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PREDATION, PREY REFUGES, AND THE STRUCTURE OF CORAL-REEF FISH ASSEMBLAGES[1]

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Abstract. We studied the influence of piscivorous fishes and prey refuges on assemblages of fishes occupying 52 model reefs in a large seagrass bed off St. Thomas, U.S. Virgin Islands. We conducted three experiments: two involving 6 reefs each, lasting 2 and 5 yr, and one involving 40 reefs, lasting 1 yr. Each experiment included replicate reefs in various combinations of five structural treatments: holeless controls, 12 and 24 small holes, and 12 and 24 large holes. Tagging studies indicated that the reefs were sufficiently isolated from each other to comprise statistically independent replicates, and that resident piscivores occupied home reefs. We observed 97 species on or near the reefs, representing all major foraging guilds, and each holed reef supported hundreds of individuals. We examined four categories of fish: (1) large reef associates (too large for the small holes; most of these fish were both predators on smaller fish and prey for larger transient piscivores), (2) moray eels (piscivores that could fit into the small holes), (3) small reef associates (potential prey that could fit into the small holes), and (4) juvenile grunts (potential prey that sporadically were extremely abundant).

We tested five a priori predictions of the general hypothesis that predation is an important process structuring reef-fish assemblages. The first two predictions dealt with the role of prey refuges. First, if reef holes function as prey refuges, then prey fish should be most abundant on reefs providing holes near their body diameters, because such holes would make the prey fish safest from predation. Seven of eight experimental comparisons supported this prediction, and five of them were statistically significant. Second, if refuge availability limits prey abundance, then prey fish should be more abundant on reefs with 12 holes than those with no holes, and should be more abundant on reefs with 24 holes than those with 12 holes. The first part of this prediction was verified by all nine experimental comparisons, seven of which were statistically significant. However, there were no strong differences between 12-hole and 24-hole reefs. Thus, between 0 and 12 holes per reef, holes limited local prey populations; between 12 and 24 holes per reef, the number of holes was not limiting. Several lines of evidence suggested that the latter pattern was due to temporary saturation of the study area with refuges when we added 40 reefs to 12 existing reefs.

The remaining three predictions dealt directly with the community-level role of predation. First, predators should affect local prey abundance either chronically, in which case a negative relationship among reefs is predicted between the average abundances of predators and prey, or sporadically, in which case a negative relationship is predicted between the abundance of predators and the maximum number of co-occurring prey ever observed at each predator abundance. The former prediction was falsified, whereas the latter was verified. Observations of extreme type III survivorship of recruit cohorts on reefs with many piscivores and occasional direct observations of piscivory bolstered the conclusion that this relationship was causal. Finally, we predicted that predators should affect the number of prey species on a reef. We observed a significant negative relationship among reefs between predator abundance and maximum prey-species richness. Comparing species' relative abundances on reefs at the extremes of this regression, piscivores appear to have nonselectively reduced and extirpated both common and rare prey species, although this relationship remains purely correlative. In our model system, high local species diversity appears to have been maintained despite rather than because of predation.

We propose a conceptual model where the local abundances of coral-reef fishes are determined by the relative magnitudes of recruitment by larvae, colonization by juveniles and adults, predation, and competition for refuges, each of which varies through time and space. Multifactorial field experiments will be necessary to test such pluralistic hypotheses.

Key words: Caribbean; colonization; coral-reef fish; field experiment; model reefs; predation; predator–prey abundances; prey refuges; recruitment; species richness; survivorship.

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INTRODUCTION

The idea that predation can strongly affect the distribution and abundance of prey species within a community is a central tenet in modern ecology. Unfortunately, documenting predation and its effects is difficult in most systems (Terborgh 1988). Therefore, community-level studies of predation have been largely confined to more manipulable assemblages, such as rocky intertidal and freshwater systems (reviews by Connell 1975, Zaret 1980, Sih et al. 1985).

Community-level studies of coral-reef fishes are especially difficult because these assemblages are extremely complex in at least three ways. First is the tremendous species richness characterizing these communities. It has been estimated that about 30–40% of all fish species inhabit coral reefs (Cohen 1970). Regional richness can be in the thousands of species, and hundreds of species can coexist locally (reviews by Sale 1980, Ebeling and Hixon 1991). In a typical sample near our study area, Smith and Tyler (1972) reported 75 species occupying a 3-m diameter patch reef at St. John, U.S. Virgin Islands. Second is the extremely high structural complexity of the coral-reef habitat, which provides a seemingly endless variety of microhabitats for fishes, and precludes accurate censuses of all but the most conspicuous species (reviews by Sale 1991, Ebeling and Hixon 1991). Third, as with most other marine organisms, reef fishes have open populations in which local reproductive output is probably unrelated to subsequent larval recruitment from the plankton, making demographic analyses very difficult.

Most community-level research on reef fishes has dealt with the complexity problem by following one of two approaches. The first approach is to focus on a few conspicuous species occupying continuous reef tracts, thus eliminating most species from analysis. The second approach is to focus on many species occupying very small, easily censusable habitat isolates (often much less than 1 m in diameter), thus eliminating habitat complexity from analysis.

Studies of the first kind have provided conclusions that species partition resources due to past or present competitive interactions (reviews by Ross 1986, Ebeling and Hixon 1991), that ecologically similar territorial species coexist by competitive lotteries involving chance recruitment events (Sale 1977, 1978), or that local assemblages are recruitment limited (reviews by Doherty and Williams 1988, Doherty 1991). As originally formalized by Doherty (1981), "recruitment limitation" occurs when mortality during the planktonic larval stage results in such low settlement that populations never reach levels where resources become limiting or substantial interactions among adults occur. At present, recruitment limitation seems to be the most popular hypothesis for explaining the structure of coral-reef fish communities.

Studies of the second kind have concluded either that local species composition and relative abundances vary unpredictably in ecological time (Sale and Dybdahl 1975, Sale and Douglas 1984, Sale and Steel 1989), or that shelter availability enhances net settlement of larvae from the plankton, especially where predators are abundant (Shulman 1984, 1985*a, b*).

A third and less common approach has been to focus on few species occupying very small isolates. Although doubly constrained from a community-level perspective, such studies have provided evidence that resident fish either positively or negatively affect net settlement of larvae (Shulman et al. 1983, Sweatman 1985, Jones 1987, Booth 1992).

What about predation?

Thus, facing the constraints imposed by the complexity of the system, most community-level studies to date have, directly or indirectly, concerned the question of whether reef-fish assemblages are structured by competition or recruitment limitation. Although predation was proposed as an important structuring process as early as the 1970s (Smith 1978, Talbot et al. 1978), this proposal has received relatively little empirical attention (reviewed by Hixon 1991). We find this situation to be problematical given, first, the importance attributed to predation in other marine and freshwater systems (reviews by Connell 1975, Zaret 1980, Sih et al. 1985), as well as terrestrial vertebrate communities (C. Krebs, *personal communication*; J. Terborgh, *personal communication*), and, second, the hypothesized role of predation in maintaining high diversity in tropical marine systems (Paine 1966).

Hixon (1991) reviewed the role of piscivores (mostly other fishes) in structuring assemblages of coral-reef fishes, and divided the limited evidence into three categories: circumstantial, correlative, and experimental. Circumstantially, piscivores, especially small generalized carnivores capable of consuming new recruits, are an abundant component of reef-fish communities, and morphological and behavioral antipredatory mechanisms are widespread among reef fishes. Correlatively, there is some evidence that more fish occur where the abundance of holes in reefs acting as prey refuges per se are more abundant (e.g., Shulman 1984, Roberts and Ormond 1987). Reef fish commonly defend and appear to compete for shelter (e.g., Smith and Tyler 1972, Shulman 1985*a*), although holes are not always in short supply (Robertson and Sheldon 1979, Robertson et al. 1981). Shulman (1985*b*) demonstrated that the closer to reefs small fish are tethered, the more quickly they are eaten. More directly, inverse relationships have been noted between the local abundances of prey fish and resident piscivores (Shulman et al. 1983, Shulman 1985*b*, Hixon and Beets 1989). Finally, most species for which there are sufficient data exhibit type III survivorship after settlement, which is consistent with high early-age mortality due to predation (Deevey 1947).

Surprisingly, only four experimental (loosely defined) studies of direct predation effects on entire reef-fish assemblages have been reported, each of which suffered problems in design or implementation. Bohnsack (1982) compared fish communities in the Florida Keys, where spearfishing had apparently reduced the abundance of predatory fish at one reef relative to others. He found little evidence that prey fish had increased in abundance where predators had been reduced. Stimson et al. (1982) attempted an unreplicated moray eel removal at Oahu, Hawaii, but did not census the eels, could not document that eel abundance had declined, and did not provide strong evidence that the abundance of prey fish responded to the removal per se. Doherty and Sale (1986) followed survivorship of new recruits settling in predator-exclusion cages vs. partial cages vs. open plots on the Great Barrier Reef. They encountered numerous artifacts, but found that new recruits of a group of sedentary species apparently suffered less mortality in the exclusion cages over a period of weeks. Finally, in an uncontrolled manipulation, Shpigel and Fishelson (1991) removed 97 of 155 piscivores from reefs in the Red Sea. After 36 mo there were 101 piscivores on the reefs and no significant changes in the estimated number of prey fish.

It is clear that the difficulty of detecting predation effects, as well as manipulating predators, have inhibited progress in understanding the role of predation in structuring reef-fish communities. Part of the problem lies in the two constrained scales of previous studies imposed by the complexity of reef-fish systems. On the one hand, piscivorous fishes inhabiting continuous reef tracts are diverse, abundant, and often wide-ranging, effectively precluding predator manipulations; whereas on the other hand, very small isolated patches seldom support resident piscivores.

Our goal was to circumvent the logistic constraints facing previous studies of predation by employing an alternative approach. We wished to expand the scale of habitat isolates to a size and complexity that would support many species and individuals, including resident piscivores, yet would be small and structurally simple enough that complete visual censuses of all resident fishes could be made. We also wished to control the size and abundance of shelter holes in the isolates in order to manipulate prey-refuge availability for resident fishes, to allow us to capture resident piscivores, and to provide true replication and randomized treatments.

We accomplished our goal by using concrete blocks to construct isolated, cubic-metre, model reefs. Although many other studies had employed similar reefs (e.g., Molles 1978, Talbot et al. 1978, Shulman et al. 1983), previous reefs were not nearly as large, as extensively replicated, nor designed for studying predation per se. Because our reefs were subject to natural recruitment by larvae and colonization by juveniles and adults, the resulting fish assemblages were clearly more "real" than those occurring in, say, artificially seeded temporary ponds (see Hairston 1989, Jaeger and Walls 1989, Morin 1989, Wilbur 1989). We draw this comparison because, despite their constraints, such pond studies have provided much insight on community structure in freshwater systems (Hall et al. 1970, Werner 1977, Morin 1983, Wilbur 1987, Resetarits and Wilbur 1989, Wilbur and Fauth 1990, and references therein). In any case, if predation was important on our model reefs, then impetus would be provided for more labor-intensive studies on larger reefs.

Hypotheses and predictions

We tested five predictions from three corollaries of the general hypothesis that piscivores strongly affect the community structure of reef fishes:

Hypothesis: Spatial refuges from predation limit the local abundance of reef fish.—If predators control the abundance of their prey, then spatial prey refuges should set an upper limit to local prey abundance (Jeffries and Lawton 1984, Holt 1987). The major prediction of this hypothesis (prediction 2 below) requires two assumptions. The first is that holes in reefs are in fact refuges from predation and do not *exclusively* serve other functions, such as nesting sites, shelters from turbulence, etc. This assumption seemed reasonable because we observed the fish consistently entering the holes in our reefs upon the approach of a piscivore or diver. Moreover, we never observed the fish using the holes for nesting or other specialized activities.

The second assumption is that fish prefer and/or differentially survive in holes near their body diameters, which would exclude larger predators and be most consistent with the shelters being prey refuges per se. This assumption, suggested by previous field observations (Randall 1963, Robertson and Sheldon 1979, Shulman 1984), we tested directly:

> Prediction 1: Holding the number of holes constant, reefs with large holes (12 cm high × 14 cm wide) will support more large reef-associated fish (>15 cm total length, TL, excluding moray eels) than reefs with small holes; conversely, reefs with small holes (4 cm high × 6 cm wide) will support more small reef-associated fish (<10 cm TL) and moray eels than reefs with large holes.

We defined "reef-associated" species as those that both occurred within a metre of the reef during a census and sheltered in or near the reef upon the approach of a piscivore or diver. This definition, which crosses foraging-guild boundaries, does not imply strict reef fidelity, but simply that the fish tend to utilize reefs for shelter. While most of the species associated with our reefs do inhabit reefs exclusively, others (such as many wrasses and parrotfishes) are often found in seagrass beds as well. In fact, a continuum exists between strictly reef-resident and strictly nonresident fishes; subdividing the many species we encountered into residency categories for analysis would have been arbitrary and subject to considerable interpretational error. If anything, pooling all reef-associated species was a statistically conservative approach, biasing our analyses against verifying our predictions because seagrass-associated species would tend to be evenly distributed among reef treatments.

