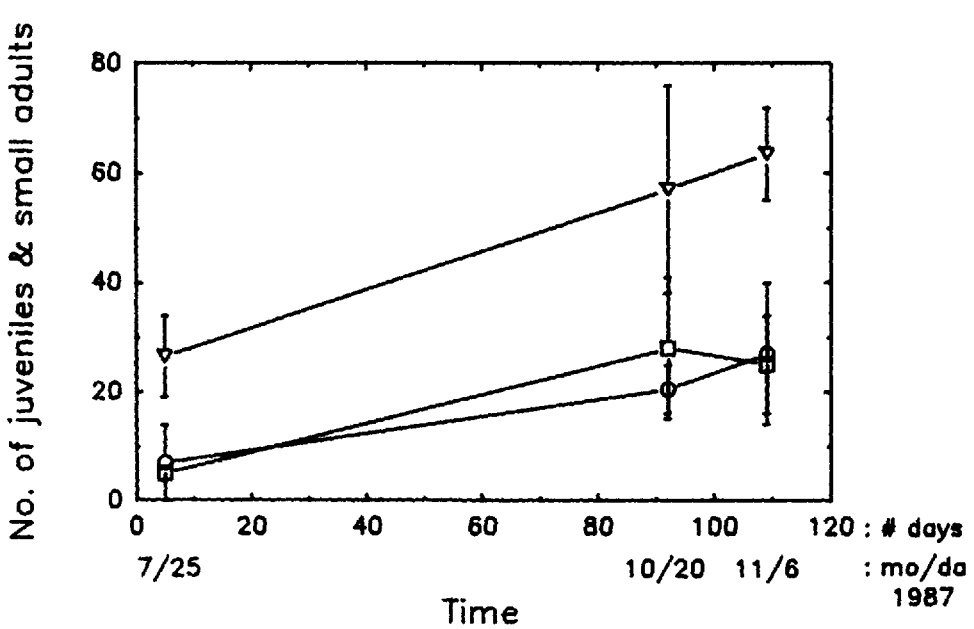


Figure 6. Experiment 3: Number of resident fish occupying six artificial reefs over 4 months (two replicates per treatment). A, large adults; B, juveniles and small adults.

reef. Moreover, there was no appreciable decline of small fishes on reefs lacking large holes, where large fishes were not abundant. This pattern suggests that small shelters may not be necessary for small fishes where piscivorous fishes are uncommon (Shulman, 1985a).

Corollary (II) states that if reef size and shelter number are held constant, then

Table 3. Experiment 3: Tests for significant treatment effects of hole size on the number of (A) large adult and (B) juvenile and small adult resident fish per reef. Analysis of variance: ns = not significant ($P > 0.05$), * = significant ($P < 0.05$). Student-Newman-Keuls (SNK) multiple comparisons: underlined means are not significantly different

A. Large adult fish: Analysis of variance:					
Source	SS	df	MS	F	P
Among treatments	4.9	2	2.5	1.3	0.39 ns
Within treatments	5.7	3	1.9		
SNK multiple comparisons:					
Treatment:		0 holes	small holes		large holes
Mean number of fish:		<u>0.2</u>	<u>1.0</u>		<u>2.4</u>
B. Juvenile and small adult fish: Analysis of variance:					
Source	SS	df	MS	F	P
Among treatments	1,219.4	2	609.7	8.9	0.05*
Within treatments	204.5	3	68.2		
SNK multiple comparisons:					
Treatment:		0 holes	large holes		small holes
Mean number of fish:		<u>18.2</u>	<u>19.4</u>		49.0

reefs with small shelters should support more small fishes than reefs with large shelters, and vice versa. In our third experiment, small fishes indeed mostly colonized small-shelter reefs and large fishes mostly colonized large-shelter reefs (Fig. 6).

Because the reefs in each experiment were constructed at the same time in the same habitat, were identical in size, were randomly distributed by treatment, and were isolated from each other, it is highly unlikely that these patterns were the result of limited recruitment or colonization. Rather, the combined results of these experiments suggest that shelter of the appropriate size was a limiting resource on our reefs.

These data corroborate and extend Shulman's (1984) small-scale experiments with juvenile fishes. She found that settlement and/or early survivorship over one-month periods increased with the availability of shelters (0 to 2 holes in conch shells) off St. Croix, USVI, some 40 nautical miles from our site off St. Thomas. Our experiments demonstrated the same pattern for both small fishes and large adults over much larger temporal and spatial scales. Shulman (1984) also compared conch shells with one small vs. one large hole. She found no significant differences in the overall abundances of larvae settling these two treatments, yet did not report differences in fish sizes. Our study showed that hole size is an important component of shelter quality—only fishes of the same general size as the holes in each experiment responded to variation in the abundance of those holes.

