

Fish community structure as a function of habitat structure on West Indian patch reefs

by

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Abstract: The fish communities of twenty-five natural patch reefs in a back-reef lagoon off northeastern St. Croix, West Indies, were censused visually during summer, 1976. These reefs fell into two morphologically distinct groups: those in the east were of consolidated carbonate pavement reaching to near the water surface; those in the west consisted of scattered large coral heads (*Porites porites* and *Montastrea annularis*) separated by sand, and in slightly deeper water. Indices of similarity were calculated for the fish faunas of all pairs of reefs based on comparisons of abundances of all species present. The resulting matrix was used to construct a dendrogram of fish faunal similarity, which corresponded to major differences in the physical makeup of the reefs. Among structurally similar reefs, fish faunas were very similar, with forty-five species distributed uniformly among similar reefs. The majority of the remaining species were rare and local or uncommon. The distribution of some of the species could be correlated with single distinctive physical parameters of the reefs such as the presence of vertical walls, caves or the proximity to oceanic water or with biological factors such as food availability. When categorized according to general trophic category, omnivores were most abundant, followed by herbivores, crustacean eaters, planktivores (nearly all nocturnally active species), piscivores, and species with other, specialized diets (e. g. sponges). Although the morphologically most dissimilar reefs collectively had the most dissimilar fish faunas, the overall trophic composition of the eastern and western groups of reefs was similar.

One of the fundamental aims of community ecology is to determine the relative roles of the various factors responsible for determining community composition and organization. Coral reef fish communities are diverse assemblages of organisms with an extremely high degree of within-habitat diversity; for example, seventy-five species were found on a single patch reef three meters in diameter in the tropical Atlantic (Smith & Tyler, 1972). A number of factors, such as chance recruitment, competition for food and space, and predation, probably play important roles in determining fish community composition. Recent evidence (Sale, 1977; Sale & Dybdahl, 1975; Russell, *et al.*, 1974) suggests that stochastic

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factors are important in determining the species composition of very small reef structures (individual coral heads or small block reefs). The use of such small structures permits experimental manipulation and excellent documentation of recruitment patterns, but the relevance of such studies to understanding the composition of fish assemblages on reefs is not entirely clear. Studies on larger, natural reefs have substantiated that there is a great amount of within-habitat diversity but have also indicated some degree of habitat specificity among reef fishes (Hiatt & Strasburg, 1960; Clarke, 1977).

In order to gain a better understanding of the role of habitat structure in determining the structure of fish communities, the fish assemblages of a series of twenty-five natural, medium-sized (average area = 1350 m²) patch reefs were analyzed in relation not to single types of habitat, but rather in relation to overall reef structure. The reefs studied fell into several distinct morphological categories which differed to a greater or lesser degree from other reefs. Replicate visual censuses permitted characterization of the fish faunas of these reefs.

METHODS

The fish assemblages of twenty-five patch reefs located in the eastern portion of the lagoon behind the Tague Bay bank barrier reef (Adey, 1975) were censused during July and August, 1976. The reefs are arrayed more or less linearly over a distance of 2.5 km starting at the eastern limit of the bay (Fig. 1). Current measurements have indicated that most of the water entering the lagoon enters via this eastern entrance (Fig. 1, arrows), relatively little entering across the reef. The reefs are sequentially numbered according to a system long in use at the West Indies Laboratory. Several of the readily measured physical parameters of these reefs are presented in Table 1. The reefs range in size from 5 m² to 4600 m², the mean size being nearly 1500 m². Nearly all the reefs are greater than 50 m apart and always beyond the visual range of all other reefs. The reefs fall into two distinct groups of very different structure: an eastern group of elevated carbonate platforms (pavement reefs, 1 to 18), and a western group consisting of clusters of the massive corals *Porites porites* and *Montastrea annularis*, separated by bare sand (*Porites* reefs, A to P). In addition to these two groups of patch reefs, a small shore-fringing reef of the coral *Acropora palmata* was censused (Fig. 1, Sh). Water depths at the bases of the reefs are fairly uniform, although the western reefs are consistently deeper. Seagrass beds (composed especially of *Thalassia testudinum* and *Syringodium filiforme*) are well developed around and between the pavement reefs, but seagrasses are sparse around the *Porites* reefs. The pavement reefs, while all similar in general morphology differ among themselves in several important respects: many of them have significant areas of structurally complex three-dimensional habitat, usually stands of *Acropora palmata* but also systems of caves; however, six of the reefs (4, 9a, 9b, 12, 14a, 14b) completely lack such habitat. Four of the reefs (1, 16, 17, 18) have greater vertical relief than the others. The easternmost reefs (especially 16, 17, 18) due to their proximity to the entrance to the lagoon, are subject to a greater oceanic influence than more western reefs.

