EFFECTS OF REEF SIZE ON COLONIZATION AND ASSEMBLAGE STRUCTURE OF FISHES AT ARTIFICIAL REEFS OFF SOUTHEASTERN FLORIDA, U.S.A.

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ABSTRACT

Fifty standard concrete modules were deployed on a sand bottom to make 16 replicated artificial reefs of 1 to 8 modules·reef [1]. Fish assemblages were monitored for species composition, abundance, and fish size, and compared to two natural control sites. We censused 127 species (107,168 fishes) from artificial reefs, 93 species (16,495 fishes) on natural control reefs, and 17 species (1,040 fishes) on sand bottom from July 1987 to March 1989. Artificial reefs supported a diverse, abundant, and dynamic assemblage of fishes that were a mixture of species found in surrounding sand and natural reef habitats. Colonization (number of species, individuals, and biomass) was very rapid. Abundance varied seasonally with recruitment episodes tending to occur in the spring and summer followed by losses for the remainder of the year. Assemblages were quite variable on and between similar sized reefs. Fish and biomass densities were higher at artificial reefs than on sand and natural reefs. Resident fish biomass varied less than resident fish numbers, because individual growth compensated for mortality after recruitment episodes. Reef size significantly influenced total numbers of species, individuals, and biomass. Smaller reefs had greater fish density while larger reefs had higher biomass density from larger, but fewer, individuals. Multiple small reefs supported more individuals and more species than one large reef of equal material. Fishes recruited by larval settlement accounted for 36% of the total resident abundance but only 2% of total biomass. As reef size increased, older juvenile or adult colonists comprised a greater percentage of total biomass (94% to 99%). Assemblage importance percentages (based on abundance, biomass, and frequency) were divided between residents (64%), visitors (20%), and transients (16%). Economically important species comprised 61% of the biomass and 55% of the individuals, among which settlers accounted for 94.3% of individuals but only 5.7% of their total biomass. The most highly valued species were visitors or residents that utilized the reefs after first settling elsewhere. These results showed that data on artificial reef assemblages based solely on the abundance of resident species are biased. Data on visitors, transients, frequency-of-occurrence, and biomass are important in evaluating bias. Results provided a partial test and support for a model predicting the importance of attraction over production for artificial reefs located in areas with high reef availability.

Greater demands for recreational fishing opportunities, habitat enhancement, and mitigation have resulted in increased deployment of artificial reefs. The number of permitted artificial reef projects has increased exponentially in the USA (Seaman and Aska, 1985; McGurrin et al., 1989). Despite the number of reefs built, relatively little is known about their benefits, how they function, and how they should be used in a comprehensive fisheries management program (Bohnsack and Sutherland, 1985; Seaman and Sprague, 1991). Bortone and Van Orman (1985) attempted to evaluate Florida's artificial reefs and concluded that there were insufficient data to make a meaningful analysis. Currently, data are critically needed to properly design, locate, evaluate, and plan for further development of artificial reefs. A major unanswered question involves the contribution of artificial reefs to new production of fish versus the concentration of existing fishes, especially when stock size has been reduced by fishing (Bohnsack, 1989; Meier et al., 1989; Polovina, 1991). Quantified knowledge about the relative importance of these two processes is essential for proper management.

A major problem for managing reef resources is the incomplete understanding of the interactions between recruitment and habitat structure. Fish recruitment is subject to at least two major constraints: appropriate habitat availability and settlement by planktonic larvae from local or distant sources. Most reef fish populations are dependent on planktonic eggs and larvae for reproduction. Habitat may be limiting because artificial reefs appear to increase or aggregate reef fish populations. However, although habitat space may ultimately be limiting, many reef fish populations are not at the carrying capacity of their environment and changes in abundance may be controlled by settlement from the plankton (Victor, 1983; Doherty and Williams, 1988; Richards and Lindeman, 1987) or by early postsettlement mortality (Sale and Ferrell, 1988). One popular justification for artificial reefs is that they increase fish populations by improving recruitment.

The goal of our research was to determine the influence of habitat structure on reef fish populations to better understand reef fish recruitment processes, artificial reef function, and artificial reef use for habitat enhancement and environmental mitigation. We specifically compared fish assemblages on natural and artificial reefs of different sizes. Concurrently, we examined the role of artificial reefs in recruiting larval fishes, attracting adult and juvenile fishes, and providing for growth and production of reef fish biomass.

Specific objectives were to: (1) quantify the relationship between reef size and the biomass and numbers of reef fishes that settle and grow on artificial reefs versus those that arrive at older stages; (2) experimentally test whether multiple small reefs can support more fish than one large reef using equal quantities of materials; and (3) compare the artificial reef assemblages of reef fishes with nearby natural and artificial habitats. Major null hypotheses tested were: (1) the size of a reef has no effect on recruitment and resulting reef fish community structure, in terms of biomass, species composition, and numbers and sizes of individuals; and (2) the standing crop biomass is primarily the result of recruits that settle at artificial reefs and grow versus those which were redistributed from other sources.

METHODS

Artificial Reef Construction and Deployment.—Artificial reefs (ARs) were constructed from 50 identical, prefabricated, concrete modules; each measured 132 × 132 × 132 cm, occupied 2.3 m³, weighed approximately 2,590 kg in air (1,555 kg in water), and had 13.2 m² exposed surface area (Fig. 1) The walls and floor were 15 cm thick. Each module was strengthened with eight embedded reinforcing rods and had four lifting rings in the floor. Modules included features considered desirable for durability and fish utilization based on research in Japan and Hawaii: open tops, side holes (two 35.6-cm-diameter holes in each side), single pour construction, and high (52%) void space (Grove and Sonu, 1985; Mottet, 1985).

Sixteen reefs were deployed in 1987 in an experimental grid with 3 × 7 cells on a 10- to 12-m-deep sand plain at 25°42'N and 80°06'W in the inshore portion of a Dade County artificial reef zone, 4 nautical mi east of Key Biscayne, Miami, Florida (Fig. 2). The three rows ran south to north parallel to shore and were separated by approximately 150 m. Reefs in each row were separated by approximately 100 m and consisted of 1, 2, 4, or 8 modules with 6, 4, 3, and 3 replicates, respectively. Modules were individually lowered into position. Reefs in row 1 (cells 11 through 16, inshore) were deployed on 8 July, row 2 (cells 22–26) on 9 July, and row 3 (cells 31–37, offshore) on 16 July along with cell 21 of row 2. Three empty cells (14, 23, 35) were used as sand bottom control sites and two cells (17, 27) were not used in this study.

Multiple unit reefs were loosely aggregated to simulate patterns of natural coral colonies. Nearest neighbor distance between modules on multiple unit reefs averaged 3.3 m (range 0.01 to 8.61 m). Modules at multiple unit sites were not precisely repositioned at set distances from each other to avoid confounding early colonization which was anticipated to be rapid based on previous studies (Stone et al., 1979; Bohnsack and Talbot, 1980). We also did not want to unnecessarily risk diver safety by moving the 2.6 mt modules or divert limited diving time away from the initial census effort.
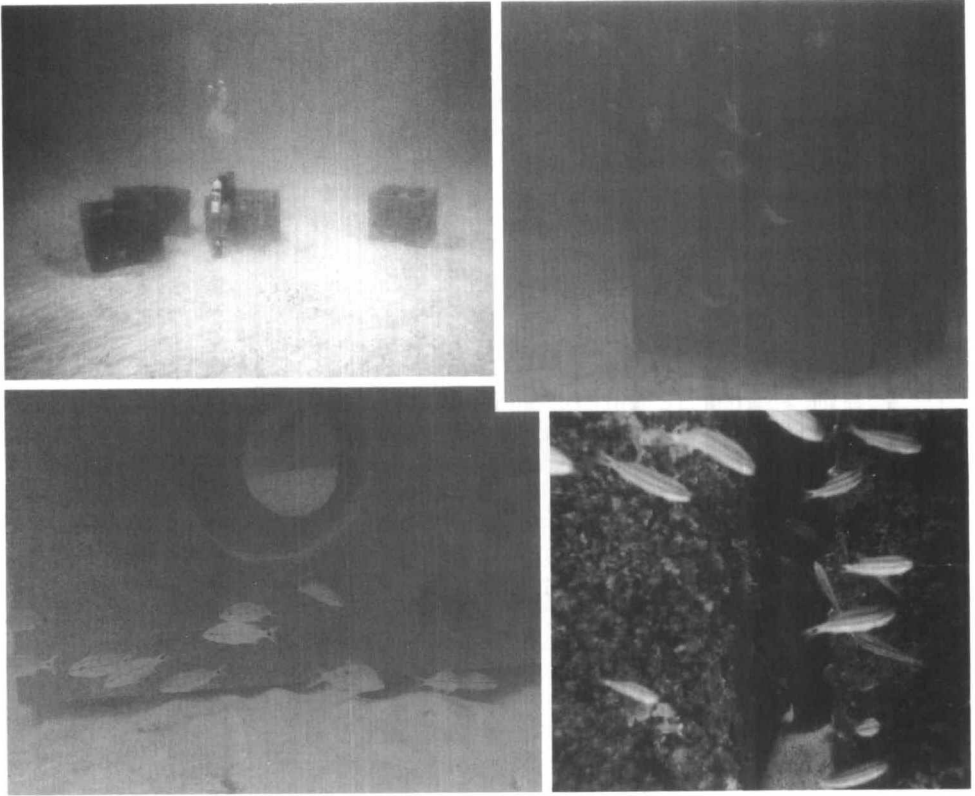
Figure 1.   Artifical reef modules showing a 4-unit reef configuration (upper left), foraging *Caranx bartholomaei* (upper right, sand cavity microhabitat (lower left), and microhabitat provided by close proximity of two modules (lower right).

Site Description.—A nearby small patch reef (SPR) and a large natural reef (LNR) were used as control sites (Fig. 3). SPR was a circular isolated patch reef approximately 150 m southwest of the experimental grid. It covered 28 m², twice the bottom area of an 8-module reef, but with approximately the same surface area as a 2-module reef. LNR is best described as a "hard bottom" reef habitat (Blair and Flynn, 1989) although previously described as "live bottom" by Jaap (1984). LNR was approximately 150 m inshore of the experimental grid and several orders of magnitude larger than any of the artificial reefs although its actual area was undetermined. LNR extended north and south beyond and parallel to the 700-m-experimental grid, varied in width, and was occasionally interrupted by sand channels. Natural reefs differed from ARs most notably in terms of topography, reduced relief, and greater coverage by sponges, octocorals, and occasional scleractinian corals. To the east, the sand plain descended into deeper water off the shelf. It was occasionally broken by exposed hard bottom and artificial reefs composed of sunken ships and other materials beginning at approximately 20 m depth (Shinn and Wicklund, 1989).

Prevailing winds were 10 to 15 km from the southeast. Wave action generally varied by season with the heaviest seas occurring in the fall and winter in association with passing cold fronts. Currents usually flowed north but occasionally ran south due to eddies from the Florida Current. Current speed varied from nil to an estimated 1 m·s⁻¹. Visibility was visually estimated to average 10 m and vary from 0.1 to 30 m.