We used 15 cm TL as the critical size defining "large" fish because preliminary observations had shown that fish above this size (except moray eels) could not or would not enter the small holes. Thus, if many large fish occupied small-hole reefs, then one could infer that holes were unimportant to those fish. Similarly, all fish <10 cm TL could enter the small holes, so we used this size to define "small" fish. Thus, because predators could enter the large holes, if small fish were equally abundant on small-hole and large-hole reefs, then one could infer that holes over the size range tested did not serve as effective refuges from predation. Although these size categories left fish of the borderline size class (10–15 cm TL) out of our analyses, this excluded only 3% of the reef-associated fish we observed.

If prediction 1 was verified, then a direct test of our hypothesis would be provided by:

> Prediction 2: Holding hole size constant, reefs with 24 holes will support more fish than reefs with 12 holes, which in turn will support more fish than holeless control reefs.

We tested this two-part prediction for large reef-associated fish using large-hole reefs, and for small reef associates and moray eels using small-hole reefs.

Hypothesis: The local abundance of piscivores and that of prey fish on a reef are causally related.—This was our fundamental hypothesis, which we approached by testing two alternative predictions: the first (prediction 3) should be true if predation is always the predominant process controlling prey abundance; the second (prediction 4) should be true if multiple processes limit predator and prey abundances and predation is important only in setting the upper limit to the number of prey occupying a reef. The number of prey fish on a reef is determined by the input rates of larval recruitment and juvenile/adult colonization, and the opposing rates of predation, nonpredatory mortality, and emigration due to many possible reasons, including competition. If predation is the predominant regulatory process, then we expect:

> Prediction 3: There will be an inverse relationship among reefs between the average abundance of reef-associated piscivores and the average number of co-occurring prey fish.

This prediction is derived from two conditions. First, the population input rates are sufficiently high to cause high prey abundances in the absence of predation (i.e., the prey are not recruitment/colonization limited), but are not so high as to swamp the predation rate when predators are present. Second, when predators are present, they limit prey populations to levels less than those set by other mortality factors and emigration. Therefore, on reefs where predators are rare, prey will always be abundant, and on reefs where predators are abundant, prey will always be rare. Sih (1984) argues that this prediction follows in general when both predators and prey are mobile (e.g., can select reefs to colonize) and prey have access to spatial refuges (e.g., holes in reefs). Correlative evidence supporting this prediction has been gathered for reef fishes (review by Hixon 1991, see *Introduction*: *What about predation?*, above) and freshwater fishes (review by McQueen et al. 1989).

If the abundances of prey fish on reefs are often limited by factors other than predation, then predation may only occasionally set the upper limit to prey populations. In such cases, we expect:

> Prediction 4: There will be an inverse relationship among reefs between the abundance of reef-associated piscivores and the maximum number of co-occurring prey fish ever observed at each piscivore abundance.

In this case, because factors such as low recruitment and colonization limit prey populations below levels set by predators, at some times on all reefs and/or at all times on some reefs, predation is only occasionally important as a regulatory process. A condition for this prediction, shared by prediction 3, is that the population input rates are not so high as to swamp the predators. Therefore, on reefs where predators are rare, prey abundances can range from low values (due to limited recruitment and colonization) to high values (limited by competition); only on reefs where predators are abundant will prey abundances always be low. Thus, prediction 4 is tested by examining the maximum number of prey fish ever observed at each predator density.

Note that both predictions 3 and 4 assume that: (1) reef-associated piscivores can consume incoming recruits or colonists at least as rapidly as the rate of recruitment or colonization; (2) reef-associated piscivores are more important than transient piscivores in influencing the local abundance of prey fishes; and (3) reef-associated piscivores spend much of their time at home reefs. Our data verified all these assumptions (see *Results*).

Meaningful tests of predictions 3 and 4 required identification of predator and prey species a priori. Randall (1967) had already identified the piscivores in our system by thorough gut analyses. We also directly observed a quarter of the 20 known piscivore species at our reefs consuming small resident fish (these piscivores being *Gymnothorax vicinus, Synodus* sp., *Holocentrus ascensionis, Epinephelus striatus,* and *Caranx bartholomaei*; see Appendix). Knowing from direct observation and Randall (1967) that the minimum size at which these species become piscivorous is ≈15 cm, and that such predators can readily consume fish as large as 10 cm, we chose these size limits to define reef-associated "predators" and "prey."

Note that these definitions ultimately resulted in most of the "large" reef-associated fish we sampled being "predators," and all of the "small" reef associates being potential "prey" (see Appendix). However, these definitions allowed for the ontogenetic reality of individuals shifting from one category to another as they grew. Of course, the "predators" we analyzed were themselves potential prey for even larger piscivores, the top predators in our study area being barracuda and sharks. This is why we expected both large and small fish to require shelter from predation.

Originally, we intended to test predictions 3 and 4 by experimental manipulations of piscivore abundances. Hurricane Hugo (September 1989) precluded this experiment by destroying our reefs and leaving a debris field of sunken uprooted trees, which abruptly ended our project. We were left with a correlative test.

Hypothesis: Piscivores affect the local diversity of their prey.—In other aquatic communities where predation is an important structuring process, predators often influence the number of co-occurring prey species (reviews by Connell 1975, Zaret 1980, Hixon 1986, Hixon and Menge 1991). We approached this hypothesis by testing the following:

> Prediction 5: Comparing among reefs, prey species richness will vary with the local abundance of piscivores.

A priori, it is impossible to predict the precise effect of predators on the local diversity of their prey without knowledge of the pattern by which predators will alter prey species composition and relative abundances (review by Hixon 1986). As with the previous predictions, Hurricane Hugo allowed us to test this prediction only by correlation.

METHODS

Study site

Our experiments required a large and uniform study area with few natural shelters but an existing food supply for reef fishes. These criteria were necessary for the model reefs to be isolated from each other, as well as from natural reefs, to inhibit movement of fish between reefs and ensure statistical independence. We chose the seagrass bed in Perseverance Bay, St. Thomas, U.S. Virgin Islands, because it met our criteria, had no beach access, and was uncommonly visited by divers or fishermen.

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

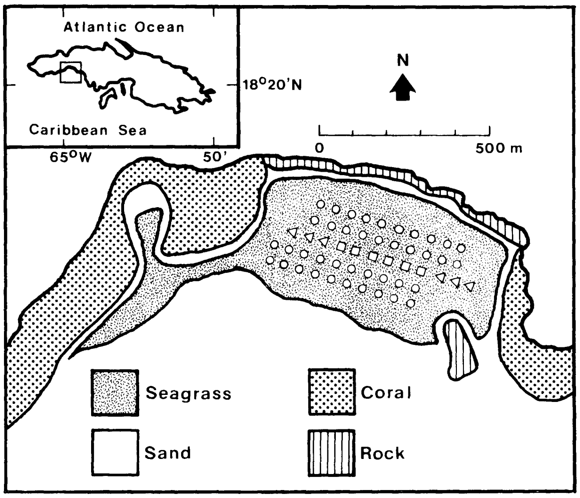

FIG. 1. Map of the study area, Perseverance Bay, St. Thomas, U.S. Virgin Islands, showing the major benthic habitats and the locations of the 52 model reefs. The central row of 6 □ and 6 △ indicates the reefs built along the 8-m isobath for experiments 1 and 2, respectively. The four rows of ○ indicate the 40 reefs for experiment 3. Note that the size of the symbols is not proportional to the size of the reefs.

Such seagrass habitats are nursery grounds for small juvenile fishes before they settle on adjacent reefs (reviews by Ogden 1988, Baelde 1990). 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 larger adults. Importantly, seagrass systems support abundant food organisms for fishes, but no shelter for larger fish (reviews by Ogden 1988, Baelde 1990), which allowed us to separate food from shelter effects during our experiments.

Experimental design

We tested our predictions with data from three overlapping experiments involving a total of 52 reefs (Table 1). Each experiment included various combinations of five reef treatments (Fig. 2): (1) control reefs, providing no holes; (2) reefs with 12 small (4 cm high by 6 cm wide) holes; (3) reefs with 24 small holes; (4) reefs with 12 large (12 cm high by 14 cm wide) holes; and (5) reefs with 24 large holes. Each experiment followed a randomized-complete-block design (Fisher 1960) with 50 m between adjacent 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.

We built each reef, measuring ≈1 m^3 and weighing 1 Mg, of concrete blocks, on thick plywood foundations, with skirts of wire mesh to prevent fish from

TABLE 1. Design of experiments examining the influences of predation on reef-fish assemblages.

Experiment	Predictions tested*	Duration	No. censuses		No. replicates by treatment†				
			Total	Analyzed	C	12S	12L	24S	24L
1	2AB (lg)	Jun 84–Jun 89	25	19	2	—	2	—	2
2	1, 2A	Jul 87–Jun 89	11	8	2	—	—	2	2
3	1, 2AB	Jul 88–Jun 89	6	6	8	8	8	8	8

* See *Introduction: Hypotheses and predictions* for numbered predictions. Prediction 2 was tested by comparing control and 12-hole reefs (2A) and by comparing 12-hole and 24-hole reefs (2B). Experiment 1 tested prediction 2 only for large fish. All experiments were used to test predictions 3 to 5.

† Reef treatments: C = holeless control; 12S = 12 small holes; 12L = 12 large holes; 24S = 24 small holes; 24L = 24 large holes (see Fig. 2). "—" indicates that the given experiment did not use the given treatment.

creating shelters by burrowing. The completed reefs were reinforced with stainless steel bands, and all crevices were sealed with nontoxic marine putty. Thus, each reef provided only the shelter it was designed to provide.

Each of the first two experiments involved six reefs, positioned along the 8-m depth contour (Fig. 1), and each comprised two replicates of three treatments (Table 1). The first experiment was designed to test prediction 2 for large fish, and began in June 1984, with all reefs constructed on the same date. This experiment compared control reefs to reefs with 12 and 24 large holes. We did not adequately reinforce this first set of reefs, which eventually formed gaps and crevices, so we reconstructed the reefs immediately adjacent to their original locations, three in September 1986, and the others in April 1988. During and after reconstruction, resident fish remained with the reefs. We censused these reefs 25 times over their 5-yr lifespan.

The second experiment was designed to test prediction 1, and began in July 1987, with all reefs constructed on the same date. This experiment compared control reefs to reefs with 24 small and 24 large holes. We censused these reefs 11 times during their 2-yr existence.

The third experiment followed a factorial design, including eight replicates of all five reef treatments (Table 1). This design allowed tests of not only predictions 1 and 2, but also, combined with results from the other experiments, predictions 3 through 5. We built these 40 reefs in late June–early July 1988, positioning two treatment blocks (10 reefs) each along the 6-m, 7-m, 10-m, and 12-m isobaths (Fig. 1). Each block of five reefs was constructed on the same date. We censused these reefs bimonthly over the year preceding Hurricane Hugo, for a total of six censuses.

Fish censuses

We were able to census the reefs entirely, rather than relying on random sampling techniques and their potential biases. Two scuba divers observed a reef from opposite sides, slowly and repeatedly circling the reef while recording the number and sizes of each species on underwater slates (cf. Sale and Douglas 1981). From a distance of ≈3 m we recorded planktivores and other active species hovering above the reef. Then, from a distance of ≈1 m, we enumerated demersal and cryptic fishes (and macroinvertebrates). Finally, we examined each hole by flashlight and recorded the occupants. We estimated the size of dense aggregations of grunt recruits (1–2 cm TL) to the nearest 100 fish, averaging values between the two divers. We estimated the size class of each fish to the nearest 1 cm (below 30 cm TL) or to the nearest 5 cm (above 30 cm TL). The few cases with differences in census data between divers involved rare species (1 or 2 individuals) that one diver had overlooked. Each reef required ≈20 min to census; we were able to census about 12 reefs in 1 d.

Data analyses

The complete randomized-block design of our experiments facilitated tests for significant reef treatment effects by repeated-measure (i.e., repeated-census) analyses of variance (ANOVA; Winer 1971). Our first and second experiments (Table 1) involved low replication ($n = 2$ per treatment), so we used a simple one-way ANOVA of the mean number of fish per reef averaged over all censuses and grouped by treatment (df = 2), followed by Student-Newman-Keuls (SNK) multiple comparisons (Sokal and Rohlf 1981). Experiment 3 provided sufficient replication ($n = 8$ per treatment) for a more sophisticated two-way (treatments by blocks) ANOVA of the mean number of fish per reef averaged over all censuses and grouped by both treatments (df = 4) and blocks (df = 7), followed by Bonferroni multiple comparisons (Miller 1985). Note that the Bonferroni procedure can detect significant multiple comparisons despite a nonsignificant ANOVA (Miller 1985), as occurred in one case in our study. Randomizing treatments among blocks allows the "block" factor and the interaction term to be eliminated from the analysis (Winer 1971, Sokal and Rohlf 1981).