These reefs were censused by two experienced observers (the authors) working simultaneously using scuba. We swam in opposite directions around the periphery of a reef then across the top recording all species observed in one of five abundance categories: 1 = 1 fish per species per census; 2 = 2-5 fish; 3 = 6-15 fish; 4 = 16-50 fish; 5 >> 50 fish. We feel that the entire censusable

portion of the fish fauna of a reef was well characterized by this method. Twenty-five reefs were censused in this way at least once (19 eastern pavement reefs; five western, *Porites* reefs; one shore-fringing reef). All but the smallest reefs were censused at least twice, and some were censused three times. In addition to these diurnal censuses, nocturnal censuses were carried out on seven of the reefs. A total of over 100 man-hours were spent censusing. The diurnal census data for each reef (4-6 individual censuses) were averaged, with the larger values weighted more heavily since some species were missed or under-represented in some of the censuses. Although new species (up to 10%) were added to the fauna of a particular reef in censuses subsequent to the first, these additions were invariably present in low abundance, usually category 1, occasionally category 2, or were transient and highly mobile species. A comparison of nocturnal and diurnal censuses on the same reef shows that strictly nocturnal species were always censused in daytime counts but were often numerically under-represented, especially highly cryptic species such as apogonids and pempherids. For most species this under-representation was not extreme (average diurnal abundance = 1.0; average nocturnal abundance = 1.9) and was comparable on all reefs so that diurnal comparisons of nocturnally active species are valid. To obtain additional information on how representative the visual census data were of the fish fauna as a whole, a small natural patch reef just outside the bank barrier reef, adjacent to the study area, was thoroughly censused visually then poisoned with rotenone and all fish collected and counted. Twenty reef-dwelling species not censused in 3 diurnal and one nocturnal visual censuses were collected in the rotenone station. These were all small highly cryptic species rarely encountered in visual censuses: eels (7 spp.); brotulids (2 spp.); apogonids (4 spp.); small serranoids (4 spp.); blennies (2 spp.) and scorpaenids (1 sp.).

The analysis of fish community similarity was carried out in the following way. The average abundance value for each species (i) on each reef (j) was tabulated for all species (n) on twenty-five reefs. Comparisons were then made between the abundances of each species on each possible pair of reefs; for each species on each pair of reefs the lower of the two abundance values was doubled and the results added for all (n) species, then divided by the sum of abundances of all species on both reefs:

$$\frac{2 \sum_{i=1}^n x_i \text{ minimum}}{\sum_{i=1}^n x_i(j) + \sum_{i=1}^n x_i(j+1)}$$

thus obtaining an index of the similarity between the fish faunas of the two reefs being compared. This index theoretically ranges from 0 for two reefs with no species in common, to 1 for two reefs with all species present on both reefs and in the same abundances. The resulting indices of similarity were combined into a matrix following the example of Cody (1974: 92). These data were further reduced by constructing a dendrogram based on the values in the matrix, again following Cody (1974). The resulting dendrogram (Fig. 2) diagrammatically summarizes the overall similarity among the fish faunas of the twenty-five reefs. In the dendrogram, the lower the junction between two units (reefs or groups of reefs) the greater the similarity of their fish faunas.