Sampling.—Fish assemblages were monitored for species composition, abundance, and fish size. All species names used in this paper are according to Robins et al. (1991). Divers sampled grid sites by swimming down current from reef to reef. At AR and SPR sites, we censused all fishes, identified species, and estimated individual sizes using standard visual census methods (Bohnsack and Talbot, 1980; Bohnsack, 1983a, 1983b). Large fish were first censused as the diver approached the reef. Then the reefs were closely examined for small and cryptic species. A 30 cm ruler attached perpendicular
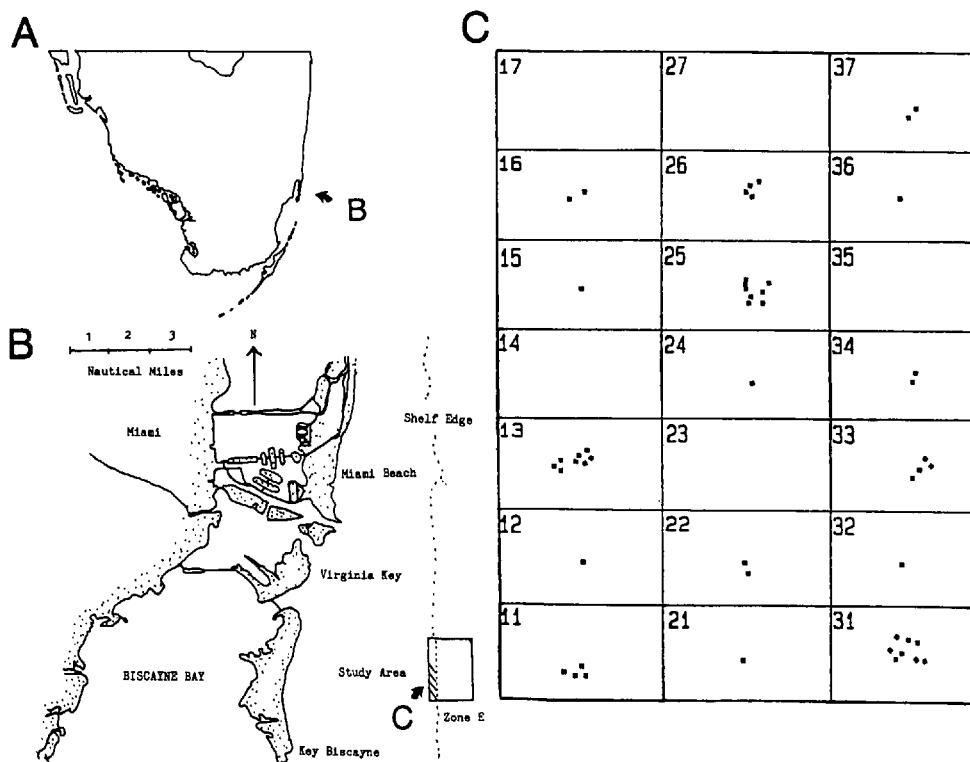
Figure 2. Study location. The scale of reef and module size within numbered grid cells is exaggerated.

to the end of a meter stick aided in making size estimates. Buddy teams would compare their census data and agree on the most complete and accurate combined data set to represent a census sample.

A total census was not possible at LNR and sand control sites. Here divers collected multiple random samples using a visual stationary sampling method (Bohnsack and Bannerot, 1986). At randomly selected points, a stationary diver recorded all species observed in 5 min within an imaginary 7.5-m-radius cylinder centered around the diver and extending from the bottom to the surface. At the end of 5 min, numbers of individuals were counted and the mean and range of sizes (fork lengths) were estimated for each listed species, working from the last recorded species to the first. These data should be considered indices of abundance and biomass because they are not complete censuses and probably underestimate absolute abundance for some species (Bohnsack and Bannerot, 1986).

The study area was repeatedly censused prior to reef construction to determine the effects of artificial reefs on the pre-existing ichthyofauna. After reefs were deployed, the experimental grid was censused daily for several days and then weekly for the first month. After that, reefs were censused approximately monthly as water and weather conditions permitted.

Analyses.—Statistical analyses were done using Lotus 123 Version 2.2 and SAS Version 6.04.[1] Biomass estimates at AR and SPR sites were made using individual length estimates and empirically derived length-to-weight conversion formulae (Bohnsack and Harper, 1988). When no conversion formula was available for a species, the formula for its nearest congener or fish with the most similar body shape was used. Biomass estimates for sand and LNR sites were based on mean size for each species instead of each individual fish.

To provide a common basis for comparing assemblages,[2] an importance index was calculated for

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[1] The National Marine Fisheries Service does not approve, recommend, or endorse any proprietary product mentioned in this publication.

[2] The term "assemblage" is used instead of "community," to refer to groups of co-occurring fishes on study reefs as recommended by Mapstone and Fowler (1988). "Community" implies coevolved, deterministic systems with emergent properties which are not necessarily associated with artificial reefs.
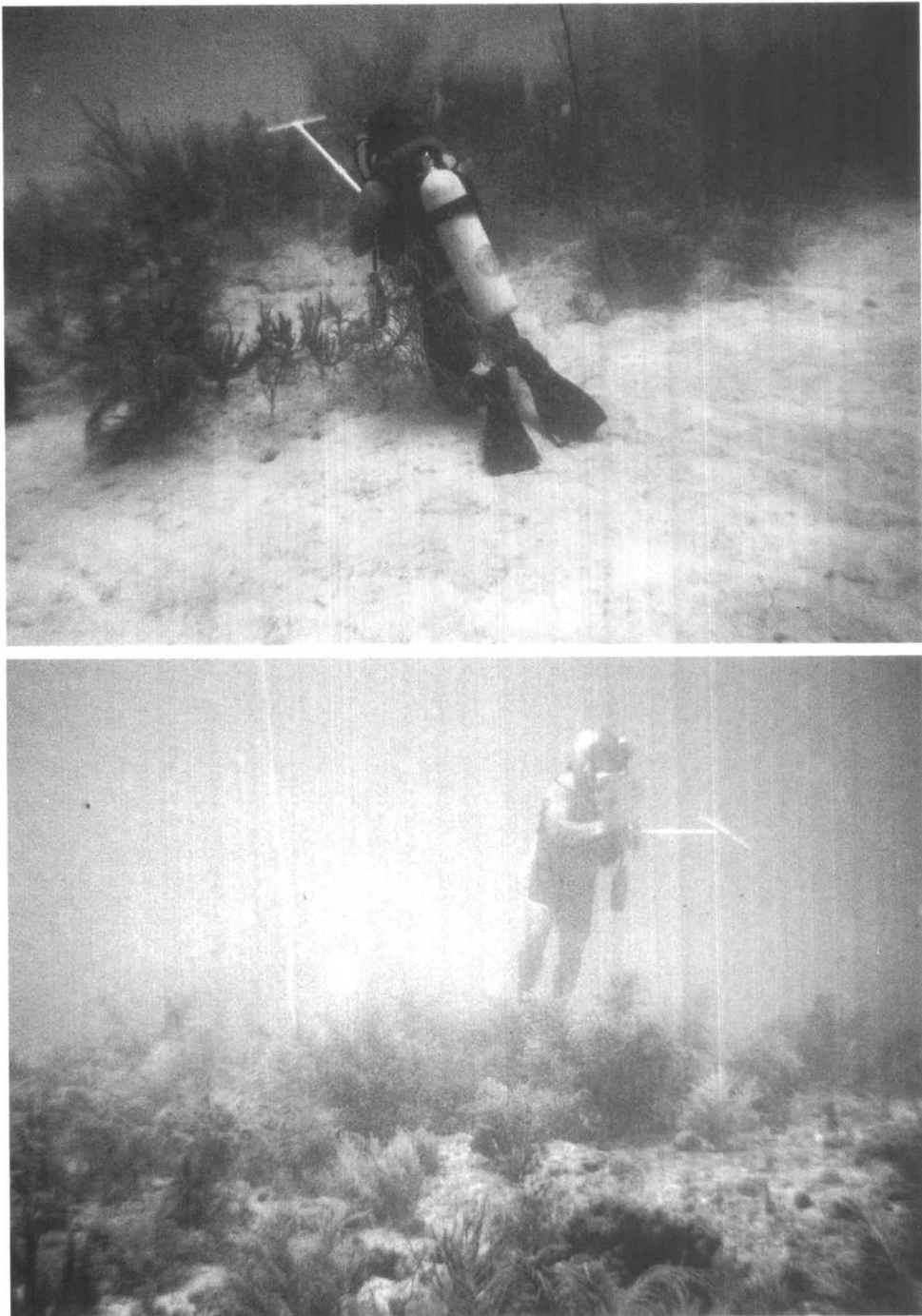
Figure 3.   Natural reef control sites: small patch reef (top), large natural reef (bottom).

each species that gave equal weight to abundance, biomass, and frequency-of-occurrence (Brower and Zar, 1977). Each of these parameters has biases for evaluating the ecological importance of a species. Number of individuals, for example, gives extreme value to small but numerous fishes while biomass gives extreme value to a few large individuals. Species richness (species lists) emphasizes rare species, although frequency-of-occurrence is useful for showing the rarity or commonness of a species. The importance percentage, IP, of a species, i, was calculated by:

$$IPi = (RA_i + RF_i + RB_i)/3$$

where RA is relative percent abundance, RF is relative percent frequency, and RB is relative percent biomass for species i. The relative percent abundance (RA) of species i is the total individuals of species i as a percentage of the sum of the total individuals censused. Relative percent frequency (RF) is the number of times (occurrence) a species was included in census samples as a percentage of the sum of the frequencies for all species. Relative percent biomass (RB) is the total biomass (weight) for a species expressed as a percentage of the total biomass for all species. The sum of the importance percentage for all species in an assemblage equals 100 percent. Although IP gives a common basis for comparing species, the information from the various components is lost.

RESULTS AND DISCUSSION

Assemblage Structure.—A total of 462 census samples containing 127 species and 107,168 fishes were collected from the artificial reef grid during 55 sampling days between 9 July 1987 and 22 March 1989 (Table 1). On natural reefs, 93 species (16,495 fishes) were censused in 83 samples. On sand, 17 species (1,040 fishes) were censused in 28 pre-deployment samples collected over 7 months between November 1985 and July 1987.

Of the 127 species observed at ARs, 92 (72%) were classified as reef residents, 22 (17%) were visitors, and 13 (10%) were transients (Table 1) according to criteria used by Russell et al. (1974), Talbot et al. (1978), and Bohnsack and Talbot (1980). Resident species tended to remain at one site and were usually observed on one or more consecutive censuses. Visitors used ARs only for temporary shelter or feeding and tended to be present only for one census. Transients were fishes that were observed near reefs but that roamed over a broad area and appeared not to react to reef presence. Resident species had a combined importance percentage of 64%, followed by visitors (20%) and transients (16%).

Mackerel scad, *Decapterus macarellus,* a transient, had the greatest importance value (18.29%). Although it occurred infrequently, it was highly aggregated and represented considerable biomass. Potentially this species could be ecologically important as a predator on fish eggs and larvae or as a competitor for planktonic food resources (Hamner et al., 1988). Although visitors and transients used ARs only temporarily, they perhaps benefitted from the foraging opportunities provided. Visitors accounted for only 1.5% of the total number of fishes and 7.8% relative frequency, but represented a disproportionate amount of the total biomass (38.8%). Most were piscivorous and therefore could have had an ecologically important influence on fish assemblages. Visitors also tended to be important fishery species (Table 1). These results suggest that use of abundance and species composition data alone may give very biased interpretations of AR ecology. Unfortunately, biomass is frequently ignored in visual studies, because with most underwater survey methods it is more difficult to estimate than abundance.

