RELATIONSHIPS BETWEEN FISHES AND MOBILE BENTHIC INVERTEBRATES ON CORAL REEFS

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ABSTRACT

Observations of 3 types of artificial reefs at 20 m depths show that fish predation alters the pattern of colonization of stomatopods, the largest and most mobile members of the cryptic reef fauna. Recruitment by polychaetes probably is adversely affected by the presence of fish predation also. Possibly because of their secretive habits, the densities of the remaining taxa of cryptic invertebrates were unaffected by fish predators. The data also suggest that the presence of an invertebrate biota influences the colonization and abundance of invertebrate-eating fishes.

INTRODUCTION

The importance of predator-prey interactions in governing community structure has been demonstrated for some marine systems (e.g., Paine, 1966; Dayton, 1975; Menge and Sutherland, 1976; and many others), but their role in coral reef communities remains poorly understood. Coral-eating fishes can influence the structure of coral reefs (Kaufman, 1977; Neudecker, 1979; Wellington, 1982), and herbivores exert both direct and indirect effects upon coral reef communities (Ogden and Lobel, 1978; Hay, 1981; Hixon and Brostoff, 1983). In laboratory microcosm experiments, Brock (1979) showed that parrotfish grazers influence the abundance and diversity of the benthic flora and fauna, and that the presence of refuges (3-dimensional surfaces) is an even more important determinant of benthic community structure than the densities of consumers. Additionally, it has been suggested that a variety of structural, behavioral, and chemical defense mechanisms found in benthic reef organisms represent adaptations to strong predation pressures in reef environments (e.g., Bakus, 1966, 1981; Vermeij, 1978; Reaka, 1980a, 1980b; Reaka and Manning, 1981). However, astonishingly little experimental and quantitative information is available regarding the relationships between fish predators and the abundant invertebrate fauna that inhabits the reef substrate in the field. Most of this benthic biota lives in cryptic refuges under and within the coral substrate. Jackson and Buss (1975) have suggested that the cryptic sessile fauna currently does not experience strong predation. Many of these encrusting organisms grow in inaccessible sites, and particularly the colonial organisms exhibit chemical defenses that are used in competitive interactions (see also Buss and Jackson,

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1979). However, virtually no field studies have quantatively investigated the effects of fish predators upon the teeming mobile cryptic fauna that inhabits this environment. Also, while these invertebrates are the primary food source for many reef fishes (Randall, 1967), no studies have experimentally examined the importance of this mobile invertebrate fauna for the colonization and maintenance of populations of reef fishes. In July 1980 we initiated a 2½ year of study that experimentally investigated reciprocal interactions between fishes and the mobile cryptic invertebrate fauna in Salt Canyon, St. Croix. A preliminary analysis of the first 6 months of the data is presented here. A more thorough analysis of data from the entire 2½ year period is in progress.