RESULTS

The degrees of similarity between the fish faunas of different reefs and groups of reefs are summarized in Figure 2. The major dichotomies in fish faunal similarity are correlated with obvious differences in the physical makeup of the reefs on each side of the dichotomy. The greatest dissimilarity (first dichotomy) occurs between the fish faunas of the nineteen pavement reefs (and shore-fringing reef) and those of the five *Porites* reefs. The most likely explanation for this is the profound difference in reef structure between the two groups of reefs. The second dichotomy, within the group of pavement reefs, is between reefs 14a and 14b and all the others. This is primarily due to the extremely small size of those two reefs in comparison with the others (Table 1). The third dichotomy is between the remaining pavement reefs and the small shore-fringing reef, which differs not only in lying along the rocky shore in shallow water (1.5 m maximum depth) and thus having species characteristic of inshore waters (e. g. *Abudefduf taurus*) but also in consisting almost entirely of dense *Acropora palmata*. The fauna of patch reef 12 (dichotomy # 4) is set apart from the remaining reefs, probably because it is a barren reef, having been heavily overgrazed by the urchin *Diadema antillarum* of which a large number were experimentally introduced to the reef three years prior to the present study. The next dichotomy (# 5) separates the faunas of all those pavement reefs having complex habitat (*Acropora palmata* and caves) from the remaining three reefs lacking such habitat (4, 9a, 9b). Among these thirteen reefs, # 1, 16 and 17 (dichotomy # 6) are all high reefs with greater vertical relief than the remaining reefs. Reef 18 also falls into this category, but it is much smaller than the others. Thus, the degrees of similarity of the fish faunas of the various patch reefs can be explained to a large degree by overall gross structural differences in the habitat (reef). At the level of analysis employed to this study it is difficult to further sort out precise parameters of the reefs that determine fish community structure though the spatially complex habitat provided by the large branching coral *Acropora palmata*, and to a lesser extent caves of the appropriate dimension, is one important parameter.

When the actual faunal composition of the thirteen reefs with complex habitat is analysed, it is seen that most of the species (86%) fall into one of two categories: species which are generally widespread and uniformly distributed and species which are uncommon or rare (Fig. 3). Of the total of 122 species censused, 26 species were present on all thirteen reefs in uniform abundance (standard deviation ≤ 1.0 ; Table 2). Eleven additional species occurred on twelve of the thirteen reefs. These thirty-seven generally abundant and uniformly distributed fishes were primarily members of six families: Holocentridae (3 spp.), Pomadasylidae (3 spp.), Pomacentridae (6 spp.), Labridae (4 spp.), Scaridae (5 spp.), and Acanthuridae (2 spp.). Eight additional species were uniformly distributed on all five *Porites* reefs. Of the remaining seventy-seven species, thirty-five were rare and local (three or fewer reefs, abundance less than 2.0) or uncommon (abundance less than 2.0).

The major dichotomy between the fish faunas of the pavement reefs and the *Porites* reefs is reflected in distributions and abundances of many individual species between those two groups of reefs. Inspection of Table 2 reveals that nearly half the total number of species censused (56) were absent from either the pavement reefs or the *Porites* reefs. Twenty-four species were significantly more abundant (Student's t-test, p 0.05) on the pavement reefs than the *Porites* reefs, eleven species were significantly more abundant on the *Porites* reefs, and two species occurred on the fringing reef only.

TABLE 1

Parameters of Tague Bay patch reefs

Reef #	Area (m ²)	Distance from Lagoon Entrance (m)	Water Depth (m)	Max. Vertical Side (m)	Perimeter (m)	Percent Coverage by Caves & <i>A. palmata</i>	Special Features
1	1300	1300	4.5	4.0	130	15% <i>A. p.</i> ; C+	<i>P. parites</i> +, wide halo
2	2500	1100	3.0	2.0	175	5% <i>A. p.</i> ; C+	<i>P. porites</i> ++
3	2600	880	3.5		195	10% <i>A. p.</i>	heavily grazed by <i>Diadema</i>
4	750	770	3.5		110		heavily grazed by <i>Diadema</i>
5	750	770	3.5	3.0	105	50% <i>A. p.</i> ; C+	
6	4600	690	3.5	2.5	325	10% <i>A. p.</i>	
7	350	520	3.0	1.5	70	5% <i>A. p.</i> ; C+	
8	850	630	4.0	3.0	140	50% <i>A. p.</i> ; C++	
9a	200	560	4.0+	3.5	70		heavily grazed by <i>Diadema</i>
9b	200	490	4.0+	3.0	55		heavily grazed by <i>Diadema</i>
11.	1700	450	3.0	2.5	160	20% <i>A. p.</i> ; C++	
12	250	450	3.0	1.5	80		heavily grazed by <i>Diadema</i>
13	1900	365	3.0	2.0	160	10% <i>A. p.</i> ; C+	
14a	5		2.5		10		<i>M. annularis</i> heads
14b	15		2.5		25		heavily grazed
15	3300	245	3.0	2.5	260	5% <i>A. p.</i>	
16	4500	140	4.5	3.5	245	5% <i>A. p.</i> ; C++	southern end with relief & caves
17	900	190	4.5	4.0	115	10% <i>A. p.</i> ; C++	
18	300	190	4.5	4.0	70	50% <i>A. p.</i> ; C+	
A	1800	1450	5.0				scattered heads of <i>P. porites</i> &
D	2400	1650	6.0				<i>M. annularis</i>
E	1200	1680	6.0				<i>M. annularis</i>
P	150	1650	5.0				<i>M. annularis</i>
K	500	2600	6.0				<i>M. annularis</i>
Sh	500	1680	1.5		40	50% <i>A. p.</i>	Shore