Further discussion refers only to residents unless otherwise indicated. By eliminating transients and visitors, seasonal patterns become more pronounced and variation was reduced for numbers of species, individuals, and biomass.

Colonization.—Colonization in this study was similar to other studies from southern Florida (Stone et al., 1979; Bohnsack and Talbot, 1980; Alevizon and Gorham, 1989). Colonization was very rapid with peak levels of species, individuals, and biomass being reached within two months (Figs. 4–6). Resident abundance varied

Table 1. Summary of species censused in the experimental grid between July 1987 and March 1989

Species	Common name	Primary source of recruits[1]	Residency[2]	Trophic level[3]	No.	Biomass (kg)	Freq. (N = 462)	Importance percentage	Economic value[4]
1 Abudefduf saxatilis	Sergeant major		R	P	49	0.95	28	0.30	
2 Acanthurus bahianus	Ocean surgeon	C* S	R	H	232	37.59	63	1.15	SC
3 Acanthurus chirurgus	Doctorfish		R	H	40	13.11	8	0.25	
4 Acanthurus coeruleus	Blue tang		R	H	106	44.02	50	1.07	
5 Aluterus schoepfi	Orange filefish		R	H	26	7.38	18	0.27	
6 Aluterus scriptus	Scrawled filefish	C	R	H	6	2.30	6	0.09	SC
7 Anisotremus surinamensis	Black margate	C	R	Ma	1	1.15	1	0.02	SC R
8 Anisotremus virginicus	Porkfish	C* S	R	Ma	24	7.02	21	0.30	SC
9 Apogon maculatus	Flamefish		R	P	38	0.01	10	0.11	
10 Apogon pseudomaculatus	Twospot cardinalfish		R	P	1,146	0.39	97	1.30	
11 Atherinomorus stipes	Hardhead silverside		T	P	1	0.00	1	0.01	
12 Aulostomus maculatus	Trumpetfish		R	F	31	4.50	25	0.31	
13 Balistes capriscus	Gray triggerfish	C	R	Ma	284	81.69	140	2.46	PC
14 Bodianus rufus	Spanish hogfish	S	R	MiMa	20	0.01	15	0.15	PC
15 Bothus lunatus	Peacock flounder		T	F	20	0.14	19	0.19	
16 Bothus ocellatus	Eyed flounder		T	F	3	0.01	3	0.03	
17 Calamus bajonado	Jolthead porgy	C	V	Ma	8	4.70	4	0.10	PC
18 Cantherhines pullus	Orangespotted filefish		R	H B	33	0.25	27	0.27	
20 Canthidermis sufflamen	Ocean triggerfish	C	V	P	11	15.45	10	0.29	PC
19 Canthigaster rostrata	Sharpnose puffer		R	H B	137	0.11	81	0.83	
21 Caranx bartholomaei	Yellow jack	C	V	F	441	298.60	58	4.44	SC
22 Caranx crysos	Blue runner	C	V	F	902	323.20	113	5.42	SC
23 Caranx ruber	Bar jack		V	P	182	41.18	37	0.93	
24 Chaetodipterus faber	Atlantic spadefish	C	V	Ma	1	0.85	1	0.02	SC
25 Chaetodon sedentarius	Reef butterflyfish		R	Mi	41	0.67	23	0.24	
26 Chromis cyanea	Blue chromis		R	P	17	0.00	10	0.10	
27 Chromis enchrysurus	Yellowtail reeffish		R	P	1	0.00	1	0.01	
28 Chromis flaviccauda	Cobalt chromis		R	P	1	0.00	1	0.01	
29 Chromis insolata	Sunshinefish		R	P	1	0.00	1	0.01	
30 Chromis multilineata	Brown chromis		R	P	10	0.01	7	0.07	
31 Chromis scotti	Purple reeffish		R	P	11	0.00	4	0.04	
32 Clepticus parrae	Creole wrasse		V	P	4	0.00	1	0.01	
33 Coryphopterus glaucofraenum	Bridled goby		R	H	50	0.01	19	0.20	
34 Cryptotomus roseus	Bluelip parrotfish		R	H	104	0.47	41	0.43	

Table 1. Continued

Species	Common name	Primary source of recruits[1]	Residency[2]	Trophic level[3]	No.	Biomass (kg)	Freq. (N = 462)	Importance percentage	Economic value[4]
35 Dactylopterus volitans	Flying gurnard		V	MiMa	1	0.74	1	0.02	
36 Dasyatis americana	Southern stingray		T	Ma	14	21.37	12	0.39	
37 Decapterus macarellus	Mackerel scad		T	P	33,242	607.91	35	18.29	
38 Decapterus punctatus	Round scad		T	P	969	44.17	8	0.93	
39 Diodon holocanthus	Balloonfish		R	Ma	8	1.97	8	0.10	
40 Diodon hystrix	Porcupinefish		R	Ma	22	34.48	19	0.62	
41 Diplectrum formosum	Sand perch		R	MiMaF	2,919	51.67	313	4.58	
42 Echeneis naucrates	Sharksucker		T	P	1	0.06	1	0.01	
43 Epinephelus cruentatus	Graysby	S	R	Ma	11	0.12	10	0.10	SC
44 Epinephelus fulvus	Coney	C	R	MaF	1	0.02	1	0.01	PC R
45 Epinephelus morio	Red grouper	C S	R	MaF	7	0.87	6	0.07	PC R
46 Epinephelus niveatus	Snowy grouper	S	R	MaF	3	0.03	3	0.03	PC R
47 Equetus acuminatus	High-hat		R	Mi	54	0.11	26	0.27	
48 Equetus lanceolatus	Jacknife-fish		R	Mi	92	0.17	62	0.63	
49 Euthynnus alletteratus	Little tunny	C	T	F	3	5.59	1	0.08	R
50 Ginglymostoma cirratum	Nurse shark		V	MaF	1	1.08	1	0.02	
51 Gnatholepis thompsoni	Goldspot goby		R H	Mi	144	0.04	36	0.39	
52 Gobiosoma oceanops	Neon goby		R	Mi	2	0.00	2	0.02	
53 Gobiosoma sp.	Unidentified goby		R		3	0.00	2	0.02	
54 Gymnothorax moringa	Spotted moray		R	MaF	5	1.21	5	0.07	
55 Gymnothorax vicinus	Purplemouth moray		R	F	37	44.66	16	0.73	
56 Haemulon aurolineatum	Tomtate	C S*	R	P Mi	44,098	162.11	134	17.04	SC
57 Haemulon chrysargyreum	Smallmouth grunt	C S*	R	P Mi	419	3.18	28	0.44	SC
58 Haemulon flavolineatum	French grunt	C S*	R	P MiMa	292	0.41	45	0.53	SC
59 Haemulon melanurum	Cottonwick	C S*	R	P Mi	1,023	3.43	80	1.13	SC
60 Haemulon parra	Sailor's choice	C S*	R	P MiMa	319	16.50	47	0.76	SC
61 Haemulon plumieri	White grunt	C S*	R	P MiMa	65	8.36	45	0.56	PC R
62 Haemulon sciurus	Bluestriped grunt	C S*	R	P MiMa	9	2.44	5	0.08	PC R
63 Haemulon sp.	Unidentified grunt	S	R	P MiMa	9,655	0.46	104	4.01	SC
64 Halichoeres bivittatus	Slippery dick		R	MiMa	246	1.23	91	0.97	
65 Halichoeres garnoti	Yellowhead wrasse		R	MiMa	14	0.05	13	0.13	
66 Halichoeres maculipinna	Clown wrasse		R	MiMa	5	0.00	4	0.04	
67 Halichoeres pictus	Rainbow wrasse		V	P Mi	4	0.07	2	0.02	
68 Halichoeres radiatus	Puddingwife		R	MiMa	15	0.03	15	0.15	
69 Hemipteronotus martinicensis	Rosy razorfish		R	MiMa	269	1.35	89	0.96	
70 Hemipteronotus novacula	Pearly razorfish		R	MiMa	7	0.03	4	0.04	

Table 1. Continued

	Species	Common name	Primary source of recruits[1]	Residency[2]	Trophic level[3]	No.	Biomass (kg)	Freq. (N = 462)	Importance percentage	Economic value[4]
72	Hemipteronotus splendens	Green razorfish		R	MiMa	183	1.18	72	0.77	
71	Hemipteronotus sp.	Unidentified razorfish		R	MiMa	21	0.04	7	0.07	
74	Holacanthus bermudensis	Blue angelfish		R	B	17	3.68	12	0.17	
75	Holacanthus ciliaris	Queen angelfish		R	B	4	0.02	4	0.04	
76	Holocentrus tricolor	Rock beauty		R	B	30	0.27	20	0.21	
73	Holocentrus ascensionis	Squirrelfish	S	R	MiMa	2	0.05	2	0.02	SC
77	Inermia vittat	Boga		T	P	1	0.02	1	0.01	
78	Ioglossus calliurus	Blue goby		R	P	2	0.00	1	0.01	
79	Ioglossus helenae	Hovering goby		R	P	2	0.00	1	0.01	
80	Kyphosus sectatrix	Bermuda chub		R	H	14	7.34	8	0.17	
81	Lachnolaimus maximus	Hogfish	C	R	Ma	29	13.12	12	0.29	PC R
82	Lactophrys polygonia	Honeycomb cowfish		R	B	1	0.02	1	0.01	
83	Lactophrys quadricornis	Scrawled cowfish		R	B	29	5.04	25	0.31	
84	Lactophrys triqueter	Smooth trunkfish		V	B	8	1.53	7	0.09	
85	Lutjanus analis	Mutton snapper	C	R	MaF	53	29.97	24	0.62	PC R
86	Lutjanus apodus	Schoolmaster	C	V	MaF	1	0.00	1	0.01	SC R
87	Lutjanus buccanella	Blackfin snapper	S	R	MiMaF	116	0.56	43	0.46	PC
88	Lutjanus synagris	Lane snapper	C*	S	R	MaF	1,270	211.68	58	3.61	PC R
89	Malacoctenus sp.	Unidentified blenny		R	P Mi	5	0.00	5	0.05	
90	Malacoctenus triangulatus	Saddled blenny		R	P Mi	7	0.01	5	0.05	
91	Microgobius carri	Seminole goby		R	P	78	0.02	25	0.27	
92	Microspathodon chrysurus	Yellowtail damselfish		R	H	2	0.00	2	0.02	
93	Monacanthus hispidus	Planehead filefish		R	MiMa	37	0.74	31	0.32	
94	Mulloidichthys martinicus	Yellow goatfish	C	T	Mi	1	0.01	1	0.01	
95	Mycteroperca bonaci	Black grouper	S	R	F	6	0.06	6	0.06	SC
96	Mycteroperca interstitialis	Yellowmouth grouper	C S*	R	F	13	1.76	12	0.14	PC R
97	Ocyurus chrysurus	Yellowtail snapper	S	R	MaF	52	0.17	30	0.31	PC R
98	Ogcocephalus nasutus	Shortnose batfish		V	Mi	1	0.32	1	0.01	
99	Pomacanthus arcuatus	Gray angelfish	C	R	B	69	39.85	51	1.01	SC
102	Pomacanthus paru	French angelfish	C* S	R	B	32	4.09	29	0.34	SC
100	Pomacentrus leucostictus	Beaugregory		R	H	9	0.01	9	0.09	
101	Pomacentrus partitus	Bicolor damselfish		R	HP	132	0.12	73	0.75	
103	Pomacentrus palnifrons	Three spot damselfish		R	H	1	0.00	1	0.01	
104	Pomacentrus variabilis	Cocoa damselfish		R	H	3	0.00	3	0.03	
105	Pseudupeneus maculatus	Spotted goatfish		T	Mi	13	0.47	8	0.09	