We ran these analyses using the SYSTAT microcomputer package (Wilkinson 1990), following $\ln(x + 1)$ transformations, which provided positive tests for normality (normal probability plots) and homogeneity of variances (Bartlett's tests). Means were back-transformed for presentation.

For our first experiment (Table 1), we analyzed the data gathered during our last 19 censuses (September

1985 to June 1989), which represented the period following initial colonization. Similarly, for our second experiment, we analyzed the data from our last eight censuses (April 1988 to June 1989). For both these experiments, Hixon and Beets (1989) presented data on early colonization patterns. For our limited data set from the third experiment, we analyzed all six censuses (July 1988 to June 1989), which included the initial colonization period.

Tagging study

Crucial to our experimental design was the assumption of statistical independence: that each reef was sufficiently isolated so that associated fish did not move appreciably between reefs. Most small reef fish are known to be highly site attached (review by Sale 1980, but see Robertson 1988), and those that undergo twilight foraging migrations (especially grunts) apparently return to the same reef each morning (Ogden and Ehrlich 1977). Although previous tagging studies had indicated high reef fidelity (Bardach 1958, Springer and McErlean 1962), our primary concern was larger reef associates, especially groupers and large squirrelfishes, which were the most common piscivores (see Appendix).

We tested the assumption of independence—first, by tagging and monitoring reef-associated adults, and second, by translocating tagged adults to determine their homing responses. We captured individuals in situ by prodding a fish in a hole so that it swam into a holding bag covering the opposite opening. We tagged each fish underwater with a color-coded anchor tag inserted at the base of the dorsal fin, transported it underwater, and released it unharmed. For the homing study, we tagged and translocated fish from two reefs to two other reefs 140 m from their presumed home reefs. As a control for handling and transporting, we tagged and moved fish from two other reefs half this distance, then returned them to their capture reefs.

RESULTS

Tagging study

Testing the isolation of the reefs involved two phases. The initial tag-and-observe phase during experiment 1 showed that none of 15 fish from three reefs was observed at reefs other than where each was tagged (Table 2A). The tags persisted on these fish for up to 16 mo.

The tag-and-translocate phase, run in July 1989 following our last census, tested whether fish home to specific reefs following displacement. One week after the fish were tagged and translocated, we surveyed all 52 reefs. All but two of the 19 fish in the handling-control treatment remained at the reefs where they were captured (Table 2B). Of the 32 translocated fish, 19 individuals homed within 1 wk, and 10 others eventually homed. Most importantly, we observed only two of the 51 fish in this experiment at reefs other than where they were tagged (Table 2B).

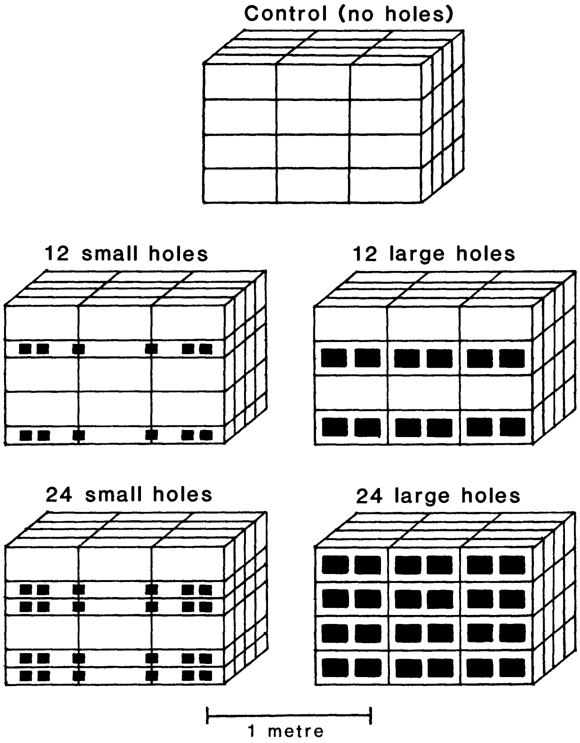

FIG. 2. Designs of the model reefs, which were constructed of concrete blocks and occupied ≈1 m^3.

Although we were unable to tag most species, large fishes (except moray eels) were numerically the most stable component of each reef assemblage, and we came to recognize many fish as individuals. Overall, we concluded that our reefs comprised adequately independent replicates for statistical analysis, and that the most common piscivores in particular showed high reef fidelity.

General patterns

Over the entire study, we observed 97 fish species from 28 families on or near the 52 model reefs (see Appendix). Of 402 reef censuses (see Table 1), 75% showed at least 10 fish species per reef, 38% showed at least 15 species, and 12% showed at least 20 species. These species comprise most of the common fishes inhabiting natural reefs in the Virgin Islands (Randall 1967, Clavijo et al. 1980). They also represent all major foraging guilds (see Appendix), suggesting that the assemblages we studied were both ecologically realistic and representative. We excluded from analysis 11 species that visited the reefs sporadically as being obvious transients (see Appendix).

Following Shulman (1985*b*, Shulman et al. 1983), we analyzed juvenile grunts (*Haemulon* spp. <10 cm TL) separately from other reef-associated small fishes because their abundance was sporadically so high that

TABLE 2. Tagging studies to determine reef fidelity of large reef-associated fish. "Home" refers to fish that were observed on the reef where they were tagged. "Away" refers to fish observed on a reef other than where they were tagged. "Tag persistence" is the number of days between the tagging date and the last date a homing fish was observed with its tag intact.

A. Tag-and-observe

	Number of fish			
Species	Tagged	Home	Away	Tag persistence (d)
Holocentrus ascensionis	12	11	0	100, 116, 207(×2), 224, 333, 397, 489(×4): $\bar{X} = 321.8$
Epinephelus striatus	2	1	0	85
Acanthurus coeruleus	1	1	0	9

B. Tag-and-translocate

	Number of fish			
Species by treatment	Tagged	Home	Away	Notes
Handling control:				
Holocentrus ascensionis	2	2	0	
Epinephelus afer	14	14	0	
Epinephelus guttatus	1	1	0	
Epinephelus striatus	2	0	1	"Away" fish on adjacent reef
Translocation test:				
Holocentrus ascensionis	1	0	0	
Epinephelus afer	27	18	1	All fish eventually homed
Epinephelus striatus	4	1	0	1 other fish homed later

they would overwhelm the abundance patterns of all other species.

There were few differences between experiments in terms of species composition and relative abundances, the major exceptions being due to unique pulses of recruitment of single species: *Myripristis jacobus* midway through experiment 1 and *Lutjanus synagris* early during experiment 3 (see Appendix). Except for obvious patterns concerning fish sizes, presented below, there were also no major differences in species composition between reef treatments. Finally, the most substantial difference in species relative abundances between the model reefs and nearby natural reefs involved grouper species: *Epinephelus afer* and *E. striatus* dominated the model reefs, whereas *E. cruentatus* and *E. fulvus* dominated natural patch reefs (Beets and Hixon, *in press*).

Prediction 1: shelter size vs. fish size

Experiments 2 and 3 provided comparisons of fish abundances between reefs of the same hole number but different hole sizes, allowing two independent tests of prediction 1 for each of the four categories of fish. As predicted, large reef associates (excluding moray eels; see Appendix for species) were always significantly more abundant on large-hole reefs than small-hole reefs (Fig. 3B and C, Table 3B and C). Conversely and also as predicted, moray eels were more abundant on small-hole reefs (Fig. 4B and C), their snake-like bodies fitting snugly into the narrower holes. This difference was statistically significant during experiment 2, but not experiment 3 (Table 4B and C).

As predicted, small reef associates (excluding juvenile grunts; see Appendix for species) were on average more abundant on small-hole reefs than large-hole reefs (Fig. 5B and C). This pattern was significant during experiment 3 (high replication), but not experiment 2 (low replication, Table 5B and C). Juvenile grunts were significantly more abundant on small-hole reefs than large-hole reefs during experiment 2 (Table 6B), but this was largely due to a single census following a recruitment pulse in mid-1988 (Fig. 6B). Grunts showed virtually no pattern in experiment 3 (Table 6C), during a period of relatively low recruitment (Fig. 6C).

In summary, seven of eight comparisons showed trends supporting the prediction of fish being more abundant on reefs with shelter holes closer to their body diameters. Five of these seven trends were statistically significant (Table 7, prediction 1), convincing us that we were justified testing prediction 2 for matching fish and hole sizes.

Prediction 2: shelter abundance vs. fish abundance

Prediction 2 had two parts. The first was that reefs with hole sizes best matching the body diameter of the fish would support more fish than reefs with no holes. All three experiments provided tests of this prediction for large reef associates, comparing holeless reefs with large-hole reefs, and all three comparisons significantly followed the prediction (Fig. 3, Table 3). Experiments 2 and 3 provided tests for the other three categories of fish, comparing holeless reefs with small-hole reefs. As predicted, moray eels were significantly more abundant

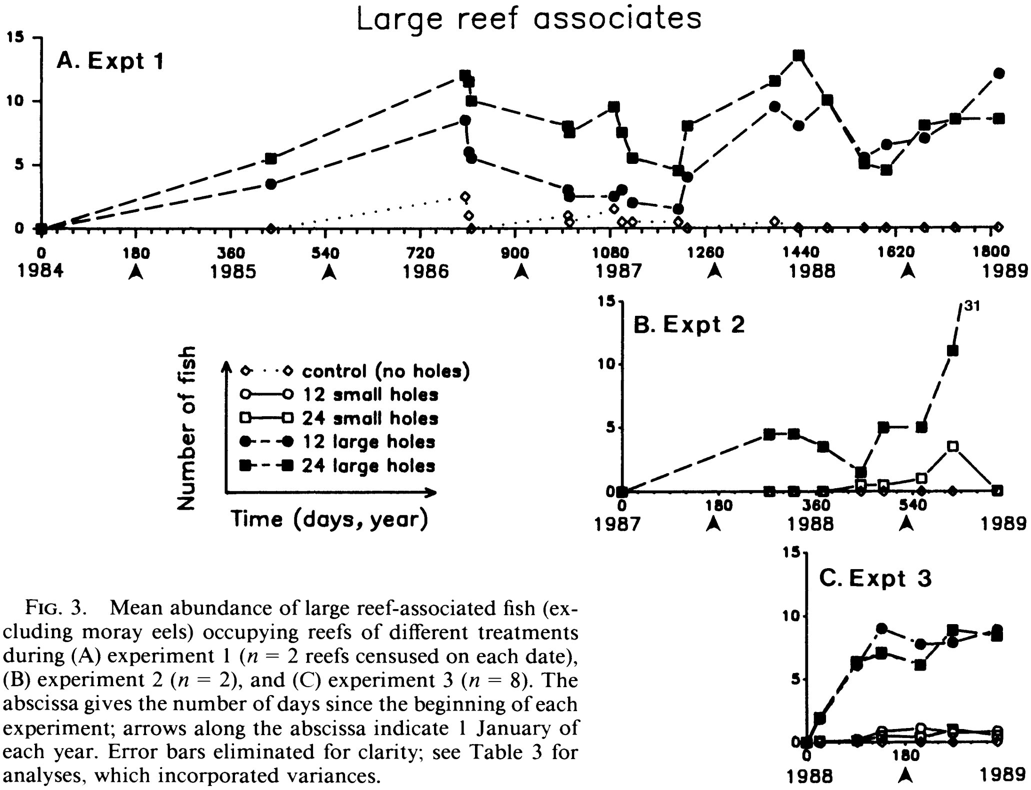

FIG. 3. Mean abundance of large reef-associated fish (excluding moray eels) occupying reefs of different treatments during (A) experiment 1 ($n = 2$ reefs censused on each date), (B) experiment 2 ($n = 2$), and (C) experiment 3 ($n = 8$). The abscissa gives the number of days since the beginning of each experiment; arrows along the abscissa indicate 1 January of each year. Error bars eliminated for clarity; see Table 3 for analyses, which incorporated variances.