TABLE 2

Synopsis of frequency and abundance data on lagoonal patch reef fishes.

	Frequency on 19 pavement reefs	Frequency on 13 pavement reefs	Avg. abundance on 13 pavement reefs	Standard deviation	Frequency on 5 <i>Porites</i> reefs	Avg. abundance on 5 <i>Porites</i> reefs	Standard deviation	Species differing significantly between pavement & <i>Porites</i> reefs
<i>Synodus intermedius</i>	9	7	.62	.65	4	1.20	.84	
<i>Myrichthys acuminatus</i>	1	1	.08	.28				
<i>Gymnothorax moringa</i>	11	10	1.08	.76	1	.20	.45	.05
<i>G. funebris</i>	1	1	.08	.28				
<i>G. vicinus</i>	7	6	.77	1.01	3	.60	.55	
<i>Muraena miliaris</i>	2	2	.15	.38				
<i>Enchelycore nigricans</i>	2	2	.15	.38				
<i>Echidna catenata</i>	1	1	.08	.28				
<i>Fistularia tabacaria</i>	1	1	.08	.28				
<i>Aulostomus maculatus</i>	15	12	2.15	.80	1	.40	.89	.01
<i>Holocentrus ascensionis</i>	18	13	2.77	.93	4	1.80	1.30	
<i>H. rufus</i>	19	13	4.54	.52	5	3.40	.89	.05
<i>Flammeo marianus</i>	4	4	.54	.88	3	1.00	1.00	
<i>Adioryx coruscus</i>	14	10	1.85	1.21	5	2.60	.89	
<i>A. vexillarius</i>	9	8	1.31	1.32	1	.40	.89	
<i>Myripristis jacobus</i>	19	13	3.85	.38	1	.40	.89	.01

<i>Sphyræna barracuda</i>	3	3	.23	.44				
<i>S. picudilla</i>	1	1						
<i>Epinephelus guttatus</i>	17	13	1.85	.55	5	2.20	.84	
<i>E. adscensionis</i>	3	3	.23	.44				
<i>E. striatus</i>	11	9	1.00	.82	5	1.80	.45	*
<i>Cephalopholis fulva</i>	10	9	.69	.48	1	.20	.45	
<i>Petrometopon cruentatum</i>	9	8	.62	.51	2	.40	.55	
<i>Alphistes afer</i>	7	5	.54	.78	1	.20	.45	
<i>Mycteroperca tigris</i>	2	1	.08	.28				
<i>Hypoplectrus puella</i>	17	12	1.85	.90	5	3.40	.55	.01
<i>H. unicolor</i>	6	6	.62	.77	5	2.60	.89	.05
<i>H. nigricans</i>					2	.80	1.10	.05
<i>H. chlorurus</i>					2	.60	.89	.05
<i>H. guttavarius</i>	3	3	.23	.44	4	1.20	.84	.01
<i>Serranus tigrinus</i>	9	7	.77	.83	4	1.40	.89	
<i>S. baldwini</i>	2	2	.23	.60				
<i>Gramma loreto</i>	12	9	1.77	1.64	1	.20	.45	*
<i>Rypticus saponaceus</i>	3	3	.23	.44				
<i>Priacanthus cruentatus</i>	8	7	.77	.83				*
<i>Apogon townsendi</i>	9	7	1.77	2.05	5	3.20	1.30	
<i>A. binotatus</i>					5	3.80	.45	.01
<i>A. maculatus</i>	7	7	1.08	1.12	1	.40	.89	
<i>A. "planifrons"</i>	6	5	.77	1.09	1	.40	.89	
<i>Pheoptyx</i> sp.	14	12	2.85	1.46	1	.60	1.34	.01
<i>Astrapogon</i> sp.	1	1	.08	.28				
<i>Caranx ruber</i>	13	12	1.92	1.26	2	.40	.55	.05
<i>C. fusus</i>	1	1	.23	.83				
<i>Trachinotus falcatus</i>	1	1	.08	.28				
<i>Lutjanus apodus</i>	5	5	.46	.66				
<i>L. mahogoni</i>	8	8	.92	1.12	1	.20	.45	

TABLE 2 (cont.)