Table 1. Continued

Species	Common name	Primary source of recruits[1]	Residency[2]	Trophic level[3]	No.	Biomass (kg)	Freq. (N = 462)	Importance percentage	Economic value[4]
106 Priolepis hipoliti	Rusty goby		R	?	1	0.00	1	0.01	
107 Rachycentron canadum	Cobia	C	T	Ma	1	0.91	1	0.02	PC R
108 Rhinobatos lentiginosus	Atlantic guitarfish		V	Ma	1	2.32	1	0.04	
109 Rypticus saponaceus	Greater soapfish		V	MaF	1	0.06	1	0.01	
111 Scartella cristata	Molly miller		R	H	1	0.00	1	0.01	
110 Scarus coeruleus	Blue parrotfish	C	V	H	1	0.00	1	0.01	SC
112 Scarus croicensis	Striped parrotfish		R	H	10	0.04	5	0.05	
113 Scorpaena plumieri	Scorpion fish		R	F	126	54.37	84	1.53	
114 Seriola dumerili	Greater amberjack	C	T	F	3	1.38	3	0.05	SC R
115 Serranus tabacarius	Tobaccofish		R	Mi	14	0.01	14	0.14	
116 Serranus tigrinus	Harlequin bass		R	Mi	4	0.00	4	0.04	
117 Sparisoma aurofrenatum	Redband parrotfish		R	H	49	1.72	35	0.37	
118 Sparisoma chrysopterum	Redtail parrotfish		R	H	30	5.82	17	0.25	
119 Sparisoma radians	Bucktooth parrotfish		V	H	2	0.01	2	0.02	
120 Sparisoma rubripinne	Yellowtail parrotfish		V	H	5	1.13	3	0.04	
121 Sparisoma viride	Stoplight parrotfish	C	V	H	4	2.20	3	0.06	PC
123 Sphoeroides spengleri	Bandtail puffer	C	R	BMi	376	27.03	179	2.18	
122 Sphyraena barracuda	Barracuda		V	?	20	338.24	18	4.41	R
124 Starksia ocellata	Checkered blenny		R	F	1	0.00	1	0.01	
125 Synodus foetens	Inshore lizardfish		V	?	1	0.01	1	0.01	
126 Synodus intermedius	Sand diver		V	F	3	0.01	3	0.03	
127 Thalassoma bifasciatum	Bluehead		R	P Mi	6,309	3.34	264	4.55	
Total					107,168	2,662	3,451	100	

[1] Recruit sources: S settle as larvae, C colonize as juveniles or adults, * primary mode.
[2] Residency classification: R, resident; V, visitor; T, transient.
[3] Trophic level: H, herbivore; B, browser; P, planktivore; Mi, microinvertivore; Ma, macroinvertivore; F, piscivore; ? Unknown.
[4] Economic value: R, recreational; PC, primary commercial; SC, secondary commercial.
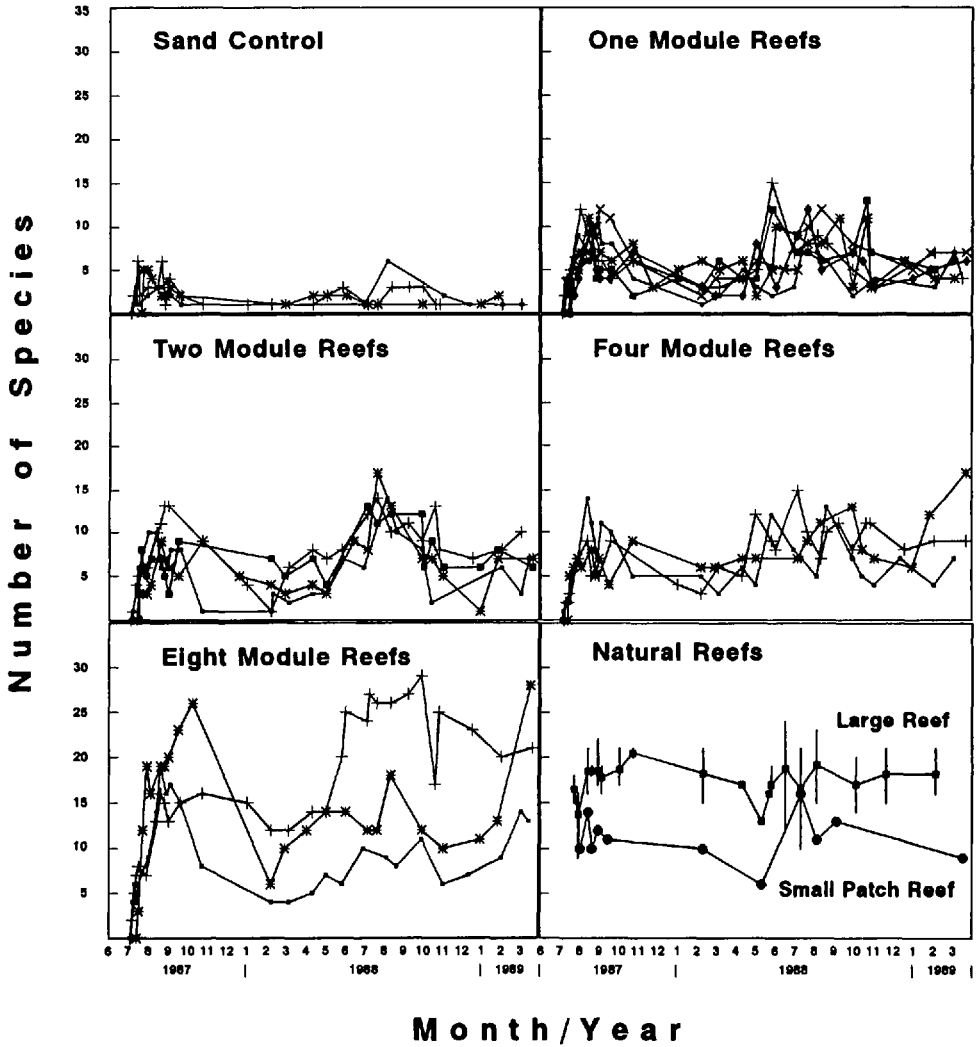
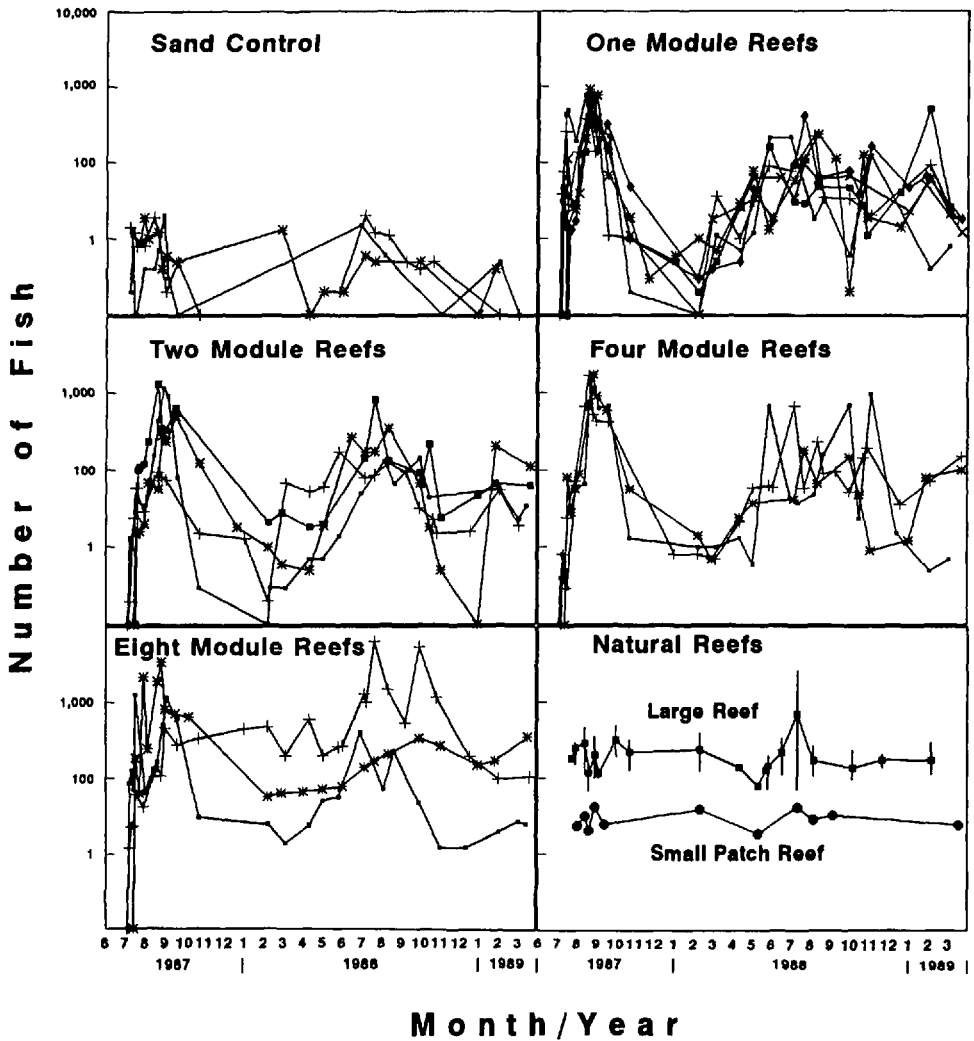Figure 4.   Number of resident species observed per sample. Vertical bars are 95% CI for the large natural reef. Symbols show different reefs but were eliminated for one module reefs for clarity. See text for details.

seasonally with recruitment episodes occurring in the spring and summer followed by reduced abundance for the remainder of the year. Variation was high within and between individual reefs.