Besides Shulman's study, prior artificial-reef studies have not tested the limited shelter hypothesis due to their experimental designs (see Introduction). Nonexperimentally, Risk (1972) at St. John, USVI, Luckhurst and Luckhurst (1978) at Curacao, and Sale and Douglas (1984) at the Great Barrier Reef examined correlations between reef structural complexity and various fish community parameters. Luckhurst and Luckhurst found that both fish abundance and the number

of fish species were positively correlated with substrate complexity, while Risk found a significant correlation only with the number of species. These correlations were presumably due to a positive association between substrate complexity and microhabitat variety, which is not necessarily equivalent to shelter availability. In the Australian study, neither fish abundance nor species richness was significantly correlated with shelter abundance, which was consistent with the apparent recruitment-limited nature of fish populations in that region (see Introduction). Hence, a definitive correlative analysis of the relationship between shelter availability and fish abundance on large coral reefs has yet to be accomplished.

Scale and Reality.—Despite the expanded scale at which the limited shelter hypothesis has now been demonstrated experimentally, we still do not know unequivocally that our results can be extrapolated to the scale of entire coral reefs. On larger reefs, the ratio of food to shelter abundance may decrease for some foragers, especially planktivores. Such patterns would tend to increase the relative importance of trophic factors in determining local distributions and abundances of fishes.

Nevertheless, two considerations suggest that our results are relevant to natural reefs. First, given that our reefs supported tens of adult and hundreds of juvenile fishes of tens of species over a period of years, each reef could certainly be considered an ecologically realistic assemblage in terms of local species-species and species-environment interactions. Second, our ongoing analyses of natural reefs indicate that our high-shelter reefs contained more (although less variable) shelter space than comparably sized natural reefs in our study area. Moreover, our artificial reefs supported more fishes than most comparably sized natural reefs. Thus, shelter limitation at the scale of our experiments was realistic. Of course, our reefs were artificial, but only by controlling the age, size, and structure of the reefs could we adequately control shelter variables and conduct a true experiment.

The Role of Predation.—Perhaps the most striking pattern from this study was the strong negative relationship between the number of piscivorous fishes on a reef and the maximum number of co-occurring potential prey fishes (Fig. 5). Shulman et al. (1983) found a similar pattern on much smaller concrete-block reefs during a 2-month study off St. Croix. Reefs which recruited small predatory snappers subsequently recruited fewer juvenile grunts. Such patterns suggest the hypothesis that resident piscivores may set an upper limit to the number of prey fishes which can occur on a reef. Testing this hypothesis would require manipulations of piscivore densities on reefs. Unfortunately, previous attempts at such manipulations, by spearfishing (Bohnsack, 1981), trapping (Stimson et al., 1982), and caging (Doherty and Sale, 1986), have been largely unsuccessful. Nonetheless, our data are consistent with the inferred importance of mortality in determining the abundance of small grunts on Caribbean reefs, as estimated by Shulman and Ogden (1987).

If true, the predation hypothesis would indicate an important indirect interaction between large shelter and small fishes: an increase in the abundance of large shelter causes an increase in the abundance of large piscivorous fishes, which in turn causes a decrease in the abundance of small prey fishes (Randall, 1963). This indirect linkage could have important ramifications for artificial reef fisheries. If an artificial structure does not provide shelter for both predators and their prey, then a persistent fish assemblage may not develop. It seems that the best reef design would provide both small shelters for small fishes (as refuges from predation) and large shelters for large predatory "target" fishes (as home sites).

ACKNOWLEDGMENTS

We are especially grateful to P. Taylor for collaboration during the early stages of the project. We thank R. Davis, J. Lucas, J. Munro, L. Patterson, T. Turner, and especially M. Sabino for field assistance, and S. Overton for statistical advice. J. Bohnsack, B. Menge, and two anonymous reviewers provided comments which improved the manuscript. This project would not have been possible without logistic support and encouragement from W. MacLean and L. Ragster, University of the Virgin Islands. Partial funding was provided by the University of Puerto Rico Sea Grant Program (seed money projects PD-33 R/LR-06 and PD-42 R/ER-40). Finally, we appreciate the timeless inspiration of R. Crumb.