	Frequency on 19 pavement reefs	Frequency on 13 pavement reefs	Avg. abundance on 13 pavement reefs	Standard deviation	Frequency on 5 <i>Porites</i> reefs	Avg. abundance on 5 <i>Porites</i> reefs	Standard deviation	Species differing significantly between pavement & <i>Porites</i> reefs
<i>L. analis</i>	6	5	.38	.51				
<i>Ocyurus chrysurus</i>	18	13	2.00	.71	5	2.20	1.10	
<i>Haemulon aurolineatum</i>					1	.80	1.79	
<i>H. chrysargyreum</i>	9	9	2.77	2.09				.01
<i>H. parra</i>	2	2	.23	.60				
<i>H. plumieri</i>	18	13	4.85	.38	4	4.00	2.24	
<i>H. carbonarium</i>	6	4	1.00	1.63				
<i>H. scïurus</i>	14	12	3.00	1.35	4	2.20	1.48	
<i>H. flavolineatum</i>	19	13	4.69	.48	5	4.40	.55	
<i>Anisotremus surinamensis</i>	1	1	.15	.55				
<i>Calamus</i> sp.	1	1	.08	.28	3	.60	.55	
<i>Odontoscion dentex</i>	5	5	.77	1.09				
<i>Equetus acuminatus</i>	10	8	.92	.86				.05
<i>E. lanceolatus</i>	1	1	.08	.28				
<i>Mulloidichthys martinicus</i>	8	8	1.54	1.39	1	.40	.89	
<i>Pseudupeneus maculatus</i>	18	13	3.54	.97	5	2.80	.45	
<i>Pempheris schomburgki</i>	5	5	1.00	1.58				
<i>Gerres cinereis</i>	15	13	2.46	.88	3	1.00	1.00	.01
<i>Eucinostomus</i> sp.								
<i>Kyphosus sectatrix</i>	3	3	.38	.77				
<i>Bothus lunatus</i>	2	2	.15	.38				

<i>Scorpaena plumieri</i>	2	2	.15	.38				
<i>Scorpaenodes caribbaeus</i>	2	2	.23	.60				
<i>Chaetodon capistratus</i>	19	13	2.77	.83	5	3.80	1.10	.05
<i>C. striatus</i>	13	9	.92	.76				
<i>C. sedentarius</i>	1	1	.08	.28				
<i>Pomacanthus paru</i>	2	2	.23	.60				
<i>Holacanthus ciliaris</i>	2	2	.15	.38	2	.60	.89	
<i>Eupomacentrus fuscus</i>	19	13	4.08	.49	3	1.60	1.67	.01
<i>E. planifrons</i>	18	13	4.00	1.00	5	4.60	.55	
<i>E. variabilis</i>	19	13	2.31	.85	5	3.00	.71	
<i>E. leucostictus</i>	19	13	3.62	1.04	5	4.20	.45	
<i>E. partitus</i>	19	13	3.31	.85	5	3.20	1.30	
<i>E. mellis</i>	12	11	1.69	.95	2	.60	.80	.05
<i>Microspathodon chrysurus</i>	16	13	2.62	1.12				.01
<i>Abudefduf saxatilis</i>	11	10	2.00	1.29				.01
<i>A. taurus</i>								
<i>Chromis cyanea</i>	1	1	.08	.28				
<i>C. multilineata</i>	3	2	.15	.38				
<i>Bodianus rufus</i>	13	10	1.38	1.04	2	.60	.80	
<i>Halichoeres bivittatus</i>	19	13	4.23	.73	5	3.00	1.00	.01
<i>H. radiatus</i>	18	13	2.77	.73				.01
<i>H. garnoti</i>	15	11	1.54	1.05	3	1.00	1.00	
<i>H. maculipinna</i>	18	13	2.46	.88				.01
<i>H. poeyi</i>	18	12	2.62	1.12				.01
<i>Thalassoma bifasciatum</i>	19	13	4.62	.77	5	4.00	.71	
<i>Sparisoma rubripinne</i>	10	10	1.85	1.34				.01
<i>S. chrysopterum</i>	13	12	1.69	1.03				.01
<i>S. viride</i>	18	13	3.15	.69	5	3.40	.89	
<i>S. aurofrenatum</i>	16	12	1.62	.77	4	2.00	1.41	
<i>S. radians</i>	13	10	1.92	1.32	1	.40	.89	.05
<i>Scarus vetula</i>	2	2	.46	1.13				
<i>S. croicensis</i>	19	13	4.85	.38	5	4.60	.55	

TABLE 2 (cont.)