Recruitment occurred by larval settlement and by colonization of older juveniles and adults. During the first week, large numbers of newly settled larval fish were observed at 10 reefs. However, most disappeared rapidly over several days after sand perch (*Diplectrum formosum*), a small predator, colonized the reefs from the surrounding area. We deduced that predation most likely caused the larval fish to disappear because we saw many direct attacks by sand perch and the continuous loss of larvae after predators arrived (described in Bohnsack, 1991). The occurrence of large numbers of newly settled larvae on new reefs suggests that a surplus of larvae were available to settle, at least during some
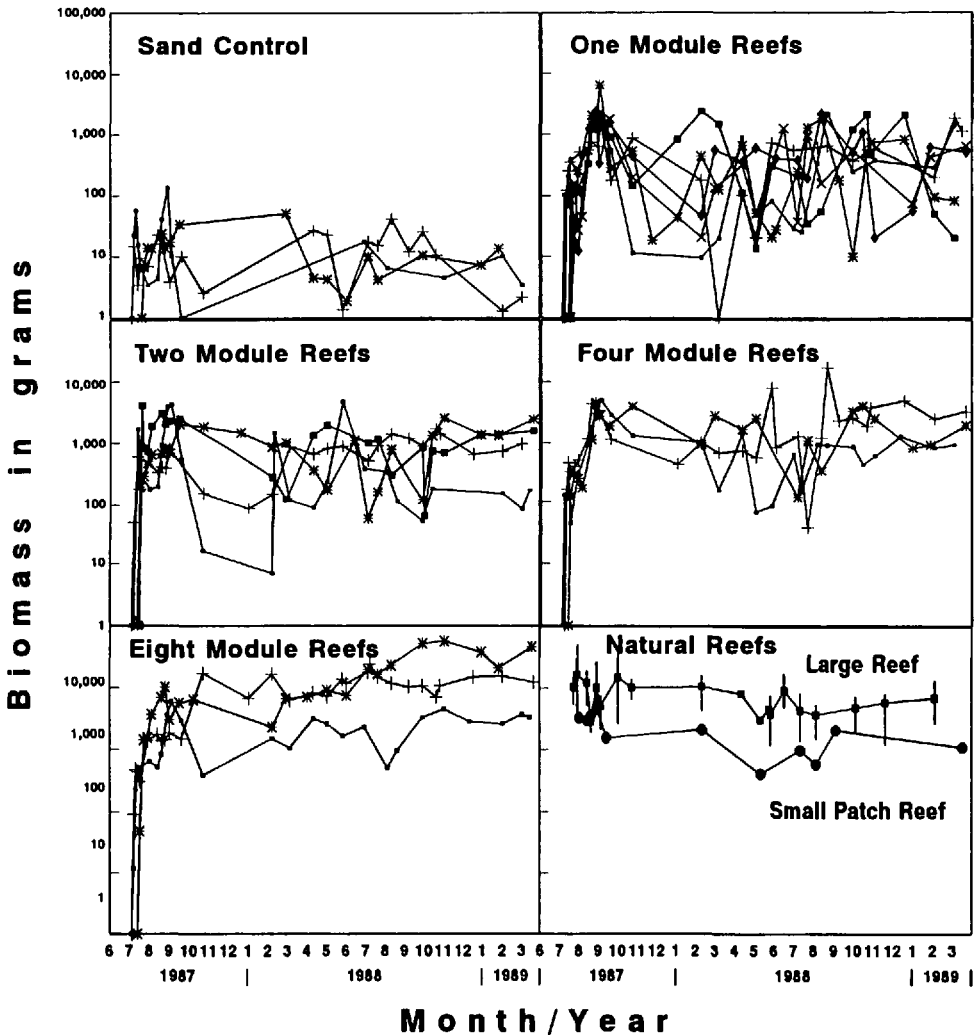
Figure 5.   Number of resident individuals observed per sample. Vertical bars are 95% CI for the large natural reef. Symbols show different reefs but were eliminated for one module reefs for clarity. See text for details.

time periods. Their rapid disappearance provides support for the "wall of mouths hypothesis" (Emery, 1973; Hamner et al., 1988) which suggests that larval fish must survive severe predation pressure at settlement. Interestingly, these initial colonization events could have been missed entirely if short sampling intervals had not been used. Sale and Ferrell (1988) found that the greatest mortality among newly settled reef fish occurred within the first 2 weeks after larval settlement. Small shelter holes were not provided by ARs which perhaps facilitated predation on larval recruits. Small holes on the scale of a few cm have been shown to be important for juvenile survival in other studies (Shulman, 1984, 1985; Shulman and Ogden, 1987; Hixon and Beets, 1989).

During fall and winter, species richness, numbers of individuals, and biomass declined, especially after periods of heavy seas and high turbidity. Recruitment

Figure 6.   Resident biomass observed per sample. Vertical bars are 95% CI for the large natural reef. Symbols show different reefs but were eliminated for one module reefs for clarity. See text for details.

peaks occurred during spring and summer. Eventually, larger reefs supported more total species, individuals, and biomass than smaller reefs although individual reefs were quite variable (Figs. 4–6). Resident biomass (Fig. 5) showed relatively less seasonal fluctuation than number of resident individuals (Fig. 6) despite recruitment peaks. Anderson et al. (1989) also found biomass to be less variable than numbers of fishes in California. Presumably growth of survivors compensated for individual mortality.

ARs were located at least 100 m apart to reduce inter-reef interactions of resident fishes (Bohnsack and Sutherland, 1985). Most residents remained close to ARs and outside the modules but would frequently move between modules on one reef. Larger fish would venture further away. Planktivores, such as juvenile grunts (Haemulidae), tended to concentrate along the upcurrent side above the modules. Only one recognizable fish was known to move between adjacent reefs:

a large surgeonfish, *Acanthurus coerulus,* first colonized the reef in cell 25 (8 modules) in December 1987 and was present for 11 censuses before moving to cell 26 (4 modules) in September 1988 where it remained for the rest of the study. Schooling fishes, such as grunts (Haemulidae), usually could not be distinguished as individuals; however, consistent abundance patterns observed between reefs implied that strong site fidelity existed under normal conditions.

Three microhabitat features could have influenced patterns of reef fish colonization and resulting assemblages: presence of sand cavities, proximity of neighbor modules, and biofouling of exposed surfaces (Fig. 1). Sand cavities often formed under edges of modules after scouring from heavy seas or strong currents. Once started, cavities appeared to be further excavated and maintained by invertebrates and fishes that used them as habitat. Some fishes would dive into these cavities when predators approached. At times these cavities would fill and fishes would attempt to hide inside the modules. Close proximity of two modules also provided a structural microhabitat that could affect the reef fish fauna. Morays (Muraenidae) and cardinalfishes (Apogonidae), for example, tended to persist on multiple unit reefs with modules in close proximity (Fig. 1). Finally, biofouling by algae, sponges, and other invertebrates could have affected the fish assemblages by providing food and shelter. Filamentous algae appeared within a week and by the end of the first year, modules appeared fully covered by fouling organisms. Fouling coverage varied between reefs apparently due to differences in grazing activity (Bohnsack et al., 1991). Algae appeared more luxuriant on small reefs, probably because fewer resident herbivores were present (discussed later).

Comparisons of Habitat Assemblages.—Habitat assemblages were compared based on all species with greater than 2% IP in each habitat (Table 2). At ARs, these included 11 out of 127 species with a combined IP of 70.99%. On LNR, 11 out of 85 species were included with a combined value of 65.11%. On SPR, 14 out of 36 species were included with a combined value of 81.38%. On sand, razor fish (*Hemipteronotus* sp.) and barracuda (*Sphyraena barracuda*) dominated pre-deployment sand control (PSC) and within-grid sand control (SC) samples (Table 2). Species composition was similar except that two carangids, *Caranx bartholomaei* and *C. crysos,* had a much greater IP after the ARs were deployed. We attribute this increase to ARs attracting more carangids into the experimental grid area. Carangids were frequently observed moving between reefs and making foraging passes at residents (Fig. 1); thus, they were more likely to be observed in sand control samples between ARs than in the predeployment surveys which had no attractants.

On the natural reefs, there were obvious differences between LNR and SPR in that only four species common to both sites had an IP greater than 2%. The most obvious difference was that tomtate (*Haemulon aurolineatum*) had a high IP at LNR (26.42%), but was insignificant at SPR (0.51%). Although only two control reefs were available locally, they represented extremes in size and probably represented extremes in assemblage structure. The fish assemblage observed at LNR was probably representative of large reefs in the region because it covered at least three orders of magnitude more bottom than all the modules combined and it was sampled at random locations. However, the fish assemblage at SPR, the small control site, was much less likely to be typical of small reefs because chance variation is more likely to influence small reef assemblages. It was, unfortunately, the only small reef that we could locate close to the study area.

AR assemblages were intermediate between sand bottom and natural reef assemblages (Table 2). In comparison to natural reefs, ARs tended to have more

Table 2. Comparison of importance percentages of dominant species between habitats (figures only shown if greater than 2% importance percentage)

Species	Predeployment sand (PSC)	Exper. grid sand (SC)	Artificial reefs (AR)	Small natural reef (SPR)	Large natural reef (LNR)
Hemipteronotus spp.	50.27	30.88	**	*	
Sphyraena barracuda	34.33	20.34	4.41		**
Haemulon aurolineatum	4.45	*	17.04	*	26.42
Microgobius carri	2.01	4.72			
Cryptotomus roseus	1.33	6.01	*		*
Caranx crysos	*	18.74	5.42		*
Caranx bartholomaei		3.93	4.44	**	*
Diplectrum formosum	**	2.25	4.58	*	*
Decapterus punctatus			18.29		
Thalassoma bifasciatum			4.55	13.40	8.02
Haemulon sp.			4.01		2.08
Lutjanus synagris			3.61		*
Balistes capriscus			2.46	**	*
Sphoeroides spengleri	*	*	2.18	**	*
Acanthurus bahianus			**	14.73	3.73
Lachnolaimus maximus			*	8.23	*
Priacanthus cruentatus				6.64	
Calamus calamus		*	*	5.09	
Halichoeres bivittatus			*	4.95	*
Haemulon plumieri			*	4.07	**
Pomacentrus partitus			*	4.54	7.62
Acanthurus chirurgus			*	4.50	*
Chaetodon sedentarius				3.80	**
Aulostomus maculatus			*	3.38	*
Sparisoma aurofrenatum			*	2.92	2.97
Calamus bajonado			*	2.75	
Canthigaster rostrata			*	2.38	**
Acanthurus coeruleus			**	*	3.68
Sparisoma viride			*		3.28
Scarus croicensis			*		2.67
Haemulon flavolineatum			*		2.44
Halichoeres garnoti			*	**	2.20
Total percent IP	95.70	88.21	80.68	88.97	73.50
Number of samples	28	70	462	11	72
Total species observed	17	24	127	37	85

* = <1.00.
** = >1.00.

planktivores (especially juvenile grunts) and benthic feeding fishes that tended to feed nocturnally away from the reef (i.e., lutjanids). Herbivores, especially larger individuals, were generally absent from ARs and SPR. Parrotfishes (Scaridae) for example, had an IP of 12.73% at LNR but only 0.80% at ARs and 3.36% at SPR. Ogden and Buckman (1973) suggested that parrotfishes were not supported on small patch reefs because of a lack of food resources. This explanation is consistent with our observations. Surgeonfishes (Acanthuridae) were also herbivorous with low importance (2.47% IP) at ARs and greater values at LNR (8.04%) and SPR (19.29%).