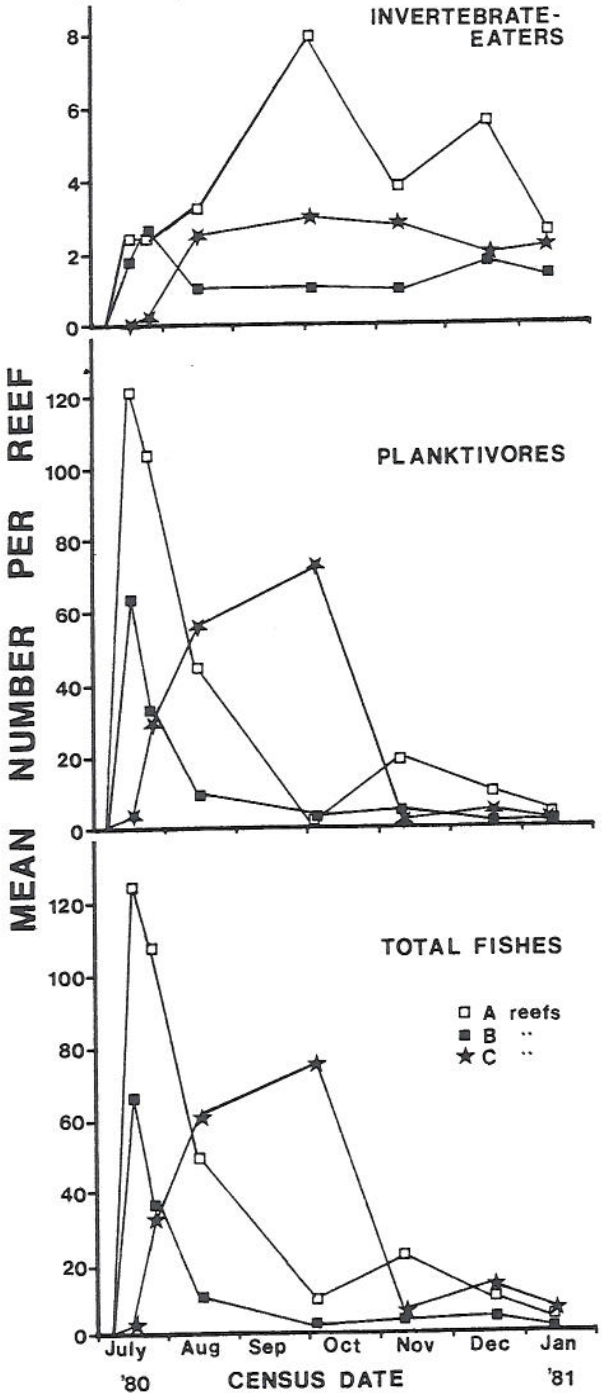
MATERIAL AND METHODS

Using the Hydrolab, an underwater habitat operated by NOAA on St. Croix, U.S. Virgin Islands, 15 artificial reefs were established at a depth of 20 m in Salt River Canyon in July 1980. Salt River Canyon is a submarine canyon 70-100 m wide with a sand floor flanked by a vertical and a sloping coral reef wall. Five reefs provided habitat for fishes and invertebrates (A reefs); each consisted of 11 cinderblocks arranged in a pyramid 2 blocks wide and 3 blocks high, with 6 pieces of sun-dried dead coral rubble placed around the pyramid base. The components were tied together with nylon rope and anchored in place with iron reinforcement bars. Five reefs consisted of a cinderblock pyramid without rubble, providing habitat for fishes but little shelter for invertebrates (B reefs). Five reefs, each composed of rubble arranged in the same pattern as in the A reefs but lacking a cinderblock pyramid, provided habitat more suitable for cryptic invertebrates (C reefs). The 15 reefs were arranged serially (ABCABC...) 10 m apart and 10 m out from the sloping east wall of the canyon. Fishes on the reefs were censused visually one week after establishment, and at approximately 30-day intervals thereafter. Using information from the literature (Randall, 1967; Clavijo, et al., 1980) and personal observations, we assigned each individual to a feeding guild (planktivore, herbivore, piscivore, piscivore-invertivore, invertivore) based on its size class (post-larval, juvenile, adult) and species (Appendix Table 1). We have included fishes that eat only invertebrates and those that eat both invertebrates and smaller fishes here as "invertebrate-eaters", since both prey on invertebrates. The invertebrate-eaters and planktivores (which prey upon invertebrate larvae as well as holoplankton) are the fishes most likely to influence benthic prey populations; hence, these taxa are emphasized in this report. After 6 months, cryptic invertebrates in half of the rubble from each of the A and C reefs were sampled quantitatively by sealing the rubble in plastic bags in situ. On shore, the rubble was chiselled into small pieces and sieved (0.7 mm mesh), retaining all of the resident cryptic biota. These samples were preserved in formalin and sorted, counted, and measured microscopically (see Reaka, 1981, 1983, for more details).

RESULTS

All fishes colonized both types of cinderblock reefs (A,B) quickly, while >2 months passed before fishes on the rubble reefs (C) reached peak abundances (lower graph, Fig. 1). On all 3 types of reefs, total numbers of individuals subsequently declined (and remained low throughout the winter; numbers increased again following spring recruitment; Reaka, 1981, 1983). Planktivores (mostly juvenile grunts, Haemulidae) were by far the most abundant guild, so their pattern of colonization followed that described above for total numbers of fishes (Fig. 1). Invertebrate-eating fishes were less abundant than planktivores. The number of invertebrate-eating fishes on reefs with rubble-dwelling invertebrates (A, C) did not peak until 2-5 months after establishment of the reefs. This period coincided with the time

FIGURE 1. Mean numbers of fishes observed on different types of reefs. All 5 guilds are included in total fishes. Species included in these guilds are listed in Appendix Table 1. The A reefs (open squares) are comprised of cinderblocks and rubble, the B reefs (closed squares) are built of cinderblocks only, and the C reefs (stars) are made of rubble only. For purposes of illustration, error bars are omitted here, but they are included in Reaka, 1981, 1983.



required for full colonization of the new rubble habitat by invertebrates (Reaka, 1981, 1983). In all guilds, fishes on the C reefs generally were smaller than those on the cinderblock reefs (Wolf, Bermingham, et al., unpub. data).