	Frequency on 19 pavement reefs	Frequency on 13 pavement reefs	Avg. abundance on 13 pavement reefs	Standard deviation	Frequency on 5 <i>Porites</i> reefs	Avg. abundance on 5 <i>Porites</i> reefs	Standard deviation	Species differing significantly between pavement & <i>Porites</i> reefs
<i>S. taeniopterus</i>	19	13	4.85	.38	5	4.60	.55	
<i>S. coeruleus</i>	10	8	1.08	1.04	5	2.20	.45	.05
<i>S. guacamaia</i>	4	4	.69	1.10				
<i>Ophioblennius atlanticus</i>	11	10	1.77	1.24				.01
<i>Malactoctenus</i> sp.	10	9	1.08	.95	3	.60	.55	
<i>Paraclinus</i> sp.	2	2	.15	.38				
<i>Gnatholepis thompsoni</i>	15	12	2.31	1.38	3	1.60	1.67	
<i>Coryphopterus glaucofrenum</i>	11	10	1.69	1.40	5	4.80	.45	.01
<i>Gobiosoma</i> sp.	19	13	3.38	.87	3	2.20	2.05	
<i>Acanthurus coeruleus</i>	17	13	2.92	.76	3	1.80	1.79	
<i>A. bahianus</i>	19	13	3.46	.78	5	2.60	.55	.05
<i>A. chirurgus</i>	7	6	.69	.85	3	1.20	1.64	
<i>Balistes vetula</i>	2	1	.08	.28				
<i>Monacanthus tuckeri</i>	4	4	.38	.65				
<i>Cantherhines pullus</i>	5	5	.46	.66	2	.40	.55	
<i>Lactophrys triqueter</i>	8	8	.77	.73	3	1.20	1.10	
<i>L. bicaudalis</i>	4	4	.46	.78	2	.60	.89	
<i>L. trigonus</i>	2	2	.15	.38	1	.60	1.34	
<i>Acanthostracion polygonius</i>					1	.40	.89	
<i>Canthigaster rostrata</i>	15	12	1.38	.77	5	3.00	.71	.01
<i>Diodon holacanthus</i>	1	1	.08	.28	2	.80	1.10	.05
<i>D. hystrix</i>	13	12	1.38	.65	2	.40	.55	.01
dactyloscopid sp.					1	.20	.45	

The distributions and abundances of a number of individual species are correlated primarily or secondarily with single physical parameters of the reefs. The most evident of these physical parameters are presented in Table 3 along with the number of species in the present study which are more or less limited by that factor and an example in each case.

TABLE 3

Distribution and abundance of species of fishes

Environmental Parameters	N ^o of Species	Example
Grassbed only	5	<i>Fistularia tabacaria</i>
Large caves	1	<i>Anisotremus surinamensis</i>
Vertical walls or overhangs	1	<i>Gramma loreto</i>
High energy zones	3	<i>Kyphosus sectatrix</i>
Reef flats	2	<i>Eupomacentrus mellis</i>
Proximity to oceanic water	7	<i>Pomacanthus paru</i>
a) source of planktonic food	2	<i>Chromis cyanea</i>
Inshore	2	<i>Abudefduf taurus</i>