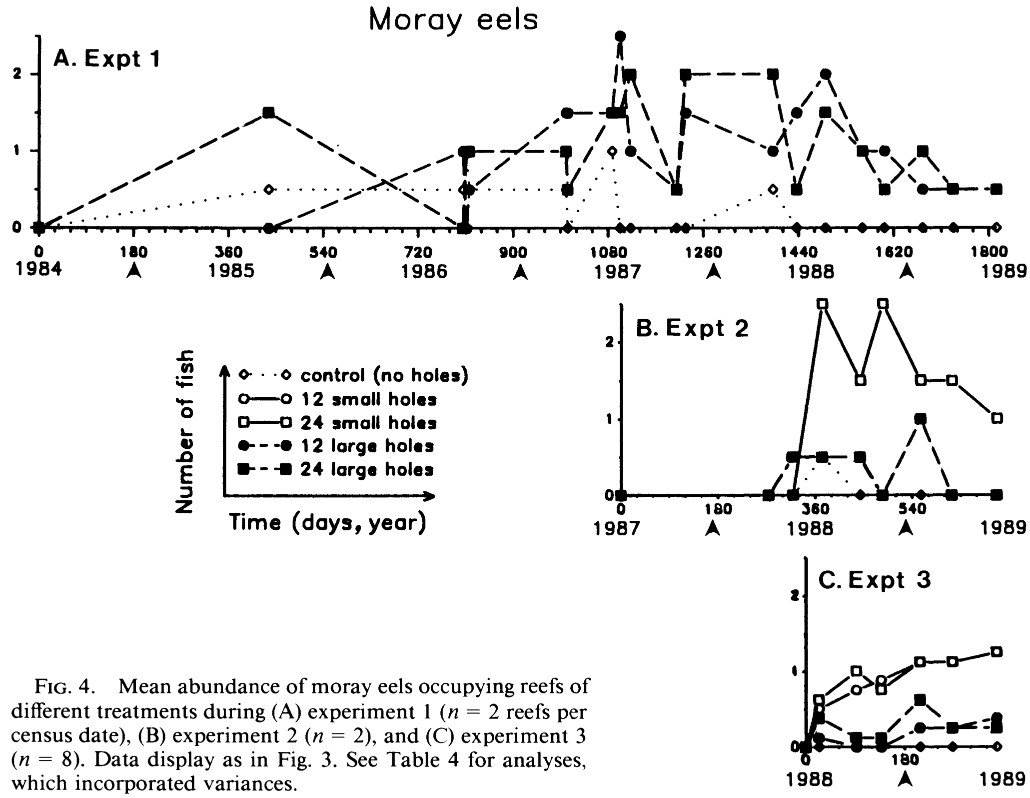

FIG. 4. Mean abundance of moray eels occupying reefs of different treatments during (A) experiment 1 ($n = 2$ reefs per census date), (B) experiment 2 ($n = 2$), and (C) experiment 3 ($n = 8$). Data display as in Fig. 3. See Table 4 for analyses, which incorporated variances.

TABLE 3. Analysis of the abundance of large fish (excluding moray eels) occupying reefs of different hole size and abundance treatments. Data were $\ln(x + 1)$-transformed prior to computations; means presented here have been back-transformed.

A. Experiment 1

One-way analysis of variance:

Source of variation	SS	df	MS	F	P
Among treatments	3.97	2	1.98	39.29	.007**
Within treatments	0.15	3	0.05		

Student-Newman-Keuls multiple comparisons†

Treatment (no. and size of holes):	0 holes	12 large	24 large
Mean number of fish:	0.4	5.7	8.4

B. Experiment 2‡

Kruskal-Wallis test: $H = 4.71$, df = 2, $P < .05$*

Wilcoxon signed-ranks tests†

Treatment:	0 holes	24 small holes	24 large holes
Mean number of fish:	0.0	0.7	8.2

C. Experiment 3

Repeated-measures analysis of variance:

Source of variation	SS	df	MS	F	P
Treatment	126.40	4	31.60	32.62	$\ll .001$***
Error	27.12	28	0.97		

Bonferroni multiple comparisons†

Treatment:	0 holes	24 small	12 small	24 large	12 large
Mean number of fish:	0.0	0.4	0.6	6.5	6.9

† In multiple comparisons (and Wilcoxon signed-ranks tests), means sharing a common underline are not significantly different ($P > .05$).

‡ Because no large fish occupied the 0-hole control reefs during experiment 2 (i.e., zero variance), the ANOVA was replaced by a Kruskal-Wallis test (Siegel 1956).

on small-holed than holeless reefs during both experiments (Fig. 4B and C, Table 4B and C). Small reef associates followed the same pattern (Fig. 5B and C), but this was significant only during the relatively highly replicated experiment 3 (Table 5B and C). Similarly, juvenile grunts followed the same pattern (Fig. 6B and C), but this was significant only during experiment 2 (Table 6B and C). In summary, all nine comparisons followed the predicted pattern, although two of these were not statistically significant (Table 7: prediction 2A).

The second part of prediction 2 was that reefs with 24 holes best matching the diameter of the fish would support more fish than reefs with 12 holes of the same size. Experiments 1 and 3 provided tests of this prediction for large reef associates, comparing reefs with 12 vs. 24 large holes. Although the predicted pattern occurred during experiment 1, in neither experiment was there a significant difference between treatments (Fig. 3A and C, Table 3A and C). Only experiment 3 tested this prediction for the other three categories of fish, comparing reefs with 12 vs. 24 small holes. The prediction was falsified outright for small reef associates (Fig. 5C, Table 5C). On average, moray eels and juvenile grunts were more abundant on 24-small-holed than 12-small-holed reefs, as predicted, but this pattern was never significant (Figs. 4C and 6C, Tables 4C and 6C). In summary, reefs with 24 holes did not support significantly more fish than reefs with 12 holes (Table 7: prediction 2B).

Prediction 3: piscivore abundance vs. mean prey abundance

If predation is the predominant process regulating the number of reef-associated prey fish, then there should be a negative relationship among reefs between the mean number of predators and the mean number of prey per reef averaged over all censuses (see Appendix for predator and prey species list). In fact, there was little pattern when these data were plotted for all 52 reefs (Fig. 7A). Many reefs, especially control reefs and reefs from experiment 3, always supported few fish; numerous points near the origin actually caused a slightly positive regression ($b = 7.62$, $r^2 = 0.10$, $n = 52$, $P = .02$). The regression became nonsignificant when the 12 holeless control reefs were excluded from analysis. Even considering each of the five reef treatments separately, no negative relationship emerged (ranges: $b = 3.53$–98.31, $r^2 = 0.02$–0.69, $n = 8$–12, $P = .001$–$.67$). Only on the nine reefs averaging >5 pred-

TABLE 4. Analysis of the abundance of moray eels occupying reefs of different hole size and abundance treatments. Data were $\ln(x + 1)$-transformed prior to computations; means presented here have been back-transformed.

A. Experiment 1

One-way analysis of variance:

Source of variation	SS	df	MS	F	P
Among treatments	0.33	2	0.16	16.79	.023*
Within treatments	0.03	3	0.01		

Student-Newman-Keuls multiple comparisons†

Treatment:	0 holes	12 large	24 large
Mean number of fish:	0.2	1.0	1.0

B. Experiment 2

One-way analysis of variance:

Source of variation	SS	df	MS	F	P
Among treatments	0.63	2	0.32	19.60	.019*
Within treatments	0.05	3	0.02		

Student-Newman-Keuls multiple comparisons†

Treatment:	0 holes	24 large	24 small
Mean number of fish:	0.1	0.3	1.3

C. Experiment 3

Repeated-measures analysis of variance:

Source of variation	SS	df	MS	F	P
Treatment	11.52	4	2.88	9.55	$\ll .001$***
Error	8.45	28	0.30		

Bonferroni multiple comparisons†

Treatment:	0 holes	12 large	24 large	12 small	24 small
Mean number of fish:	0.0	0.2	0.3	0.9	1.0

† In multiple comparisons, means sharing a common underline are not significantly different ($P > .05$).

ators did a negative regression result, but the relationship was nonsignificant ($b = -11.31$, $r^2 = 0.19$, $n = 9$, $P = .25$). From any perspective, prediction 3 was clearly falsified.

Prediction 4: piscivore abundance vs. maximum prey abundance

If predation only sets the upper limit to the number of reef-associated prey fish, then there should be a negative relationship among reefs between the number of predators and the maximum number of prey ever observed at each predator abundance. Over all 402 reef censuses (see Table 1), we encountered only 17 different predator abundances, ranging from 0 to 34 reef-associated piscivores. To examine the maximum number of prey fish ever observed at each of these predator abundances, we had to ensure that no single reef was used twice in the regression (so that the regressed points comprised independent observations). We accomplished this by working from the highest to the lowest predator abundance observed, allowing any particular reef to be used only once. Note that this algorithm conservatively biased the analysis *against* the predicted negative regression; because we had to eliminate prey maxima at low predator abundances so that no reef was used twice, selecting second- or third-highest prey abundances lowered the left side of the regression and flattened the slope.

As predicted and despite the conservative bias, the maximum number of reef-associated prey fish ever observed at each predator abundance declined significantly with increasing predator abundance (Fig. 8A; $b = -40.49$, $r^2 = 0.35$, $n = 17$, $P = .01$). We observed the same significant pattern in a separate analysis midway through experiment 1 (Hixon and Beets 1989). An identical analysis for transient piscivores (see Appendix for species) revealed the same negative relationship, although the regression was not quite significant ($b = -128.87$, $r^2 = 0.58$, $n = 6$, $P = .08$).

Recruit cohort survivorship

Because predators were large fish found mostly on large-hole reefs, and prey were small fish found mostly on small-hole reefs (as demonstrated in our test of prediction 1), the significant negative relationship between predator abundance and maximum prey abundance would be spurious if larvae settled selectively on small-holed reefs and/or avoided large-hole reefs. To

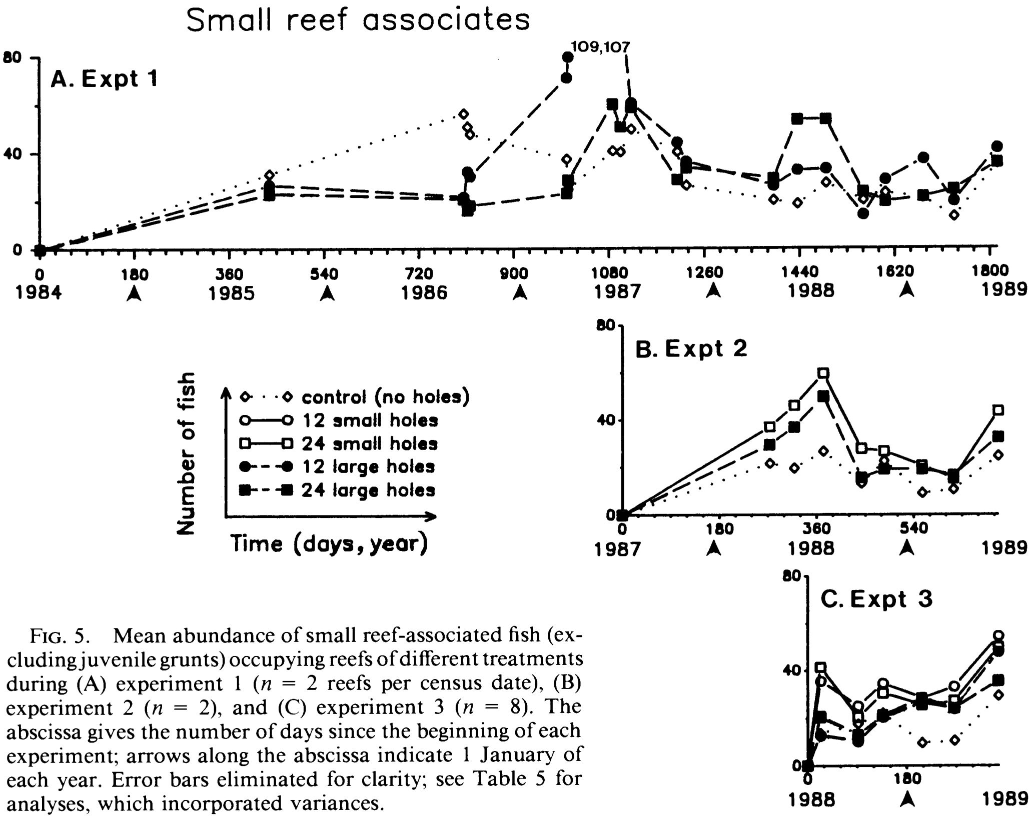

FIG. 5. Mean abundance of small reef-associated fish (excluding juvenile grunts) occupying reefs of different treatments during (A) experiment 1 ($n = 2$ reefs per census date), (B) experiment 2 ($n = 2$), and (C) experiment 3 ($n = 8$). The abscissa gives the number of days since the beginning of each experiment; arrows along the abscissa indicate 1 January of each year. Error bars eliminated for clarity; see Table 5 for analyses, which incorporated variances.