Fish and biomass densities were much higher at ARs than natural reefs and sand bottom (Table 3) as commonly observed in other studies (Ambrose and Swarbrick, 1989; Bohnsack, 1991). However, AR density calculations overestimate true density because the sand area surrounding reefs was not considered in

Table 3. Comparison of fish assemblages. Artificial reef data exclude initial colonization (before 12 August 1987)

Site	Sand	Artificial reefs (no. of modules)				Small patch reef (SPR)	Large natural reef (LNR)	500 tires*	Natural patch reef*
		AR 1	AR 2	AR 4	AR 8				
Sample method†	SS	Census	Census	Census	Census	Census	SS	Census	Census
Sample size (N)	57	119	79	62	62	10	66	8	8
Sample or reef area (m²)	177	1.75	3.5	7	14	28	177	153	113
Residents									
Mean species	na	5.6	7.2	8.0	15.0			40 ± 9	41 ± 8
Mean individuals	4.1	129.0	147.4	262.7	350.0	28.5	217.6	667	786
95% C.I.	3–5	94–164	92–202	164–362	217–483	23–34	141–294	—	—
Range	0–20	1–922	92–1,310	5–1,700	8–3,110	17–41	65–2,579	—	—
Density (m²)	0.03	70.9	40.5	36.1	24.0	1.0	1.5	4.4	6.8
Density (m³)	na	56.1	32.0	28.6	19.0	na	na	2.1	3.4
% Settlers	na	47.2%	31.2%	37.6%	30.1%	na	na	—	—
% Colonizers	na	52.8%	68.8%	62.4%	69.9%	na	na	—	—
Mean biomass (kg)	0.0117	0.71	0.97	2.05	10.21	2.02	7.09	—	—
95% C.I.	0.01–0.02	0.56–0.86	0.75–1.2	1.44–2.7	7.16–13.3	1.5–3.6	7.2–10.7	—	—
Range	0–0.14	0.00–6.5	0.00–4.7	0.01–16	0.38–57	0.41–4.8	1.19–36.3	—	—
Density $g \cdot m^{-2}$	0.077	390	266	282	701	72	47	—	—
% Settlers	na	6.5%	2.8%	4.2%	1.2%	na	na	—	—
% Colonizers	na	93.5%	97.2%	95.8%	98.8%	na	na	—	—
Total individuals									
Mean species	1.9	6.1	7.5	8	16.4	—	—	—	—
Mean individuals	6.8	237.1	154.1	377.0	557.3	29.7	224.2	—	—
Mean biomass (kg)	1.31	3.85	2.04	7.52	19.63	2.54	8.98	—	—

* Reference: Stone et al., 1979; 500 tires; 25°42'N, 80°06'W; depth 14 m.
† SS = Stationary sample of fishes observed from one point with a 7.5 m radius.
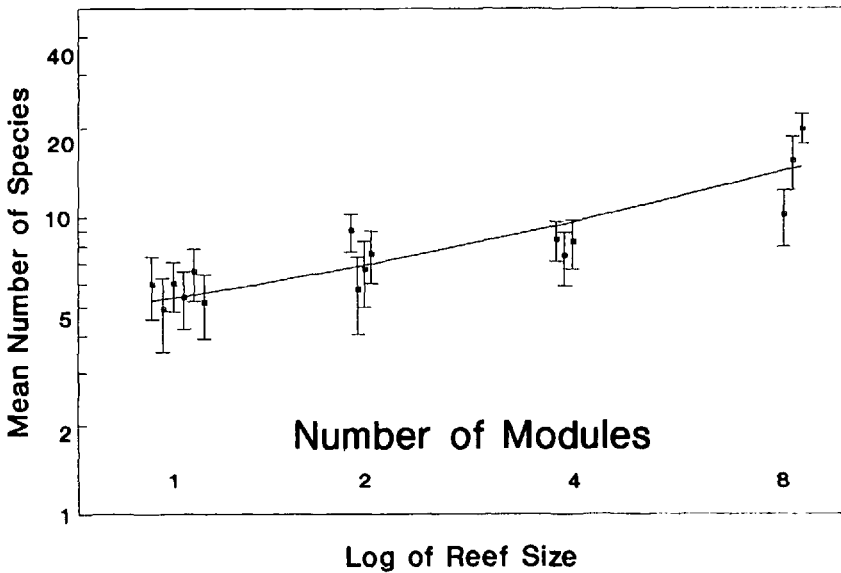
Figure 7.   Effects of artificial reef size on the mean number of resident species.

the calculations. Many resident fishes had "areas of activity" that included bottom area much greater than the actual reef.

Reef size significantly influenced the average number of species, individuals, and biomass of AR fish assemblages (Table 3, Figs. 7–9). In making these comparisons we excluded data from the initial colonization phase (prior to 12 August 1987). The log mean number of species per reef increased linearly as function of the log of reef area (Fig. 7) as commonly observed for a variety of communities (MacArthur and Wilson, 1967). Several small reefs held more total and resident species than a single reef of equivalent size (Fig. 8) based on data drawn once from each site on a randomly selected date during the summer of 1988. In this comparison, we added to random samples from single modules on other dates to the 6 single unit reefs in order to provide balanced numbers for comparison with the 4 and 8 unit reefs. Several possible factors could explain the greater cumulative number of species on the smaller reefs. Several small reefs have greater edge effect in that they offer more ecotone habitat based on a higher ratio of perimeter to reef area. Additionally, dispersing fauna may have a better chance of locating several small reefs than one large reef (Bohnsack, 1991). Further, because small reefs have higher fish density, they could have more species by chance (MacArthur and Wilson, 1967).

Using the average number of individuals and biomass on single module reefs, we predicted values on larger reefs assuming a linear relationship with reef size (Fig. 9). Larger reefs had significantly fewer individuals ($P < 0.001$) but greater biomass ($P < 0.05$) than predicted. The average number of fish increased as a linear function of reef size but at a slower rate than predicted based on single module reefs. We speculate that the reason for this relationship is that mortality is higher on larger reefs. Mean biomass increased exponentially with reef size because larger reefs tended to have larger residents.

AR fish assemblages were also compared to data from a study of an artificial reef constructed with tires approximately 35 km south of our study site (Table 3;
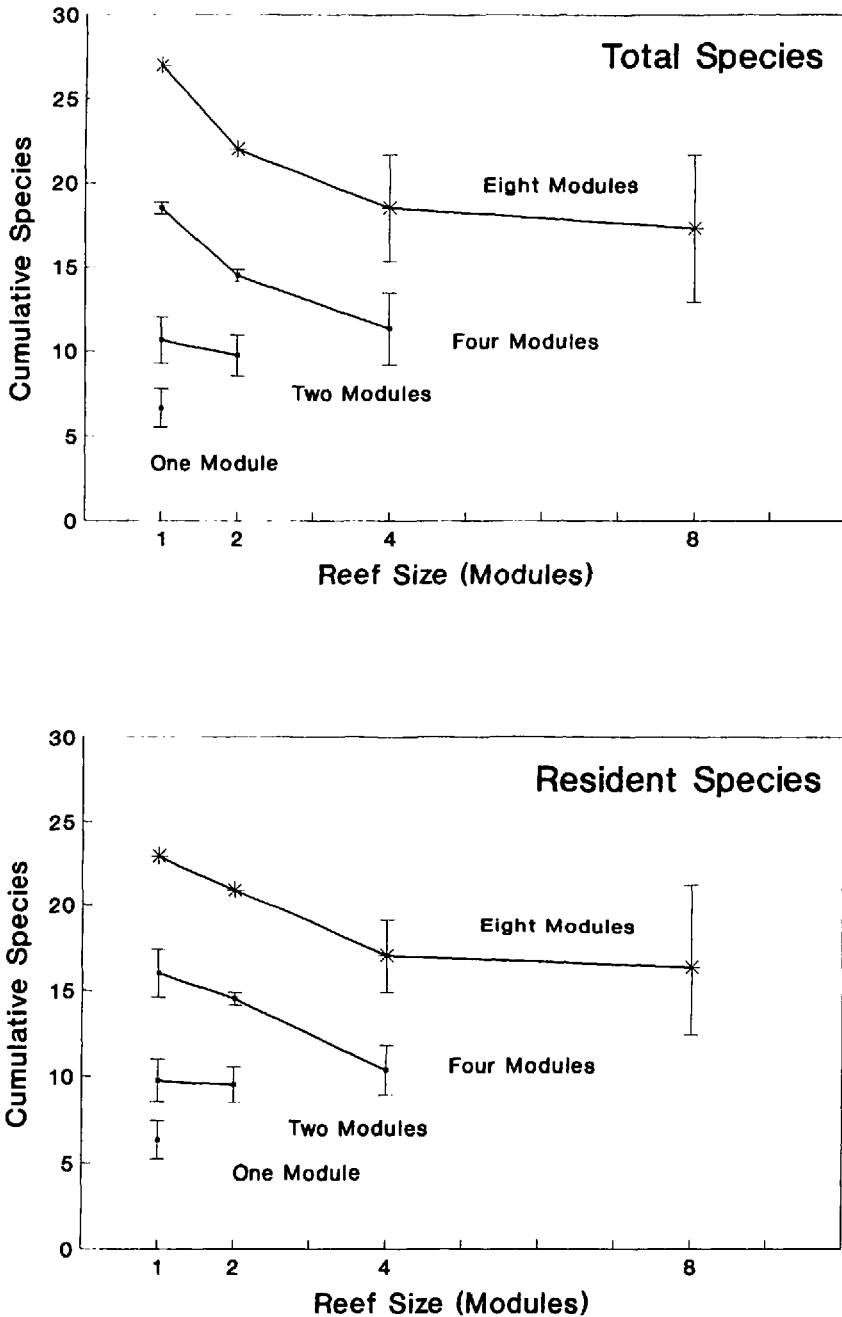
Figure 8. Mean number of total (top) and resident (bottom) species on several small versus a single large reef of the same amount of material. Data were used once from all reefs on a randomly drawn date in the summer of 1988. Error bars show 95% confidence intervals. Two random samples from single modules were added to data from the 6 single unit reefs to allow balanced comparison with the 4 and 8 unit reefs.
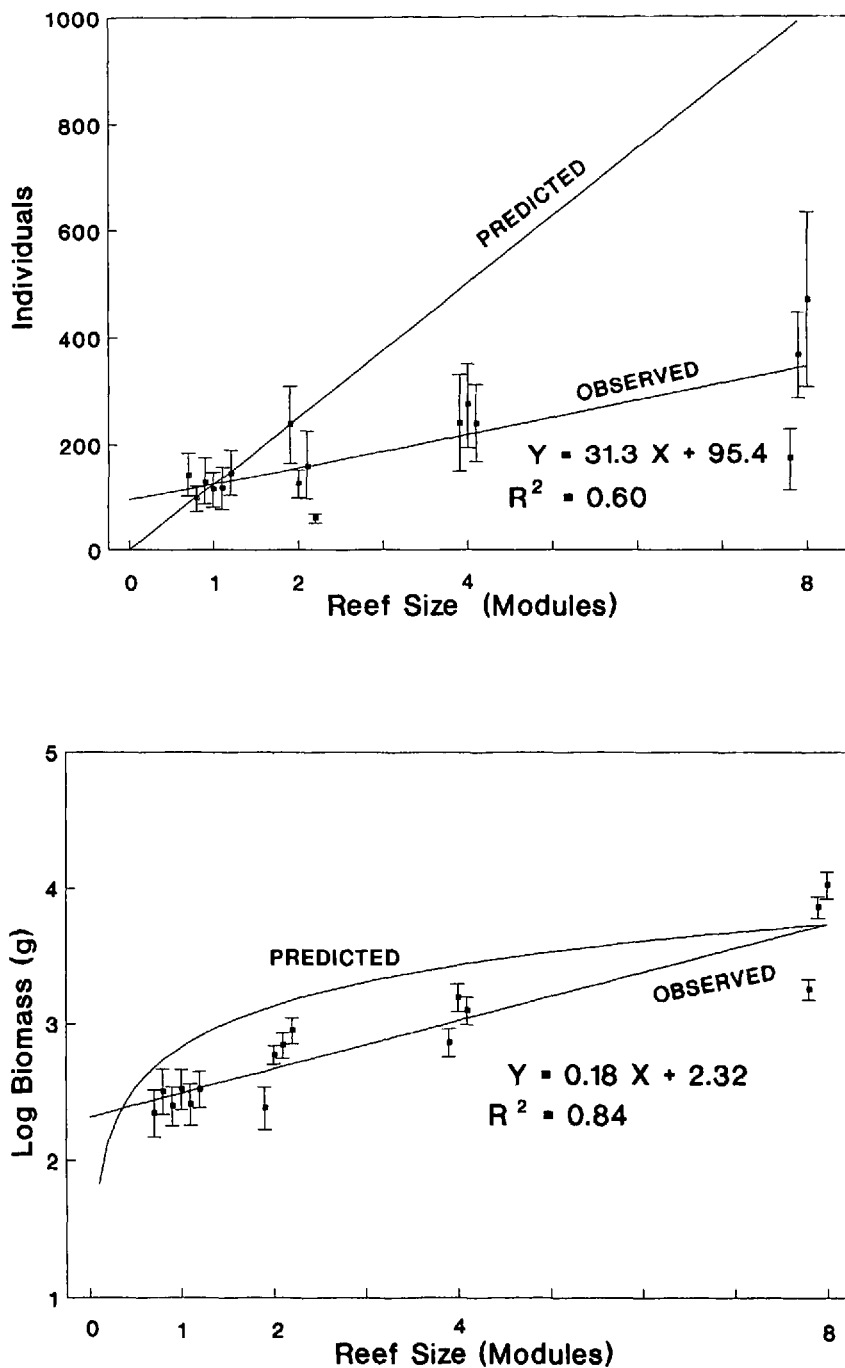
Figure 9.   Predicted and observed relationships of mean resident individuals (top) and mean total biomass (bottom) with reef size.