The data in Figure 1 suggest that reefs with habitat for invertebrates (A) generally were characterized by higher numbers of fishes than reefs without habitat for invertebrates (B). Specifically, the number of invertebrate-eaters per reef was significantly higher on A reefs than on B reefs in August and October, and the data showed a strong tendency in that direction in November (Mann Whitney U tests; $p < 0.02$, $p<0.01$, and $p<0.058$, respectively). In addition, the total numbers of invertebrate-eaters per census on the 5 type A reefs were consistently higher than those recorded on the 5 type B reefs for the 6 month interval (Wilcoxon matched-pairs signed-ranks test, $p < 0.01$).

Population levels of invertebrates may be affected by invertebrate-eaters that prey upon reef residents, and by planktivorous fishes that eat invertebrate larvae swimming near or settling on the reef. The total numbers of invertebrate-eating fishes per census on the 5 type A reefs were consistently higher than those on the 5 type C reefs throughout the study period (Wilcoxon matched-pairs signed-ranks test, $p < 0.01$). However, there was no significant difference in the numbers of planktivorous fishes per census on A vs. C reefs over the 6 month interval (Wilcoxon matched-pairs signed-ranks test, n.s.). The number of

invertebrate-eaters per reef was lower on the C than on the A reefs in the first two censuses (July 1980) (Mann Whitney U tests; $p < 0.02$, $p < 0.058$, respectively). Although fewer planktivores were recorded on A than on C reefs in July and November, individual C reefs were populated by more small planktivores than were the A reefs in October 1980 (Mann Whitney U tests; $p < 0.0001$, $p < 0.03$, $p < 0.05$, respectively).

TABLE 1. Numbers of individuals of major invertebrate taxa collected per piece of rubble in control (natural reef) and experimental reefs (A and C reefs) in January 1981 (6 months after establishment of the experimental reefs). Results of a one-way classification analysis of variance (df = 2,37) are given under F value. Means and standard errors (in parentheses) are based on raw data. All data were tested for homogeneity of variance (Bartlett's test), and, if necessary, transformed by ln (x+1). A superscript t indicates that test results are based on transformed data. Superscripts a and b indicate means that are significantly different by a Student Neuman Keuls test; means with the same subscript are not significantly different.

Taxon	Control Reef Wall	A Reefs (cinderblock + rubble)	C Reefs (rubble only)	F value (df=2,37)		Bartlett's Test Value
Stomatopods	0.5(±.2)^{b}	1.0(±.2)^{b}	1.8(±.3)^{a}	3.31	p<0.05	4.29 N.S.
Snapping shrimps	7.1(±1.3)	6.3(±1.1)	8.3(±.9)	0.90	N.S.	1.26 N.S.
Other shrimps (non-alpheids)	10.3(±1.5)	10.7(±2.0)	10.3(±1.6)	0.02	N.S.	2.30 N.S.
Crabs	17.9(±2.0)	12.5(±2.4)	13.7(±2.0)	1.90	N.S.	0.69 N.S.
Peracarids	73.3(±17.5)	62.7(±13.6)	87.3(±15.2)	0.74	N.S.	0.16 N.S.
Sipunculans	18.5(±5.8)	17.8(±4.6)	11.7(±2.5)	0.80	N.S.	5.47 N.S.
Polychaetes	180.0(±60.7)^{a}	55.6(±12.2)^{b}	76.9(+16.8)^{ab}	4.54^{t}	p<0.05	6.32^{t}N.S.
Ophiuroids	4.9(±0.7)^{a}	2.3(±0.6)^{b}	2.1(±0.4)^{b}	9.53	p<0.05	2.89 N.S.
Gastropods	6.2(±0.5)	6.5(±0.9)	6.5(±0.8)	1.28	N.S.	4.87 N.S.
Bivalves	10.5(±2.1)	9.4(±1.9)	6.8(±0.9)	0.84^{t}	N.S.	1.30^{t}N.S.
Chitons	0.2(±0.1)	0.1(±0.1)	0.1(±0.1)	0.10	N.S.	1.02 N.S.