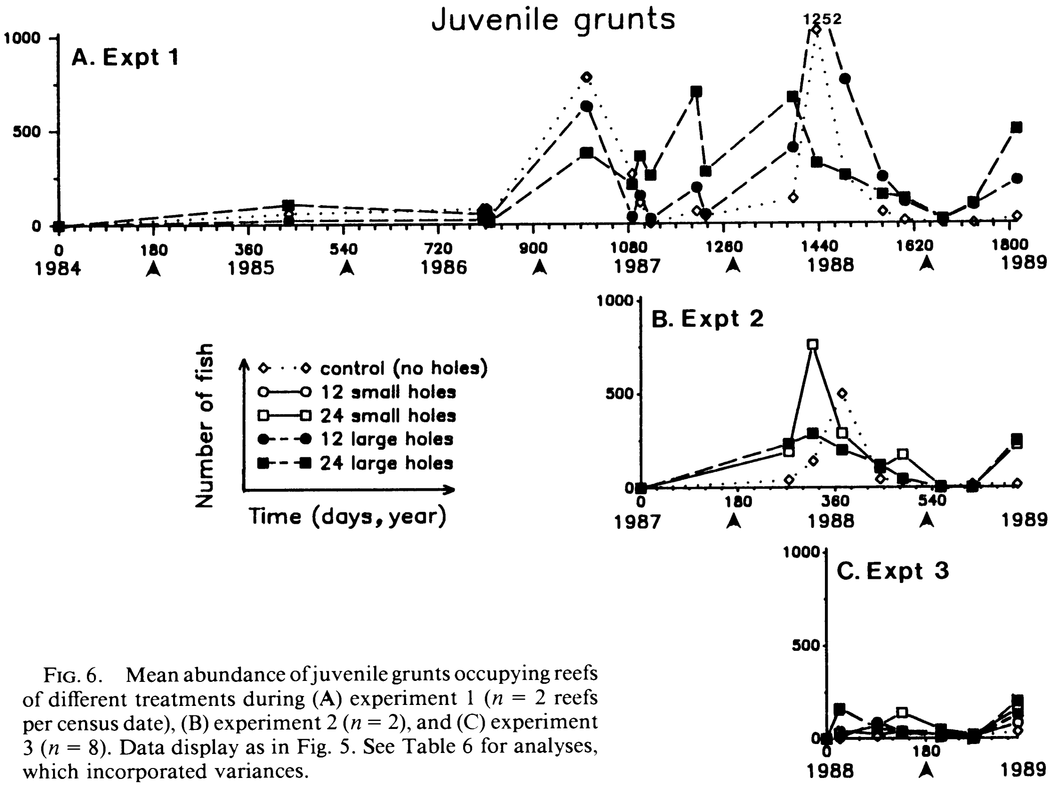

FIG. 6. Mean abundance of juvenile grunts occupying reefs of different treatments during (A) experiment 1 ($n = 2$ reefs per census date), (B) experiment 2 ($n = 2$), and (C) experiment 3 ($n = 8$). Data display as in Fig. 5. See Table 6 for analyses, which incorporated variances.

TABLE 5. Analysis of the abundance of small fish (excluding juvenile grunts) occupying reefs of different hole size and abundance treatments. Data were ln(x + 1)-transformed prior to computations; means presented here have been back-transformed.

A. Experiment 1

One-way analysis of variance:

Source of variation	SS	df	MS	F	P
Among treatments	0.12	2	0.06	2.00	.280$^{\mathrm{NS}}$
Within treatments	0.09	3	0.03		

Student-Newman-Keuls multiple comparisons†

Treatment:	0 holes	24 large	12 large
Mean number of fish:	32.6	32.6	44.6

B. Experiment 2

One-way analysis of variance:

Source of variation	SS	df	MS	F	P
Among treatments	0.37	2	0.18	5.37	.102$^{\mathrm{NS}}$
Within treatments	0.10	3	0.03		

Student-Newman-Keuls multiple comparisons†

Treatment:	0 holes	24 large	24 small
Mean number of fish:	18.4	27.4	34.4

C. Experiment 3

Repeated-measures analysis of variance

Source of variation	SS	df	MS	F	P
Treatment	18.33	4	4.58	8.84	$\ll$.001***
Error	14.51	28	0.52		

Bonferroni multiple comparisons†

Treatment:	0 holes	12 large	24 large	24 small	12 small
Mean number of fish:	17.1	23.7	23.9	32.4	35.2

NS = not significant.

† In multiple comparisons, means sharing a common underline are not significantly different (P > .05).

approach the problem of whether this negative relationship was in fact due to predators reducing prey abundances, we followed the survival of distinct cohorts of recruits that settled on both small- and large-hole reefs. Our reasoning was that type III survivorship (sensu Deevey 1947) in the apparent absence of non-predatory mortality sources would indicate that predation had reduced the size of the cohort, especially because of the general trend for smaller and younger animals to be more susceptible to predators than larger and older individuals (see Murdoch and Oaten 1975, Taylor 1984, Werner and Gilliam 1984, Hixon 1991).

Two of the most distinct recruit cohorts occurred during experiment 1, with a pulse of settlement of ≈100 *Myripristis jacobus* (soldierfish) on a 12-large-hole reef in mid-1987 (see peak in Fig. 5A) and a pulse of about 2000 *Haemulon aurolineatum* (grunts) on another 12-large-hole reef in mid-1988 (see peak in Fig. 6A). As evident in Fig. 9, and typical of other cohorts, both groups suffered high mortality shortly after settlement, displaying definite type III survivorship. (Logarithmic plots of these data were still hyperbolic.)

There was no evidence that this mortality was due to any source other than predation. There were no physical disturbances during this period, such as storms and hypo- or hyperthermal events, and no evidence of disease. Moreover, both species are highly reef associated as juveniles (and as adults in the case of *Myripristis*), so emigration was unlikely. On the contrary, we occasionally observed reef-associated piscivores consuming these fish.

In the 18-mo decline of the soldierfish (Fig. 9A), during which the average size of the censused fish increased from 8 to 19 cm TL, the reef supported 6.2 ± 2.1 ($\bar{X}$ ± 1 SD) piscivores. In the one-yr decline of the grunts (Fig. 9B), during which the average size of the censused fish increased from 5 to 18 cm TL, the reef supported 7.0 ± 2.3 piscivores. Because both these reefs were large holed, the recruits had few structural refuges that were inaccessible to predators.

Stronger inference was provided by a "natural experiment" comparing recruit survivorship among reef treatments. This fortuitous event occurred when nearly equal numbers of 1-cm TL *Chromis cyanea* (a strongly reef-associated damselfish) settled simultaneously on three adjacent reefs in April 1988, during experiment 2 (Fig. 10). Consistent with our predictions, survivorship was greatest on a 24-small-hole reef (safest from predation: only 1.2 ± 1.5 reef-associated piscivores), moderate on a holeless control reef (susceptible to tran-

TABLE 6. Analysis of the abundance of juvenile grunts occupying reefs of different hole size and abundance treatments. Data were ln(x + 1)-transformed prior to computations; means presented here have been back-transformed. Raw data from experiment 2 were analyzed directly because they were more homogeneous and normally distributed than transformed data.

A. Experiment 1

One-way analysis of variance:

Source of variation	SS	df	MS	F	P
Among treatments	0.11	2	0.05	0.60	.603^{NS}
Within treatments	0.27	3	0.09		

Student-Newman-Keuls multiple comparisons†

Treatment: (no. of holes)	0 holes	24 large	12 large
Mean number of fish:	200.9	258.8	262.7

B. Experiment 2

One-way analysis of variance:

Source of variation	SS	df	MS	F	P
Among treatments	14513.69	2	7256.84	15.06	.027*
Within treatments	1445.77	3	481.92		

Student-Newman-Keuls multiple comparisons

Treatment:	0 holes	24 large	24 small
Mean number of fish:	98.4	142.4	217.6

C. Experiment 3

Repeated-measures analysis of variance:

Source of variation	SS	df	MS	F	P
Treatment	57.67	4	14.42	2.52	.064^{NS}
Error	160.29	28	5.72		

Bonferroni multiple comparisons†

Treatment:	0 holes	12 small	12 large	24 small	24 large
Mean number of fish:	16.8	36.4	50.9	76.4	78.4

NS = not significant.

† In multiple comparisons: underlined means are not significantly different ($P > .05$).

sient piscivores: only 1.2 ± 1.3 reef-associated piscivores), and least on a 24-large-hole reef (susceptible to both reef-associated and transient piscivores: 4.7 ± 0.6 reef-associated piscivores). During the time we followed these cohorts, the fish grew to 4 cm TL. Note, however, that all three cohorts disappeared within 6 mo, suggesting that prey refuges in this particular case lowered the mortality rate only on a short-term basis. Complete extirpation of recruit cohorts was unusual for all other species. Moreover, because these observations were unreplicated, no statistical analysis is possible.

Prediction 5: piscivore abundance vs. prey richness

Matching our two alternative analyses of the relationship between predator and prey abundances (predictions 3 and 4 above), we similarly examined the

TABLE 7. Summary of experimental tests of predictions 1 and 2 for each of four categories of fishes (predictions are stated in *Introduction: Hypotheses and predictions*), as detailed in Tables 3–6. "Y" indicates that the given comparison followed the predicted pattern, with asterisks denoting those patterns that were statistically significant. "N" indicates that the given comparison did not follow the predicted pattern; none of these cases were statistically significant. "—" indicates that the given experiment did not provide the given comparison.

Prediction:	1 (small vs. large holes)		2A (holeless vs. holed)			2B (12 vs. 24 holes)	
Experiment:	2	3	1	2	3	1	3
Large reef associates:	Y*	Y*	Y*	Y*	Y*	Y	N
Moray eels:	Y*	Y	—	Y*	Y*	—	Y
Small reef associates:	Y	Y*	—	Y	Y*	—	N
Juvenile grunts:	Y*	N	—	Y*	Y	—	Y

* $P < .05$.

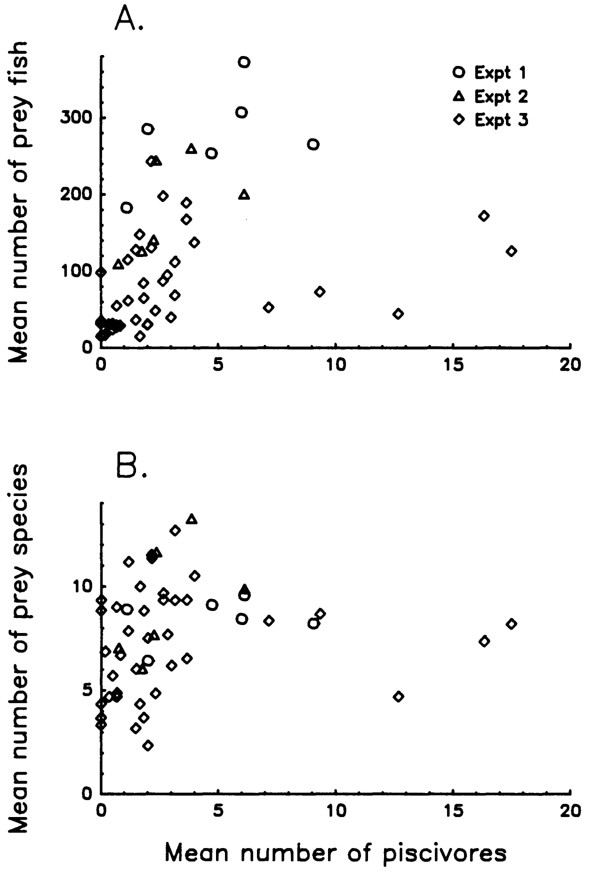

FIG. 7. (A) Average number of potential prey fish as a function of the number of reef-associated piscivorous fish. Each point represents a different reef ($n = 52$) averaged over all analyzed censuses (see Table 1). (B) Average number of prey species corresponding to each point in graph A.

species richness of reef-associated prey fishes as a function of the abundance of reef-associated predators. Just as prediction 3 was falsified, there was no relationship between the mean number of predators and the mean number of prey species per reef averaged over all censuses (Fig. 7B). This was true when all 52 reefs were regressed ($b = 0.11$, $r^2 = 0.03$, $n = 52$, $P = .26$), when the 12 holeless control reefs were excluded from analysis ($b = 0.04$, $r^2 = 0.004$, $n = 40$, $P = .71$), and when each of the five reef treatments was analyzed separately (ranges: $b = 0.12$–1.49, $r^2 = 0.02$–0.42, $n = 8$–12, $P = .08$–$.67$). Moreover, curvilinear regression (second-degree polynomials) did not substantially improve the fit to these data.

We examined the relationship between predator abundance and maximum species richness of prey in two ways, both of which produced the same pattern. First, for each point (reef and census) used in the regression of piscivore abundance vs. the maximum number of prey fish (see Fig. 8A), we substituted the corresponding number of prey species for that reef and census (Fig. 8B). Second, by the same regression procedure used to test prediction 4, we examined the maximum number of prey species ever observed at each predator abundance (Fig. 11A). (Fig. 11B shows the corresponding prey abundances, which form the same pattern as Fig. 8A, albeit nonsignificant [$b = -4.98$, $r^2 = 0.03$, $n = 17$, $P = .50$].) In other words, Fig. 8B examines the number of prey species corresponding to the maximum number of prey individuals ever observed at each predator abundance, whereas Fig. 11A examines the maximum number of prey species ever observed at each predator abundance.