Stone et al., 1979). Both studies showed high seasonal variation in abundance and dominance by *H. aurolineatum,* which accounted for 57% of the individuals observed at the tire reef and 79% of the residents observed during this study. Because the tire reef was larger than the largest reef used in this study (113–315 m² vs. 14 m²), it had a higher average number of species (40 ± 9 SD vs. 15.0 ± 5.8) and individuals (667 ± 359 SD vs. 350 ± 525 SD). Mean fish density, however, was considerably higher in this study (24–71 vs. 2 ind·m⁻²) most likely because of a greater perimeter to area ratio (edge effect) on the small sized reefs (DeMartini et al., 1989; Ambrose and Swarbrick, 1989). We did not make a more detailed comparison between assemblages because the tire reef was not directly comparable to this study: it was built close (21 m) to a natural patch reef; was partially surrounded by sea grasses (Stone et al., 1979: figs. 2, 3); and changed shape, expanding from 12 m to 20 m dia.

Alevizon and Gorham (1989) also studied comparably sized artificial reefs in a similar habitat in the Florida Keys. Although they did not provide sufficient information for a detailed quantitative comparison, their results appear to approximate those in this study: a marked increase in numbers of local resident reef fishes on new artificial reefs, rapid colonization, high variability in space and time, high abundances of snapper and grunt, etc. The slightly slower colonization curve obtained during their study was most likely because their reefs were deployed in winter (Russell et al., 1974; Talbot et al., 1978; Bohnsack and Talbot, 1980). Despite similarities in the two studies, they concluded that the availability of suitable habitat was limiting and that artificial reefs could increase the production of some species. We submit, based on the rapid recruitment, that a more parsimonious explanation for their results is that fishes were attracted into their study area from surrounding areas. They noted that snapper recruitment was primarily from redistributed (i.e., attracted) adults (pg. 654) and that grunts "recruited as juveniles and sub-adults" (pg. 655). Fish redistribution does not necessarily mean that habitat was limiting or that production was increased. Unfortunately, they did not provide data on the relative contribution of larval settlement versus later stage migration and their study ended in summer when abundance is usually at peak levels due to settlement.

Mode of Recruitment.—The importance of recruitment mode for AR fish assemblages was evaluated by classifying fishes as either colonizers or settlers and then following their growth and mortality (disappearance). Settlers were presumed to have arrived by larval settlement from the plankton. Colonizers were juveniles or adults that clearly had migrated to ARs after having settled elsewhere. Individuals were classified based on their size when first observed and using liberal criteria favoring settlement. These criteria included allowances for growth between censuses and possible errors in counting and estimating size. Fishes were presumed to be settlers when first observed unless they were obviously too large to have settled since the previous census. The actual size used depended on the species and the time since the last census. Questionable individuals were assumed to have settled. Because of potential measurement errors in estimating size, new settlers included individuals somewhat larger than those we would have expected to have recently settled. Thus, fishes in subsequent samples could be larger, somewhat smaller, and up to 100% more abundant than in the previous sample and still be considered derived from settlement. In some cases these criteria would overestimate the importance of settlement because (1) a settler that disappeared but was replaced by a colonist would still be considered a settler if the two could not be distinguished; (2) fishes that both colonized and settled within the same size cat-

egories would be considered settlers; and (3) some increased abundance between censuses due to colonization would be considered a counting error and attributed to settlement.

Settlement on a cumulative basis accounted for 36.3% of total AR fish abundance (N = 70,961) but only 2.2% of the total biomass (952 kg). Smaller reefs had higher proportions of settlers (Table 3). The relative proportion of settlers and colonizers varied seasonally with settlers being numerically most abundant following larval settlement episodes (Fig. 10). However, colonizing fishes, because they tended to be large, dominated biomass throughout the year. The proportion of biomass from settlers decreased significantly ($P < 0.01$) as reef size increased based on a regression of arcsine transferred percentage data (Fig. 11). Although the percentage of settlers appeared to be less on larger reefs (Fig. 11), the trend was not statistically significant ($P > 0.05$). These results indicate that all reefs had significant numbers of settlers but that persistence was poor, especially on larger reefs. Biomass was more sensitive to changes than abundance because it reflects growth. Apparently greater predation or competition on larger reefs caused higher loss of settlers.

Based on the 2 years of data, there was no indication that the settlement contribution would increase over time. In fact, the proportion of settlers declined the second year (Fig. 10), most likely because they faced greater predation and competition from a larger resident population. The predator, *D. formosum*, which initially colonized ARs, dropped from a mean of 10.8 individuals per sample in 1987 (N = 196) to 3.4 in 1988 (N = 225), apparently having been displaced by other fishes. It is also possible, however, that fewer settlers were observed after the first year because of natural recruitment variation (Doherty and Williams, 1988).

Loss of fish over time could be caused by mortality (probably through predation) or by emigration. We deduced that gradual and consistent attrition of individuals over time was primarily due to predation but cannot entirely exclude the possibility of some emigration. We did observe carangids attacking grunts. Occasionally, however, entire schools disappeared between censuses, especially in the fall or winter. These disappearances were more likely due to accidental storm events or ontogenic changes with growth rather than from predation. Ogden and Ehrlich (1977) noted that *Haemulon flavolineatum* would normally return to the same home reef except after periods of extreme water turbidity when they apparently become disoriented and lost. Such periods of high turbidity were frequently observed in the fall or winter in association with weather fronts that forced turbid Biscayne Bay water into the study area. Also, some fishes may have emigrated due to growth-related changes in habitat requirements. *H. aurolineatum*, for example, appeared to be small, predominantly planktivorous individuals on ARs, but at LNR most tended to be larger benthic feeding adults. The fact that many individuals immigrated to ARs implies that they settled and emigrated from someplace else, either inside or outside the experimental grid. Although the survival of the later stage emigrants from ARs is unknown, few had originated as direct settlers to ARs based on following cohorts. Although ARs contributed relatively little to successful larval settlement, many fishes used ARs during older stages.