LITERATURE CITED

- Anderson, G. R. V., A. H. Ehrlich, P. R. Ehrlich and J. D. Roughgarden. 1981. The community ecology of coral reef fishes. *Am. Nat.* 117: 476-495.
- Bohnsack, J. A. 1981. Effects of piscivorous predator removal on coral reef fish community structure. Pages 258-267 in G. M. Cailliet and C. A. Simenstad, eds. Gutshop '81: fish food habits studies. Univ. Wash. Sea Grant Pr., Seattle, WA. 312 pp.
- and F. H. Talbot. 1980. Species-packing by reef fishes on Australian and Caribbean reefs: an experimental approach. *Bull. Mar. Sci.* 30: 710-723.
- Collette, B. B. and F. H. Talbot. 1972. Activity patterns of coral reef fishes with emphasis on nocturnal-diurnal changeover. *Bull. Nat. Hist. Mus. Los Angeles Co.* 14: 98-124.
- Doherty, P. J. 1982. Some effects on the juveniles of two species of tropical, territorial damselfish. *J. Exp. Mar. Biol. Ecol.* 65: 249-262.
- . 1983. Tropical territorial damselfishes: is density limited by aggression or recruitment? *Ecology* 64: 176-190.
- and P. F. Sale. 1986. Predation on juvenile coral reef fishes: an exclusion experiment. *Coral Reefs* 4: 225-234.
- Ebersole, J. P. 1977. The adaptive significance of interspecific territoriality in the reef fish *Eupomacentrus leucostictus*. *Ecology* 58: 914-920.
- Fisher, R. A. 1951. The design of experiments. Oliver and Boyd, Edinburgh. 6th Ed. 244 pp.
- Gladfelter, W. B. and W. S. Johnson. 1983. Feeding niche separation in a guild of tropical reef fishes (Holocentridae). *Ecology* 64: 552-563.
- , J. C. Ogden and E. H. Gladfelter. 1980. Similarity and diversity among coral reef fish communities: a comparison between tropical western Atlantic (Virgin Islands) and tropical central Pacific (Marshall Islands) patch reefs. *Ecology* 61: 1156-1168.
- Hobson, E. S. 1972. Activity of Hawaiian reef fishes during the evening and morning transitions between daylight and darkness. *Fish. Bull. U.S.* 70: 715-740.
- and J. R. Chess. 1978. Trophic relationships among fishes and plankton in the lagoon at Enewetak Atoll, Marshall Islands. *Fish. Bull. U.S.* 76: 133-153.
- Low, R. M. 1971. Interspecific territoriality in a pomacentrid reef fish, *Pomacentrus flavicauda* Whitley. *Ecology* 52: 648-654.
- Luckhurst, B. E. and K. Luckhurst. 1978. Analysis of the influence of the substrate variables on coral reef fish communities. *Mar. Biol.* 49: 317-323.
- Molles, M. C. 1978. Fish species diversity on model and natural reef patches: experimental insular biogeography. *Ecol. Monogr.* 48: 289-305.
- Randall, J. E. 1963. An analysis of the fish populations of artificial and natural reefs in the Virgin Islands. *Caribb. J. Sci.* 3: 31-47.
- . 1967. Food habits of reef fishes of the East Indies. *Stud. Trop. Ocean., Univ. of Miami* (5): 665-847.
- Risk, M. J. 1972. Fish diversity on a coral reef in the Virgin Islands. *Atoll Res. Bull.* 153: 1-6.
- Robertson, D. R. and J. M. Sheldon. 1979. Competitive interactions and the availability of sleeping sites for a diurnal coral reef fish. *J. Exp. Mar. Biol. Ecol.* 40: 285-298.
- , S. G. Hoffman and J. M. Sheldon. 1981. Availability of space for the territorial Caribbean damselfish *Eupomacentrus planifrons*. *Ecology* 62: 1162-1169.
- Sale, P. F. 1976. The effect of territorial adult pomacentrid fishes on the recruitment and survival of juveniles on patches of coral rubble. *J. Exp. Mar. Biol. Ecol.* 24: 297-306.
- . 1977. Maintenance of high diversity in coral reef fish communities. *Am. Nat.* 111: 337-359.
- . 1978. Coexistence of coral reef fish—a lottery for living space. *Env. Biol. Fish.* 3: 85-102.
- . 1984. The structure of communities of fish on coral reefs and the merit of a hypothesis-testing, manipulative approach to ecology. Pages 478-490 in D. R. Strong, D. Simberloff, L. G. Abele and A. B. Thistle, eds. *Ecological communities: conceptual issues and the evidence*. Princeton Univ. Pr.; Princeton, NJ. 613 pp.