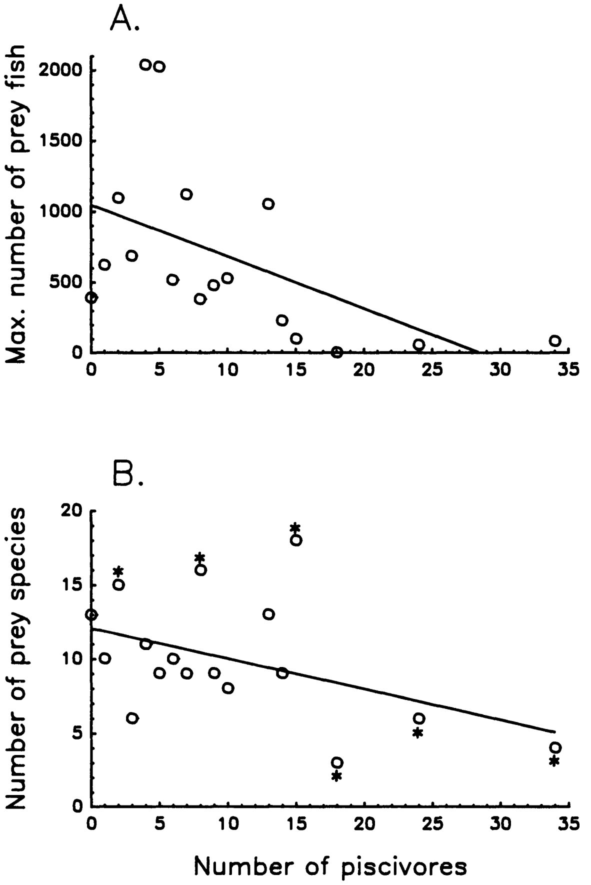

FIG. 8. (A) Maximum number of potential prey fish ever observed at each abundance of reef-associated piscivorous fish. Each point represents a different reef ($n = 17$ observed piscivore abundance levels). (B) Number of prey species corresponding to each point in graph A. The points with asterisks above are the three most speciose reefs (low predator abundance), whereas those with asterisks below are three of the least speciose reefs (high predator abundance); these prey assemblages are examined in Fig. 12A.

In both regression analyses, prey species richness decreased significantly with increasing piscivore abundance (Fig. 8B: $b = -0.20$, $r^2 = 0.31$, $n = 17$, $P = .02$; Fig. 11A: $b = -0.40$, $r^2 = 0.42$, $n = 17$, $P = .005$). The same pattern occurred midway through experiment 1 (Hixon 1991). Identical analyses for transient piscivores revealed no relationship between their abundance and prey richness ($b = 0.03$ and -0.78, $r^2 = 0.001$ and 0.32, $n = 6$, $P = .96$ and $.24$, respectively).

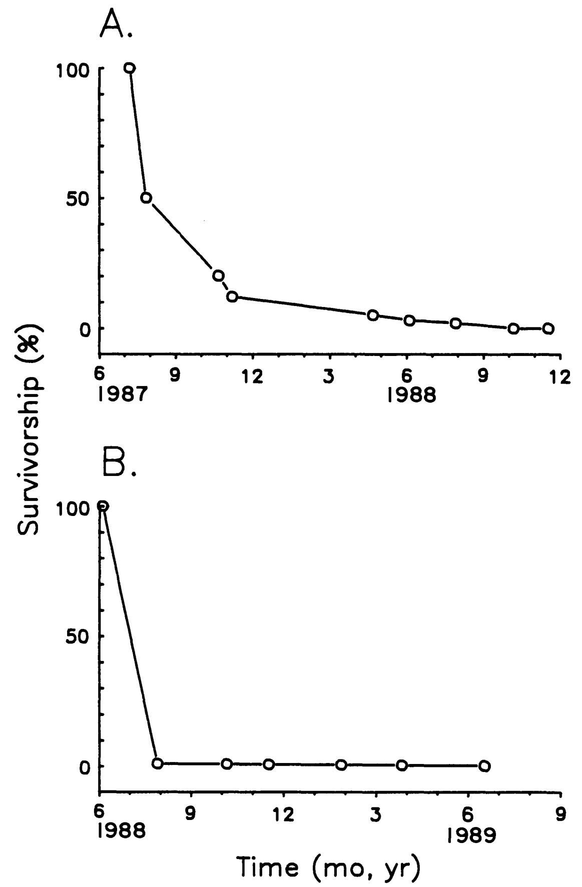

FIG. 9. Survivorship curves for recruit cohorts of (A) *Myripristis jacobus* (blackbar soldierfish; ≈100 individuals), and (B) *Haemulon aurolineatum* (tomtate, a grunt; ≈2000 individuals) on large-hole reefs during experiment 1.

To examine a posteriori the possible mechanisms by which reef-associated piscivores appeared to have limited prey richness, we compared the relative abundance patterns of prey species on the three reefs with the highest maxima of prey richness (and few piscivores) with those on the three reefs with lowest maxima of prey richness (and many piscivores). These reefs are indicated by asterisks on Figs. 8B and 11A.

As illustrated in Fig. 12, reef-associated piscivores appeared to have reduced prey abundances in a fairly generalized, nonselective pattern, decreasing the local population sizes of prey species that were common at low predator abundance as well as those that were rare (Table 8). At least half the prey species potentially present at low predator abundance were absent at high predator abundance.

Only one prey species (*Canthigaster rostrata,* a puffer, species rank 22 in Fig. 12A) was significantly more abundant where predators were more abundant. Although this species followed the same trend in the other analysis (rank 15 in Fig. 12B), the pattern was not significant. Interestingly, members of this genus are among the most highly toxic of reef fishes, which suggests that they actually may not be potential prey for piscivores (Gladstone and Westoby 1988).

In summary, there was no evidence that predation allowed any prey species to increase in abundance or any new prey species to colonize the system. Predation appeared only to limit the number of species that could occur on a reef; the greater the abundance of reef-associated predators, the lower the maximum possible number of co-occurring prey species.

DISCUSSION

Although predation was hypothesized to be an important process structuring communities of coral-reef fishes as early as the 1970s (e.g., Smith 1978, Talbot et al. 1978), research on this topic, relative to studies of competition and recruitment limitation, has been sparse (reviews by Doherty and Williams 1988, Doherty 1991, Ebeling and Hixon 1991, Hixon 1991, Jones 1991, Sale 1991, Williams 1991). Some of the more compelling recent evidence for population-level effects of predation and prey refuges has been provided by Shulman (1984, 1985*a, b,* Shulman and Ogden 1987).

Combined with previous evidence, the data from our study of 52 model reefs, involving naturally recruited assemblages of tens of species and hundreds of individuals, are largely consistent with the hypothesis that predation can affect the structure of reef-fish assemblages. To bolster inferences from our data, we tested and verified two important assumptions concerning our major predictions: first, that reef-associated fish prefer and/or differentially survive on reefs providing holes near their body sizes; and second, that large reef associates, especially the most common piscivores, inhabit and home to specific reefs. Verifying the former assumption bolstered the idea that reef holes function as prey refuges. Verifying the latter assumption was

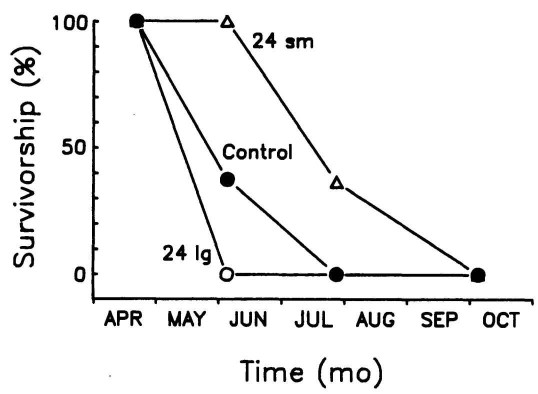

FIG. 10. Survivorship curves for recruit cohorts of *Chromis cyanea* (blue chromis) settling simultaneously on three adjacent reefs during experiment 2 in 1988: 11 fish on a 24-small-hole reef, safest from predation (24 sm); 8 fish on a holeless reef, susceptible to transient piscivores (Control); and 11 fish on a 24-large-hole reef, susceptible to both resident and transient piscivores (24 lg).

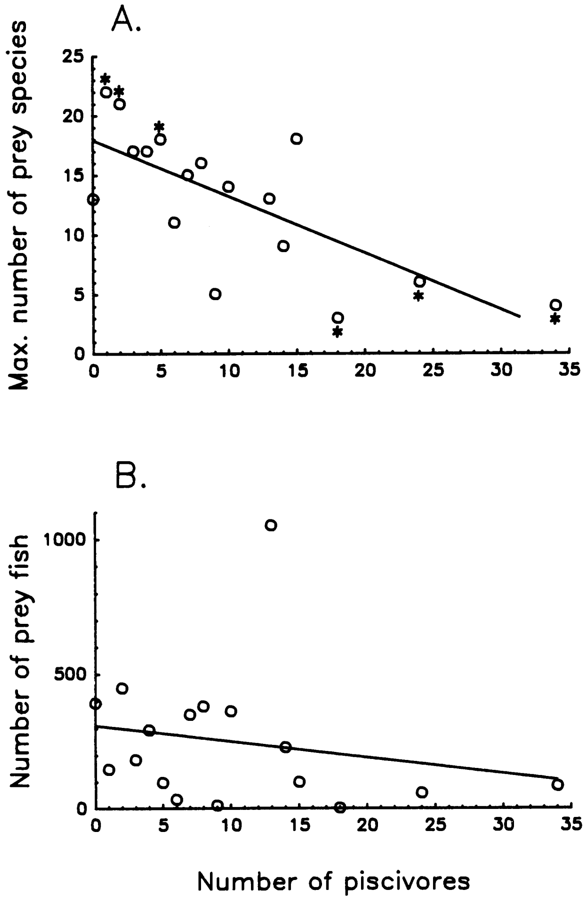

FIG. 11. (A) Maximum number of potential prey fish species ever observed at each abundance of reef-associated piscivorous fish. Each point represents a different reef (n = 17 observed piscivore abundance levels). The points with asterisks above are the three most speciose reefs (low predator abundance), whereas those with asterisks below are three of the least speciose reefs (high predator abundance); these prey assemblages are examined in Fig. 12B. (B) Number of prey individuals corresponding to each point in graph A.

crucial for treating the reefs as independent replicates in our statistical analyses.

Are prey refuges limiting?

Our experiments comparing fish abundances on identically sized reefs with variable hole abundance indicated that structural refuges of the appropriate size limited the abundance of fish on some reefs, but only up to a point. Small and large reef associates, both of which are prey for larger piscivores, were on average always more abundant on reefs with holes than on holeless control reefs, and this pattern was statistically significant in seven of nine comparisons. However, 24-hole reefs never supported significantly more fish than 12-hole reefs.

Two alternative explanations of this pattern seem plausible. First, the risk of predation by resident and/or transient piscivores may necessitate reef fish remaining near refuges, but limited recruitment and colonization and/or some nonpredatory mortality source keeps the overall abundance of fish so low that refuges are never limiting. This possibility seems to be the case for the rarest species in our and other systems. The second alternative is that refuges may normally be limiting, but the 40 reefs of our third experiment temporarily saturated the study area with refuges.

Our data on all fish combined are consistent with the second alternative. In our first and second experiments, which involved only six reefs each, at least a year was required for the reefs to become reasonably saturated with fish (Hixon and Beets 1989). The reefs of our third experiment were in place only about 1 yr when they were destroyed by a hurricane. Before the third experiment started there were more fish on 12-hole reefs than control reefs, and more fish on 24-hole reefs than 12-hole reefs, indicating that refuges at that time were limiting (Hixon and Beets 1989). Additionally, during the last census *before* our third experiment, the 12 reefs of experiments 1 and 2 supported an av-

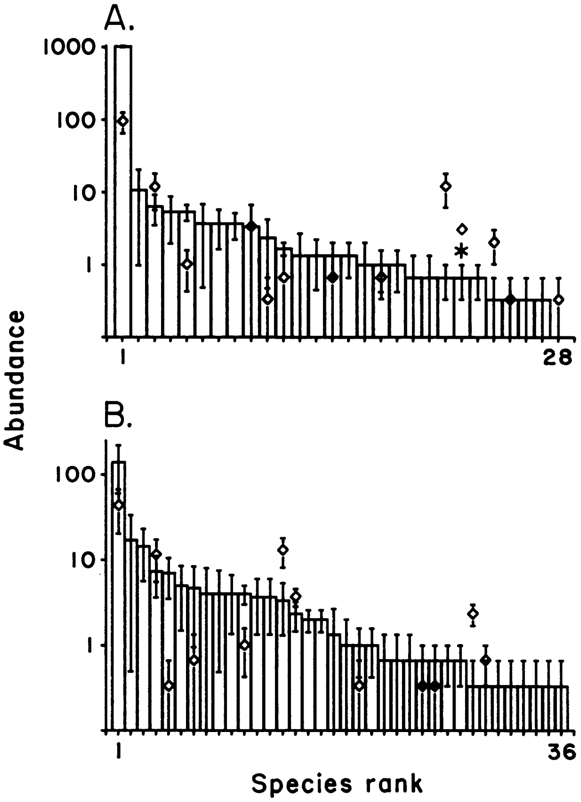

FIG. 12. Relative abundances ($\bar{X}$ ± 1 SE, $n = 3$) of potential prey species occupying the most speciose reefs (low predator abundance), indicated by bars, and least speciose reefs (high predator abundance), indicated by diamonds, as illustrated in (A) Fig. 8B, and (B) Fig. 11A. The asterisk indicates the sole case in which a prey species was significantly more abundant where predators were more abundant (see Table 8). Bars lacking associated diamonds indicate prey species that were absent at high predator abundance.