$\rightarrow$

Figure 10.   Changes in the percentages of resident settlers and colonizers with reef size. Lines show a three-point running mean.
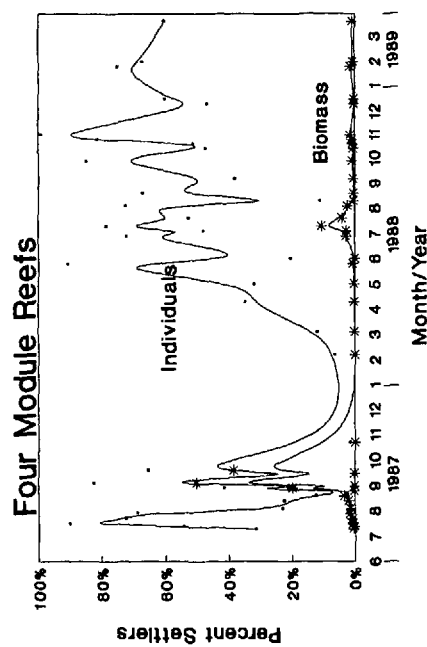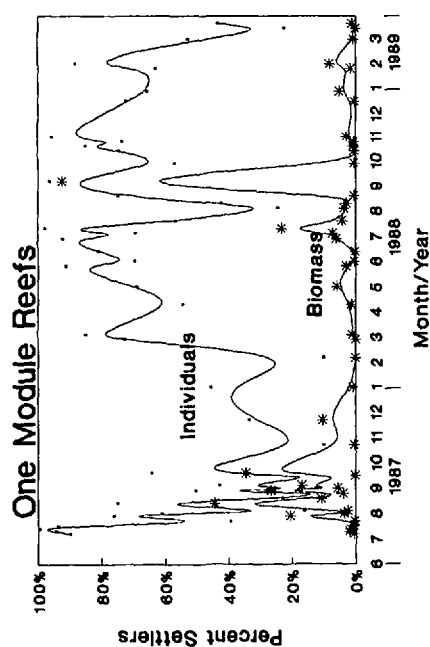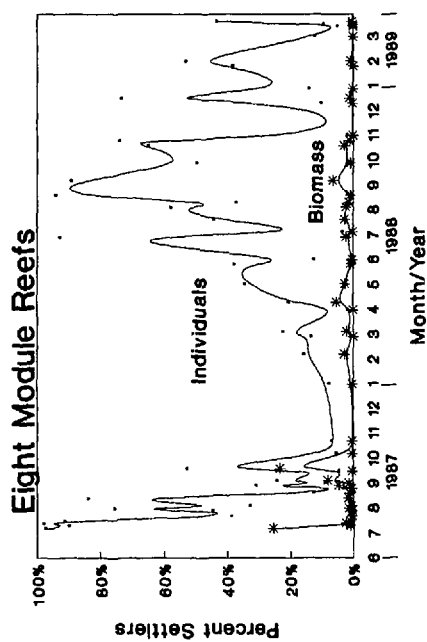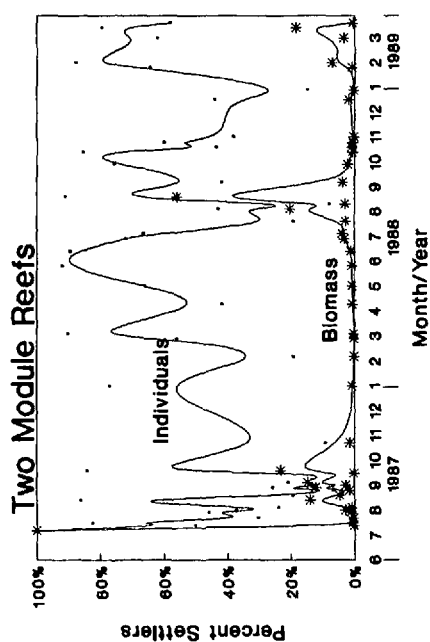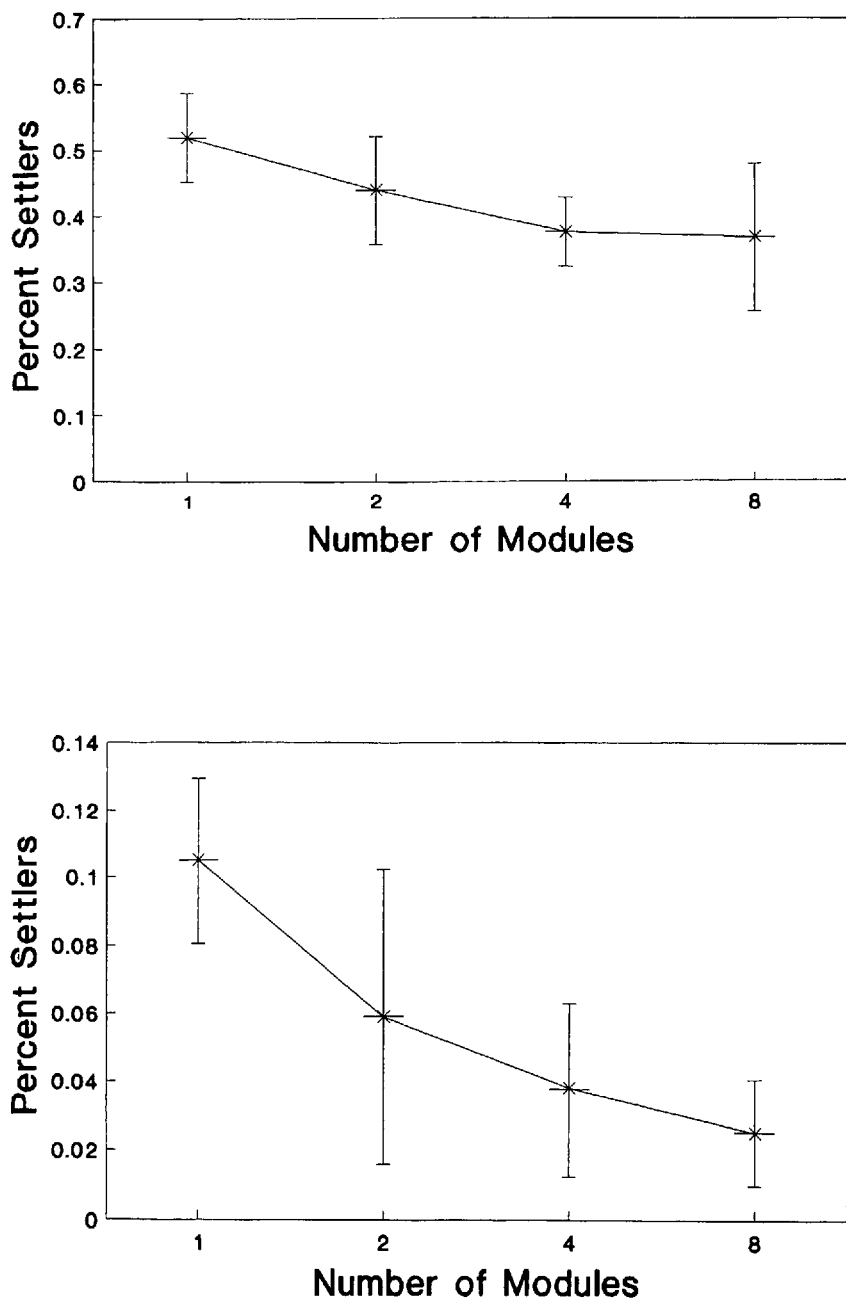
Figure 11.   Effects of reef size on settlers as a percentage of resident numbers (top) and biomass (bottom). Error bars show 95% CI.

Economically Important Species.—A total of 41 species (including unidentified larval grunts), 59,508 individuals, and 1,620 kg of fishes censused at ARs had some primary or secondary commercial or recreational value (Table 1). These represented 55.5% of all censused individuals, 60.9% of the biomass, and 50.7% IP. Some species, including most snapper and grouper, were desired by both com-

mercial and recreational fishermen; some species had commercial value (Suther-land and Harper, 1983) but limited recreational value; and others, like barracuda (*Sphyraena barracuda*) had recreational but no commercial value.

Among the economically important species, eight only settled and nine pri-marily settled, accounting for 94.3% of economically important individuals but only 12.4% of their total biomass. Twenty species only colonized and four species primarily colonized, accounting for only 5.7% of economically important indi-viduals and 87.6% of their total biomass. Colonizers included 13 visitors or tran-sient species that were primarily predators.

A total of 28 economically important species were residents: seven were col-onizers, eight were settlers, and 13 did both. Three species settled in small num-bers and did not persist (*Epinephelus niveatus, Holocentrus ascensionis,* and *Ocyurus chrysurus*). Several *Lutjanus buccanella* settled and appeared to do well before disappearing, possibly having migrated to deeper water which is their nor-mal adult habitat. Of the 13 species that both colonized and settled ARs, eight mostly settled, four mostly colonized, and one (*Epinephelus morio*) had one in-dividual in each category. One *Mycteroperca interstitialis* settled at 7 cm between 20 and 27 May 1988 and remained there for several months before disappearing between 13 and 19 October at 20 cm. Tomtate both settled and colonized and accounted for 74% of all economically important individuals but only 10% of their biomass. Because of their small average size, *H. aurolineatum* had very low commercial and recreational value in southern Florida.

Although many individuals of economically important species settled at artifi-cial reefs, few persisted. Most individuals of the highly prized species did not settle directly at ARs but colonized after having settled elsewhere. Some species, including most groupers (Moe, 1969; Keener et al., 1988), most snappers (Starck, 1970), hogfish (Davis, 1976), and barracuda (de Sylva, 1963) are known to first settle in inshore habitats such as seagrass beds before migrating to offshore reefs. Triggerfish probably colonized from drift flotsam. Although few fishes of eco-nomic importance would have had a chance to settle and grow to adults over the 2-year study, it is unlikely that a longer study would have shown any increased importance of settlers to the AR assemblages because survival of settlers was so low. Very few settlers of economically important species persisted on ARs during the study over the two years.

CONCLUSIONS

The experimental artificial reefs supported a diverse, abundant, and dynamic assemblage of fishes that were a mixture of species found in surrounding sand and natural reef habitats. As in other artificial reef studies from southeastern Florida, colonization was very rapid for number of species, individuals, and bio-mass; fish and biomass densities were higher at artificial reefs than on sand and natural reefs; assemblages were quite variable on and between the same sized reefs; and abundance varied seasonally with recruitment episodes tending to occur in the spring and summer. Resident biomass was less variable than resident in-dividuals, presumably because individual growth compensated for mortality after recruitment episodes. Economically important species were a major component of the artificial reef fish assemblage, comprising 41 species, 61% of biomass, and 55% of individuals, although most individuals were grunts with relatively low economic value. Few individuals of high economic importance settled directly on the artificial reefs; most were either visitors or residents that utilized the reef as juveniles or adults after having first settled elsewhere.

Although resident fishes dominated abundance, visitors and transients were frequently present, represented considerable biomass and a high proportion of economically important species, and were potentially important sources of competition and predation for residents. These results suggest that studies based solely on the abundance of resident species provide a biased perspective on the ecology of artificial reef fish assemblages. Data on visitors, transients, frequency-of-occurrence, and biomass must also be considered.

Reef size had a major impact on fish and biomass density as well as on total numbers of species, individuals, and biomass. Smaller reefs had higher fish density than larger reefs, while larger reefs had higher biomass density from larger, but fewer, individuals. On the scales tested, several small reefs could support more individuals and the same or more species than one large reef of equal material. For fisheries application, larger reefs may be better for fishing while smaller reefs may be better for overall recruitment. Although the proportion of settlers was not significantly different between different sized reefs, there was a significant decline in mean total biomass of settlers as reef size increased from 1 to 8 modules. We interpret these results as evidence that although larval settlement was similar at different sized reefs, mortality was higher on larger reefs due to increased competition and predation from larger resident populations and larger individual fishes.

The hypothesis that standing crop biomass was primarily the result of larvae that settle and grow at artificial reefs was not supported. At times many larval fishes were available for settlement, however, most quickly disappeared after settling, most probably due to predation. After the initial colonization phase, larval settlement accounted for 36% of the resident individuals, but only 2% of the resident biomass. Most residents colonized as juveniles or adults from other areas. Despite high rates of settlement, the low survival and the small contribution of settlers to total biomass does not support the commonly postulated hypothesis that artificial reefs provide critically limiting habitat that enhances the recruitment and survival of larval fishes, at least for these reefs in this environment. The lack of persistence by settlers and the reduced contribution of settlement in the last year of study suggests that the survival of settlers would not increase over time.

Despite supporting large numbers of fishes, these artificial reefs are unlikely to significantly increase the population size of species that are recruitment-limited or that experience heavy fishing mortality. A considerable amount of scientific literature indicates that adult abundance of many reef fishes is more likely to be limited by recruitment variability than habitat availability (Doherty and Williams, 1988; Mapstone and Fowler, 1988; Polovina and Sakai, 1989). The hypothesis that artificial reefs improve recruitment by providing critical habitat for settlers was not supported, especially for most highly exploited species which first recruited to other habitats before colonizing artificial reefs. Where settlement habitat is limiting for exploited species, then seagrass or other shallow water habitats are more likely to limit adult population size than offshore artificial reef habitat.

Many studies have noted the importance of showing the relative importance of artificial reefs for attracting and redistributing reef fishes versus increasing fish abundance and biomass. Our results provided a partial test and support for a model predicting a greater importance of attraction over production for artificial reefs located in areas with high reef availability (Bohnsack, 1989). The prediction that fish production would increase under conditions of low natural habitat availability, however, was not tested. Despite rejecting the most commonly postulated hypothesis on how artificial reefs increase fish production, we did not answer all questions or eliminate other possible mechanisms by which production could be

increased (Bohnsack, 1989, 1991; Polovina 1991). For example, there is no way to discern (1) whether fishes that settle or that were attracted to the artificial reefs would have found suitable habitat if these reefs were not present; (2) whether fishes had better survival or faster growth at artificial reefs than in natural habitat; (3) whether foraging success and food web efficiency was improved by artificial reefs; and (4) whether habitat vacated by fishes moving to artificial reefs was reoccupied so that total population size increased (Alevizon and Gorham, 1989). We postulate that the most likely way that these artificial reefs could increase production is through growth by allowing more efficient exploitation of underutilized foraging areas and by offering better foraging opportunities for roving predators. Of course in terms of fisheries application on a broader scale, high fishing mortality on a concentrated resource could still counteract any potential gains.

Although results from this study only directly apply to these reefs, they may provide a useful basis from which to evaluate other structures in terms of fish density, species composition, size, and total biomass per unit area or volume of reef material.

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