- and R. Dybdahl. 1975. Determinants of community structure for coral reef fishes in an experimental habitat. *Ecology* 56: 1343–1355.
- and W. A. Douglas. 1981. Precision and accuracy of visual census technique for fish assemblages on coral patch reefs. *Env. Biol. Fish.* 6: 333–339.
- and ———. 1984. Temporal variability in the community structure of fish on coral patch reefs and the relation of community structure to reef structure. *Ecology* 65: 409–422.
- , P. J. Doherty, G. J. Eckert, W. A. Douglas and D. J. Ferrell. 1984. Large scale spatial and temporal variation in recruitment to fish populations on coral reefs. *Oecologia* 64: 191–198.
- Shulman, M. J. 1984. Resource limitation and recruitment patterns in a coral reef fish assemblage. *J. Exp. Mar. Biol. Ecol.* 74: 85–109.
- . 1985a. Recruitment of coral reef fishes: effects of distribution of predators and shelter. *Ecology* 66: 1056–1066.
- . 1985b. Coral reef fish assemblages: intra- and interspecific competition for shelter sites. *Env. Biol. Fish.* 13: 81–92.
- and J. C. Ogden. 1987. What controls tropical reef fish populations: recruitment or benthic mortality? An example in the Caribbean reef fish *Haemulon flavolineatum*. *Mar. Ecol. Prog. Ser.* 39: 233–242.
- , J. C. Ogden, J. P. Ebersole, W. N. McFarland, S. L. Miller and N. G. Wolf. 1983. Priority effects in the recruitment of juvenile coral reef fishes. *Ecology* 64: 1508–1513.
- Smith, C. L. 1978. Coral reef fish communities: a compromise view. *Env. Biol. Fish.* 3: 109–128.
- and J. C. Tyler. 1972. Space resource sharing in a coral reef fish community. *Bull. Nat. Hist. Mus. Los Angeles Co.* 14: 125–170.
- and ———. 1973. Population ecology of a Bahamian suprabenthic fish assemblage. *Am. Mus. Nov.* 2528: 1–38.
- and ———. 1975. Succession and stability in fish communities of the dome-shaped patch reefs in the West Indies. *Am. Mus. Nov.* 2572: 1–18.
- Stimson, J., S. Blum and R. Brock. 1982. An experimental study of the influence of muraenid eels on reef fish sizes and abundance. *Hawaii Sea Grant Quarterly* 4(4): 1–6.
- Sweatman, H. P. A. 1985. The influence of adults of some coral reef fishes on larval recruitment. *Ecol. Monogr.* 55: 469–485.
- Talbot, F. H., B. C. Russell and G. R. V. Anderson. 1978. Coral reef fish communities: unstable, high-diversity systems? *Ecol. Monogr.* 48: 425–440.
- Victor, B. C. 1983. Recruitment and population dynamics of a coral reef fish. *Science* 219: 419–420.
- . 1986. Larval settlement and juvenile mortality in a recruitment-limited coral reef fish population. *Ecol. Monogr.* 56: 145–160.
- Walsh, W. J. 1985. Reef fish community dynamics on small artificial reefs: the influence of isolation, habitat structure, and biogeography. *Bull. Mar. Sci.* 36: 357–376.
- Wellington, G. M. and B. C. Victor. 1985. El Niño mass coral mortality: a test of resource limitation in a coral reef damselfish population. *Oecologia* 68: 15–19.
- and ———. 1988. Variance in components of reproductive success in an undersaturated population of coral reef damselfish: a field perspective. *Am. Nat.* 131: 588–601.
- Williams, D. M. 1980. Dynamics of the pomacentrid community on small patch reefs in One Tree Lagoon (Great Barrier Reef). *Bull. Mar. Sci.* 30: 159–170.
- . 1983. Daily, monthly and yearly variability in recruitment of a guild of coral reef fishes. *Mar. Ecol. Prog. Ser.* 10: 231–237.
- Winer, B. J. 1971. Statistical principles in experimental design. McGraw-Hill, New York.

DATE ACCEPTED: April 26, 1988.

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NOTE ADDED IN PROOF

In the year since writing this paper, we have continued to monitor the 12 reefs studied here and have constructed and begun monitoring 40 new reefs. The new reefs comprise 8 replicates each of the four treatments described above plus a 12-small-hole treatment. The old reefs have continued to display the patterns reported here and the new reefs have developed the same patterns. We plan to test these patterns further with factorial manipulations of both shelter availability and piscivore abundance.