TABLE 8. Summary of differences in prey species relative abundances between reefs with low predator abundance and reefs with high predator abundance. Abundance differences tested by Mann-Whitney U tests at $\alpha = .07$ (two-tailed, $n = 3$), which claimed significance when all values of one sample were greater than all values of the other.

Prey at low predator abundance	No. prey species at high predator abundance			
	Extirpated	Less abundant	More abundant	No difference
From Fig. 12A:				
14 most abundant species	7	2	0	5
14 least abundant species	8	0	1	5*
From Fig. 12B:				
18 most abundant species	11	2	0	5
18 least abundant species	13	0	0	5

* One species occurred only on reefs with high predator abundance, but the difference was not significantly different from zero.

erage of 668 fish/reef (a total of 8016 fish), whereas during the very last census of the study, the 52 reefs of all three experiments supported a much lower average of only 181 fish/reef (a total of 9412 fish). Moreover, 26 of the 40 reefs comprising experiment 3 supported on average <100 prey fish and <5 predators, clustering near the origin of Fig. 7A.

If experiment 3 did produce refuge saturation, this does not necessarily mean that the system shifted from refuge limitation to recruitment limitation by way of reducing the number of larvae settling on each reef (sensu Doherty 1981). In fact, the number of newly settled recruits per reef did not change detectably as the number of model reefs increased from 6 to 12 to 52 (Fig. 13), and the distributions of new recruits were largely independent of reef treatments and local population sizes (M. A. Hixon and J. P. Beets, *unpublished data*). Therefore, we suspect that had all three experiments continued for at least another year, there would have eventually been significantly more fish on 24-hole reefs than 12-hole reefs. In any case, we can only conclude at present that refuges are necessary for reef fishes, but that refuge abundance is not always limiting.

In previous studies, Fricke (1980) and Shulman (1984, 1985*b*) demonstrated experimentally that shelter availability enhances recruitment and survivorship of reef fishes, and Roberts and Ormond (1987) showed that the abundance of fish on natural reefs is positively correlated with the abundance of natural shelter holes per se (as opposed to habitat complexity in general). However, field experiments by Robertson and Sheldon (1979) and Robertson et al. (1981) detected no population responses to manipulated shelter, demonstrating that shelter is not always limiting.

Do piscivores affect prey abundance?

Our regression analyses indicated that reef-associated piscivores do not always control the number of co-occurring prey fish, but rather set the upper limit to the number of prey fish that can occupy a reef. Examining average abundances through time, prey abundance decreased with increasing predator abundance only on reefs supporting more than about five predators (Fig. 7A). However, examining the maximum number of prey fish ever observed at each predator abundance, there was a clear negative relationship among reefs (Fig. 8A). The rapid mortality of recruit cohorts on reefs with resident piscivores (type III survivorship), combined with occasional direct observations of predation, indicated that these correlations were causal.

These patterns indicate that predation was the predominant process limiting fish abundance on some reefs at some times, but certainly not on all reefs at all times. As discussed above, many of the 40 reefs from our last

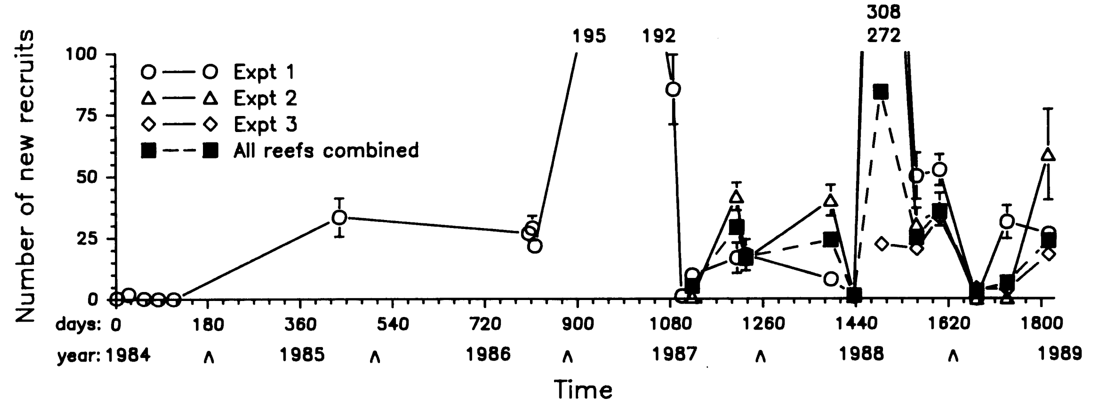

FIG. 13. Number per reef ($\bar{X} \pm 1$ SE) of newly settled recruits (≈1 cm total length) of all species during each experiment (experiment 1, $n = 6$ reefs censused on each date; experiment 2, $n = 6$; experiment 3, $n = 40$). Arrows along the abscissa indicate 1 January of each year.

experiment were incompletely colonized during their yearlong existence. In such cases, predation was clearly not a major regulatory process.

Predator–prey dynamics in open assemblages with refuges: a model

The above conclusions suggest a simple conceptual model of predator–prey abundances that may be relevant to any assemblage of open populations. The basic assumptions are threefold. First, typical of open populations (but not always of reef fishes, see Shulman et al. 1983, Sweatman 1985, Jones 1987, Booth 1992), the recruitment/colonization rates of both the predator and prey assemblages can be independent of local population sizes. Second, both the prey and the predators occupying a patch of habitat can make use of spatial refuges from predation. The resident predators require large refuges from still larger transient predators (barracuda and sharks in our system), and the resident prey require smaller refuges from both resident and transient predators. Third, the refuges are not absolute, in that some predators can enter all refuges (moray eels in our system) and/or individuals must spend time outside refuges (in reef-fish systems, individuals cannot spend their entire lives in holes).

As illustrated in Fig. 14A, a negatively sloped curve P_f, which need not be linear, represents the maximum number of prey that can occupy the patch as a function of the number of resident predators. Empirically, curve P_f is somewhat analogous to the regression illustrated in Fig. 8A. The left-hand endpoint of curve P_f occurs at the maximum possible abundance of resident prey set by competition for food or other nonrefuge resources (*F* along ordinate). This limit is reached when, (1), the prey are not limited by recruitment, colonization, or refuges, and, (2), resident predators are absent—presumably rare conditions in reef fishes.

The right-hand endpoint of curve P_f occurs at the maximum possible abundance of resident predators set by competition for food (i.e., prey) or other nonrefuge resources (*F* along abscissa). Of course, resident predators cannot persist when prey are altogether absent, so this endpoint necessarily lies above the abscissa. Essentially, this point comprises the lowest possible standing stock of prey that represents sufficient turnover in prey (high recruitment/colonization balanced by high predation) to support the highest possible standing stock of resident predators. This limit is reached only when, (1), the resident predators are not limited by recruitment, colonization, or refuges, and, (2), the combined consumption rate of the predators balances the recruitment/colonization rates of the prey.

With this foundation, consider systems in which the prey either are or are not limited by recruitment/colonization. First, when prey are not limited by these inputs and predators are present, prey abundance will be limited either directly by predation per se or indirectly by limited refuges. If prey refuges are not limiting, the local assemblage will lie somewhere along curve P_f, whereas if prey refuges are limiting, the assemblage will lie along curve P_r, somewhere below P_f. The precise location of the assemblage along these curves depends upon what limits the abundance of resident predators. The more that predators are limited by either recruitment/colonization or refuge availability, the closer the assemblage will be confined to the left end of the relevant *P* curve. In the case of refuges for the predators being more limiting than food or other nonrefuge resources, the predator assemblage will be bounded below some limit by competition for refuges

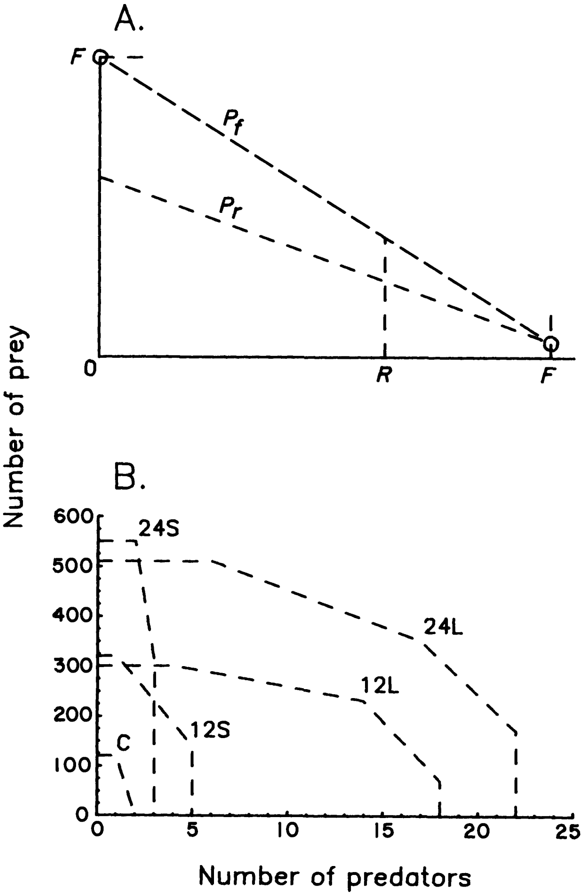

FIG. 14. (A) A model of predator–prey dynamics in an assemblage of open populations occupying a habitat patch with spatial refuges. Curves P_f and P_r give the maximum possible prey abundances set by predation when prey are initially food and refuge limited, respectively. When resident predators are limited by refuges from transient predators, their abundance will also be bounded by some upper limit (*R*). When recruitment limitation occurs, the assemblage can lie anywhere below the bound set by P_f or P_r and the bound set by *R*, and will approach the origin when both predators and prey are strongly limited. (B) Minimum convex polygons enclosing all censuses of each reef type from experiment 3: C = holeless control; 12S = 12 small holes; 24S = 24 small holes; 12L = 12 large holes; 24L = 24 large holes. Each polygon encloses 46 censuses, representing 95% of all 48 censuses of each reef type (8 reefs × 6 censuses, see Table 1).

(for example, point R along abscissa). Obviously, when refuges for both predators and prey are extremely limiting, the system will be bounded near the origin despite high recruitment or colonization.

Second, when prey are limited by recruitment or colonization, the predator–prey assemblage can lie anywhere *below* the relevant P curve within the bound set by the availability of refuges for predators (R). Thus, the assemblage will lie near the origin when either recruitment/colonization or refuge availability strongly limits both predator and prey populations.

If the model illustrated in Fig. 14A is accurate, then one can expect assemblages occupying a particular kind of habitat under specified conditions to range within a certain region of the predator–prey phase space. For reef fishes, if predation is important, both predator and prey refuges are ultimately limiting, and recruitment/colonization varies widely, these expectations are: (1) holeless reefs should remain near the origin; (2) small-hole reefs should range near the ordinate, since such reefs should always support few resident predators; (3) reefs with more small holes should range higher along the ordinate (higher prey abundances); and (4) reefs with more large holes should range further along the abscissa (higher predator abundances).

Examining the data from the 40 reefs of our third experiment, these expectations are realized. Plotted in Fig. 14B are minimum convex polygons that enclose 95% of all censuses of all reefs of a particular type. The 95% limitation excludes outlying points, so that each polygon encloses 46 of the total 48 censuses of each reef type (8 reefs × 6 censuses, see Table 1). Illustrating each of the above expectations, the resulting patterns are: (1) holeless control reefs did cluster near the origin; (2) small-hole reefs rarely supported more than five predators (mostly moray eels); (3) reefs with 24 small holes ranged to higher prey abundances than those with 12 small holes; and (4) reefs with 24 large holes ranged to higher predator abundances than those with 12 large holes. Combined, these patterns suggest that both predators and prey on these reefs were, (1), at times recruitment/colonization limited, and, (2), at times refuge limited.