Using Randall's (1969) data on the food habits of West Indian reef fishes, all species fell into six main categories (Table 4). The average abundances of the species in each category were summed to obtain a cumulative abundance value for each trophic category. The absolute values for each trophic group has relatively little meaning in terms of total number of individuals present, since a total value of 10 can represent 10 individuals (ten species each with an abundance of 1) or hundreds of individuals (two species each present with an abundance of 5). Nevertheless the relative abundance ranking of the trophic group is probably valid. The overall trophic composition of the thirteen pavement reefs with complex habitat was compared with that of the five *Porites* reefs and was found to be remarkably similar, considering the dissimilarity in species composition and abundance on the two groups of reefs (Table 3). On both groups of reefs omnivores (diet not dominated by one or two items) include the greatest number of species as well as being the most abundant group. This group was dominated by labrids (opportunistic invertebrate eaters), pomadasyids (nocturnal, generalized foragers in adjacent grassbeds) and pomacentrids (primarily highly territorial algal and invertebrate eaters). Herbivores represent the next most abundant group, being dominated by scarids and acanthurids (ranging widely on each reef) and territorial pomacentrids. Herbivores are somewhat underrepresented on the *Porites* reefs compared to the pavement reefs. This certainly correlated with the much lower degree of algal cover on those reefs as well as the sparseness of surrounding grassbeds. Crustacean eaters were dominated by the nocturnally active holocentrids, and to a lesser extent serranids. Planktivores were almost exclusively a nocturnally active group. The absence of diurnally active planktivores is correlated with the dearth of diurnal plankton in the lagoonal waters. Although represented by a moderate number of species (15), piscivores ranked low in overall abundance, as might be expected because of their high rank in the trophic pyramid. The smallest category consisted of a few species of specialized feeders, primarily on sponges or sea urchins.

TABLE 4

*Principal trophic categories of patch reef fishes
(based on Randall, 1967)*

Trophic category & families	No. of species	Avg. and total abundance on 13 pavement reefs	Avg. and total abundance on 5 <i>Porites</i> reefs
HERBIVORES	18	40.39	27.40
Kyphosidae	1	.38	
Pomacentridae	3	9.01	4.60
Scaridae	10	22.16	17.20
Blenniidae	1	1.77	
Acanthuridae	3	7.07	5.60
OMNIVORES	36	69.39	54.40
Carangidae	1	.08	
Pomadasyidae	6	16.31	11.40
Sparidae	1	.08	.60
Mullidae	2	5.08	3.20
Gerreidae	1	2.46	1.00
Chaetodontidae	3	3.77	3.80
Labridae	7	19.62	8.60
Gobiidae	2	4.00	6.40
Pomacentridae	4	12.93	12.00
Monacanthidae	2	.84	.40
Ostraciontidae	4	1.38	2.80
Canthigasteridae	1	1.38	3.00
Diodontidae	2	1.46	1.20
CRUSTACEAN (& FISH) eaters	23	21.32	20.20
Ophichthidae	1	.08	
Muraenidae	1	.08	
Holocentridae	5	11.01	9.20
Serranidae	8	5.93	8.80
Grammistidae	1	.23	
Lutjanidae	2	2.38	2.20
Pomadasyidae	1	.23	
Sciaenidae	2	1.00	
Scorpaenidae	2	.38	

TABLE 4 (cont.)

Trophic category & families	No. of species	Avg. and total abundance on 13 pavement reefs	Avg. and total abundance on 5 <i>Porites</i> reefs
PLANKTIVORES	13	14.94	9.00
Holocentridae	1	3.85	.40
Grammidae	1	1.77	.20
Apogonidae	6	6.55	8.40
Priacanthidae	1	.77	
Sciaenidae	1	.77	
Pempheridae	1	1.00	
Pomacentridae	2	.23	
PISCIVORES	15	10.31	5.20
Synodontidae	1	.62	1.20
Muraenidae	2	1.85	.80
Fistulariidae	1	.08	
Aulostomidae	1	2.15	.40
Sphyaenidae	2	.23	
Serranidae	3	1.70	2.20
Carangidae	2	2.15	.40
Lutjanidae	2	1.38	.20
Bothidae	1	.15	
OTHER	5	3.99	2.80
Holacanthidae	2	.38	.60
Balistidae	1	.08	
Pomadasyidae	1	.15	
Gobiidae	1	3.38	2.20

DISCUSSION

Available evidence suggests that the species composition of reef fish communities may be much more highly structured on Caribbean reefs than on Indo-Pacific reefs where the species pool is much larger (e. g. just over 500 species in the Bahamas. [Böhlke & Chaplin, 1968] compared to more than 1500 species on the northern Great Barrier Reef [Goldman & Talbot, 1976]). Sale (1977) has attributed the high degree of unpredictability of species composition on the Great Barrier Reef to small scale unpredictability of habitat. He has also pointed out that most species are generalists in their requirements for food and living space. The latter appears to hold true for tropical western Atlantic species as well (Randall, 1967; Clarke, 1977). In the present study we have demonstrated a high degree of