Examination of the invertebrate fauna in the rubble from A reefs (with fish predators) and C reefs (with fewer fish predators), and in naturally occurring rubble from the east canyon wall adjacent to the experimental reefs (with fish predators) revealed several patterns. Although the abundances of 8 of the 11 major revealed taxa did not differ in the 3 sets of rubble, stomatopods showed a significant increase in numbers on C reefs compared to either A reefs or rubble from the canyon wall (Table 1). The naturally occurring rubble from the wall contained species of stomatopods characteristic of shallow to moderate reef habitats (*Gonodactylus oerstedii*, *G. spinulosus*, *Meiosquilla schmitti*), while the experimental rubble (A and C reefs) was inhabited by different species (*Gonodactylus* sp. nov., *Meiosquilla* sp. nov., *M. tricarinata*, *Pseudosquilla ciliata*). Several of the latter species are generalists, occurring in grassbeds as well as rubble

(M. tricarinata, P. ciliata), and others (particularly Gonodactylus sp. nov.) are characteristic inhabitants of our deeper (35-50 m) control and experimental reef sites. These opportunists reached higher densities in the new rubble habitat (particularly in the absence of predation) than the populations that normally inhabit rubble on the reef slope at this depth. There were no differences in the species of stomatopods found in the A vs. C experimental reefs. Numbers of polychaetes were significantly lower on the experimental reefs exposed to predation (A) than in the control rubble from the reef wall, and intermediate numbers of polychaetes were found in rubble from the C reefs. Ophiuroids also showed relatively low recruitment to the new habitat on the experimental reefs, but were equally abundant on A and C reefs (Table 1).

DISCUSSION

Does the presence of cryptic invertebrates in rubble influence colonization by fishes?

Coral rubble harbors hundreds of invertebrates (Table 1), providing an abundant food source for some fishes. Many authors have argued that living space is more important than food in limiting (or structuring) populations of reef fishes (e.g., Sale, 1978; Smith, 1978). Although evidence of the importance of space comes from several sources (discussed in Sale, 1980), other studies show that space is not always limiting (e.g., Talbot, et al., 1978; Robertson, et al., 1981). Evidence that food directly influences numbers of fishes is limited (Tsuda and Bryan, 1973). In the present study, however, the timing of colonization suggests that fish recruitment to reefs is related to the availability of benthic food. On those reefs with rubble-dwelling invertebrate fauna (A, C), the number of invertebrate-eaters peaked after 2-5 months, which coincides with the colonization rate of invertebrates in coral rubble at this depth (Reaka, 1981, 1983, and Reaka, et al., in prep.). In addition, cinderblock reefs with rubble had more invertebrate-eating fishes than cinderblock reefs without rubble. Rubble around the base of the A reefs gave the latter a slightly more complex structure than the B reefs, but whether or not this contributed to the observed differences in fish populations is unclear. Other variations in the structure of small artificial reefs (differences in the sizes of available holes) have not been related to number of fishes present or species composition (Molles, 1978; Talbot, et al., 1978). Separation of the effects of food vs. habitat complexity in the present study would require an experiment comparing colonization of reefs with rubble initially containing a natural complement of invertebrates to that of reefs with sun-dried (defaunated) rubble.

Does the presence of fish predators influence invertebrate colonization?

Stomatopods appear to be strongly influenced by the presence of fish predators in this habitat (Table 1). After 6 months, these mantis shrimps were more abundant on the experimental reefs with fewer invertebrate-eaters (C) than on those with more and larger fish predators (A). This could not have been due to differences in location or habitat, since the positions of A and C reefs were alternated regularly down the canyon at equal distances from the reef wall. Except for octopuses (which in this habitat are very rare compared to the rubble fauna reported here), stomatopods are the largest and most active of the mobile cryptic fauna. Due to periodic movements on the surface of their rubble (Reaka, 1980b; Dominguez and Reaka, in review), stomatopods may be more exposed to predators than are many of the smaller, more secretive taxa. Ophiuroids had slow rates of colonization, but appeared unaffected by the fishes. Although recruitment of polychaetes to the new rubble also was slow, the effects of fish predators upon polychaete population levels are enigmatic. Invertivorous and planktivorous fishes possibly are responsible for decreased survivorship of settling polychaete larvae.

Cage experiments in shallow water (3 m) confirm that polychaete recruitment occurs slowly (probably via larval settlement), and that numbers of recruits are strongly decreased by exposure to fish predation compared to controls (Reaka, unpub. data). The remaining groups of major invertebrate taxa appear to be unaffected by fish predators. Finer taxonomic resolution of these taxa (in progress) may yield additional effects. It is also possible that a greater difference in predation pressures between the A and C reefs would have shown a more pronounced effect. At the moment, however, we conclude that the secretive habits of many of these cryptic invertebrates protects them from pronounced effects of predators upon their populations at this study site.

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