Overall, we see the local abundances of predators and prey determined mostly by the relative magnitudes of recruitment by larvae, colonization by juveniles and adults, predation, and competition for refuges. Competition for food and other nonrefuge resources may occasionally be important, although the evidence in reef fishes is sparse and indicates that competition for food affects individual growth rates and distributions more than it does local population sizes (reviews by Doherty and Williams 1988, Jones 1991). Such pluralistic views of reef-fish community regulation, where various processes are important in some circumstances and not in others, are relatively recent (Warner and Hughes 1988, Hixon 1991, Jones 1991, Sale 1991, but see Smith 1978, Talbot et al. 1978). To test such models adequately, multifactorial field experiments will be essential.

Do piscivores affect local prey diversity?

Our study revealed a significant negative relationship between the abundance of reef-associated piscivores and the maximum number of co-occurring prey species. The as-yet-untested implication is that maximum local reef-fish species richness decreased monotonically with increasing predation intensity. There was no evidence that piscivores enhanced local prey diversity, either by increasing prey evenness or by allowing new prey species to enter the system.

By what mechanism can local prey diversity only decrease as predation intensity increases from zero? Two general models have been proposed (review by Hixon 1986). First, predators may nonselectively reduce all prey populations in proportion to their initial relative abundances (Van Valen 1974). Second, if a competitive hierarchy exists among the prey species, then predators may disproportionally reduce the abundance of subordinate prey (Lubchenco 1978). In either case, rare or otherwise predation-susceptible species are eventually extirpated and prey species richness declines monotonically.

We hypothesize that the first model is more applicable to coral-reef fishes. The reef-associated piscivores in our system are known to be generalized carnivores (Randall 1967) and appeared to either reduce the abundance of or entirely extirpate both common and rare prey species. Because most of the prey species were rare, predators may have been forced to satisfy their requirements by consuming a wide diversity of prey, thus setting the stage for Van Valen's (1974) model through the mechanism of "diffuse predation" (sensu Hixon 1991). Terborgh (1988) has hypothesized the same effect for large felids on their small mammal prey in Amazonia. Of course, beyond the question of whether prey rarity drives the pattern of predation or is caused by predation, or both, it remains to be seen through experimental manipulations whether the negative correlation between predator abundance and local prey richness is a case of cause and effect.

Conclusions

To the extent that predators cause mortality of larvae, juveniles, and adults, predation is a process that contributes to structuring any community. Regardless of whether populations undergo recruitment limitation, predation can, (1), potentially force prey to compete for refuge space, and, (2), potentially affect local prey diversity by altering distributions and abundances (reviews by Jeffries and Lawton 1984, Hixon 1986, 1991, Holt 1987, Hixon and Menge 1991). It seems obvious that future studies of reef-fish assemblages should employ more pluralistic hypotheses and tests commensurate with the complexity of these systems, and that such hypotheses should explicitly include predation as a process that contributes substantially to community regulation.

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In Memoriam

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APPENDIX

Mean number of fish by species per reef per census during experiments 1-3. * in abundance columns denotes transient piscivores observed in the study area, but not censused at our reefs. Note that new recruits of grunts and parrotfishes could not be identified to species until they exceeded ≈2 cm in total length. Dietary data are from Randall (1967), Clavijo et al. (1980), and M. A. Hixon and J. B. Beets, *personal observation.*

		Mean no. fish per reef per census		
Family: Species	Guild†	Expt. 1	Expt. 2	Expt. 3
Muraenidae:				
Gymnothorax moringa (spotted moray eel)	F, L	···	···	0.01
Gymnothorax vicinus (purplemouth moray eel)	F, L	0.66	0.64	0.51
Clupeidae:				
Jenkinsia sp. (herring)	P, T	0.36	0.03	···
Synodontidae:				
Synodus sp. (lizardfish)	F, L, T	0.18	0.14	···
Holocentridae:				
Holocentrus ascensionis (longjaw squirrelfish)	F, L	1.49	0.52	0.71
Holocentrus coruscus (reef squirrelfish)	M	2.40	0.74	1.00
Holocentrus rufus (squirrelfish)	M	···	···	0.01
Myripristis jacobus (blackbar soldierfish)	M, L	6.91	1.09	1.79
Aulostomidae:				
Aulostomus maculatus (trumpetfish)	F, L, T	0.01	0.02	···
Serranidae:				
Epinephelus afer (mutton hamlet)	F, L	0.19	0.09	1.95
Epinephelus cruentatus (graysby)	F, L	0.10	0.17	0.04
Epinephelus fulvus (coney)	F, L	0.04	0.09	0.03
Epinephelus guttatus (red hind)	F, L	0.08	0.06	0.07
Epinephelus morio (red grouper)	F, L	···	···	0.01
Epinephelus striatus (Nassau grouper)	F, L	2.53	2.77	1.86
Hypoplectrus unicolor (hamlet)	M	0.36	0.79	0.47
Serranus tabacarius (tobaccofish)	M	0.02	0.02	0.06
Serranus tigrinus (harlequin bass)	M	0.44	0.53	0.81
Grammistidae:				
Rypticus saponaceus (greater soapfish)	F, L	0.10	0.09	0.13
Priacanthidae:				
Priacanthus cruentatus (glasseye snapper)	P	···	···	0.01
Apogonidae:				
Apogon aurolineatus (bridle cardinalfish)	P	0.19	0.09	0.20
Apogon binotatus (barred cardinalfish)	P	0.42	0.14	0.05
Apogon maculatus (flamefish)	P	0.99	0.29	0.20
Apogon quadrisquamatus (sawcheek cardinalfish)	P	0.15	···	···
Apogon sp. (cardinalfish)	P	···	0.21	0.24
Carangidae:				
Caranx bartholomaei (yellow jack)	F, L, T	0.03	···	···
Caranx latus (horse-eye jack)	F, L, T	*	*	*
Caranx ruber (bar jack)	F, L, T	1.29	0.86	···
Selar crumenophthalmus (bigeye scad)	M, L, T	0.90	···	···
Lutjanidae:				
Lutjanus buccanella (blackfin snapper)	F	0.02	···	0.01
Lutjanus griseus (gray snapper)	F, L	···	···	0.01
Lutjanus synagris (lane snapper)	F, L	0.47	0.23	1.92
Ocyurus chrysurus (yellowtail snapper)	P, L	1.66	1.45	2.24

APPENDIX Continued.

Family: Species	Guild†	Mean no. fish per reef per census		
		Expt. 1	Expt. 2	Expt. 3
Haemulidae (Pomadasyidae):				
Anisotremus virginicus (porkfish)	M	...	0.02	0.01
Haemulon aurolineatum (tomtate)	M, L	68.98	39.68	1.72
Haemulon flavolineatum (French grunt)	M	0.04	...	...
Haemulon macrostomum (Spanish grunt)	M	1.50	0.83	0.22
Haemulon melanurum (cottonwick)	M, L	0.78	0.77	0.44
Haemulon plumieri (white grunt)	M, L	1.28	5.56	3.69
Haemulon steindachneri (Latin grunt)	M	0.01	...	...
Haemulon spp. recruits	M	119.65	79.55	46.15
Sciaenidae:				
Equetus acuminatus (highhat)	M	0.10	0.24	0.55
Equetus lanceolatus (jackknife fish)	M, L	0.01	0.03	0.07
Equetus punctatus (spotted drum)	M	0.06	0.08	0.01
Mullidae:				
Mulloidichthys martinicus (yellow goatfish)	M, L, T	0.01	...	...
Pseudopeneus maculatus (spotted goatfish)	M, L, T	0.23	...	...
Chaetodontidae:				
Chaetodon capistratus (foureye butterflyfish)	M	0.30	0.53	0.35
Chaetodon oscellatus (spotfin butterflyfish)	M	0.01	...	...
Chaetodon sedentarius (reef butterflyfish)	M	...	0.03	0.01
Chaetodon striatus (banded butterflyfish)	M	...	...	0.01
Pomacanthidae:				
Holocanthus ciliaris (queen angelfish)	M	0.47	0.36	0.34
Holacanthus tricolor (rock beauty)	M	0.16	0.20	0.13
Pomacanthus paru (French angelfish)	M, L	0.05	0.06	0.08
Pomacentridae:				
Chromis cyanea (blue chromis)	P	0.31	0.85	0.16
Chromis multilineatus (brown chromis)	P	0.22	0.03	0.12
Stegastes leucostictus (beaugregory)	H	0.52	0.62	0.20
Stegastes mellis (honey damselfish)	H	...	...	0.01
Stegastes partitus (bicolor damselfish)	H	0.01	0.02	0.05
Stegastes planifrons (threespot damselfish)	H	...	...	0.01
Stegastes variabilis (cocoa damselfish)	H	0.15	0.02	0.36
Labridae:				
Bodianus rufus (Spanish hogfish)	M	0.01	...	0.01
Halichoeres bivittatus (slippery dick)	M	2.04	0.98	1.89
Halichoeres garnoti (yellowhead wrasse)	M	0.08	0.08	0.02
Halichoeres maculipinna (clown wrasse)	M	...	...	0.01
Halichoeres pictus (rainbow wrasse)	M	...	...	0.01
Halichoeres poeyi (blackear wrasse)	M	...	0.12	0.11
Halichoeres radiatus (puddingwife)	M	...	0.05	0.03
Thalassoma bifasciatum (bluehead wrasse)	M	1.67	1.05	2.45
Scaridae:				
Cryptotomus roseus (slender parrotfish)	H	...	...	0.01
Sparisoma aurofrenatum (redband parrotfish)	H, L	...	0.02	0.01
Sparisoma chrysopterum (redtail parrotfish)	H, L	0.01	0.02	0.01
Sparisoma radians (bucktooth parrotfish)	H	0.13	0.05	...
Sparisoma viride (stoplight parrotfish)	H	0.03	...	0.05
Sparisoma spp./*Scarus* spp. recruits	H	2.75	2.14	2.61
Sphyraenidae:				
Sphyraena barracuda (great barracuda)	F, L, T	*	*	*
Clinidae:				
Acanthemblemaria sp. (spinyhead blenny)	M?	0.02	0.03	0.01
Labrisomus nuchipinnis (hairy blenny)	M	0.03	...	0.02
Malacoctenus gilli (dusky blenny)	M?	...	0.03	0.01
Malacoctenus macropus (rosy blenny)	M?	0.01	0.02	0.14
Malacoctenus triangulatus (saddled blenny)	M?	0.10	0.08	0.18
Paraclinus cingulatus (coral blenny)	M?	0.02	...	0.02

APPENDIX Continued.

Family: Species	Guild†	Mean no. fish per reef per census		
		Expt. 1	Expt. 2	Expt. 3
Blenniidae:				
Entomacrodus nigricans (pearl blenny)	H	1.43	2.41	1.48
Ophioblennius atlanticus (redlip blenny)	H	···	0.02	0.01
Gobiidae:				
Coryphopterus glaucofraenum (bridled goby)	M	5.83	3.88	2.76
Coryphopterus personatus (masked goby)	M?	2.45	0.17	0.12
Gnatholepis thompsoni (goldspot goby)	M?	0.08	0.06	0.16
Gobiosoma evelynae (sharknose goby)	M	0.30	0.14	0.05
Acanthuridae:				
Acanthurus bahianus (ocean surgeonfish)	H, L	0.22	0.70	0.62
Acanthurus chirurgus (doctorfish)	H, L	0.88	0.97	0.78
Acanthurus coeruleus (blue tang)	H, L	1.38	0.85	0.76
Scombridae:				
Scomberomorus regalis (cero)	F, T	*	*	*
Balistidae:				
Balistes vetula (queen triggerfish)	M, L	0.03	0.03	0.02
Cantherhinus pullus (orangespotted filefish)	M	0.06	···	0.06
Monacanthus ciliatus (fringed filefish)	M	0.01	···	···
Monacanthus tuckeri (slender filefish)	M	0.01	0.02	0.02
Ostraciidae:				
Lactophrys bicaudalis (spotted trunkfish)	M, L	···	0.02	0.01
Lactophrys triqueter (smooth trunkfish)	M, L	0.05	···	···
Tetraodontidae:				
Canthigaster rostrata (sharpnose puffer)	M	1.31	1.65	2.09
Sphoeroides spengleri (bandtail puffer)	M	0.01	···	···
Mean total number of fish		237.79	156.13	85.56
Mean total number of species		74	66	78

† Guild codes: F = piscivore (i.e., large individuals had fish included in diet); H = herbivore; M = microcarnivore (i.e., small-invertebrate eater) for size classes occurring on our reefs; P = planktivore for size classes occurring on our reefs; L = large (i.e., individuals occurred on our reefs at total lengths >15 cm); T = transient (i.e., nonresident).