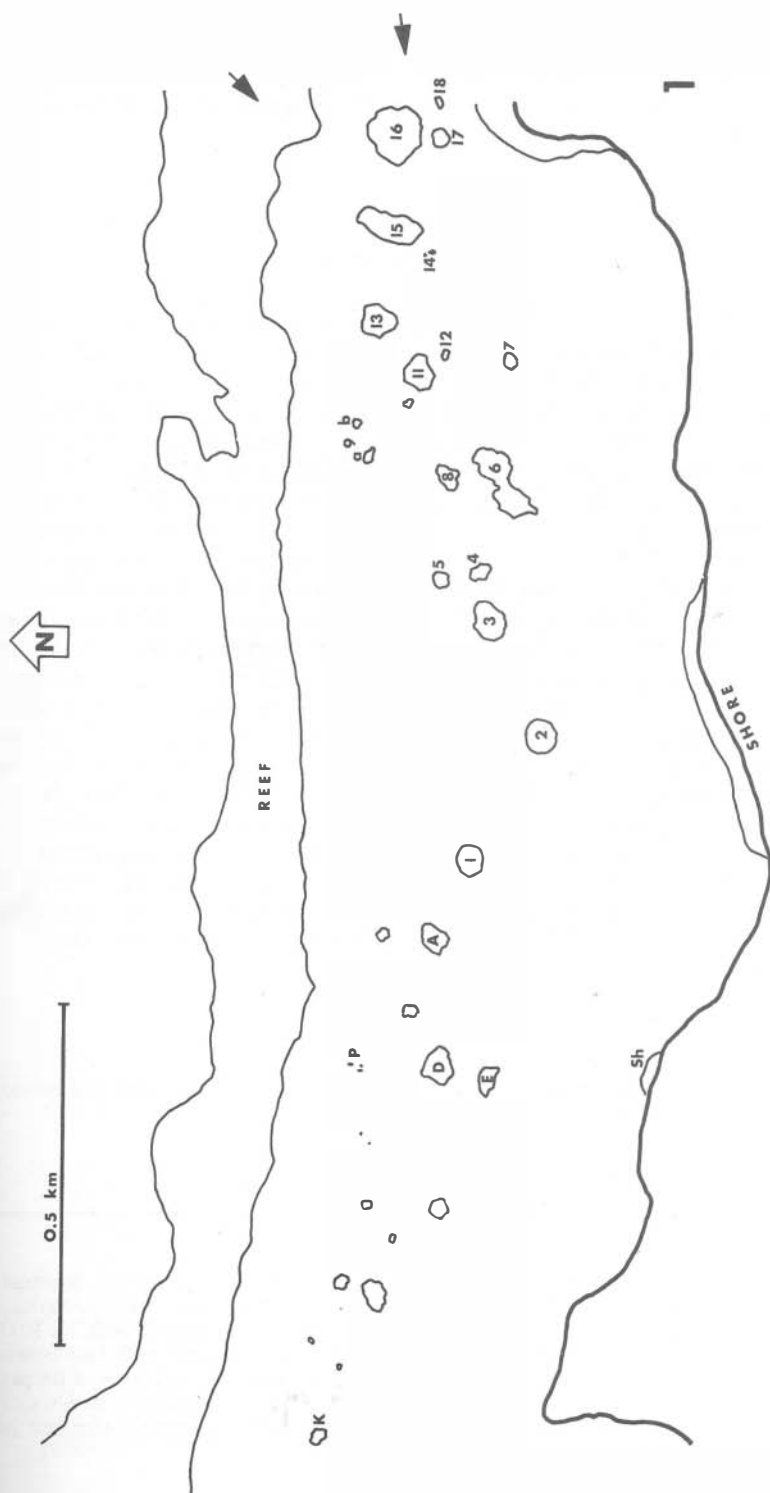
predictability (similarity) of reef fish faunal composition on replicate reefs, correlated with overall degree of similarity in reef structure, in contrast to the views of Sale (1974) and Sale & Dybdahl (1975), that species composition is due to a very large degree to chance recruitment. There are probably two reasons for this discrepancy in views. First the overall species pool on the Great Barrier Reef is much greater than in the Caribbean and it might be expected that within larger species guilds chance may play a greater role in determining the composition of the fauna on a particular reef. The second reason is that those authors worked with very small reef structures, single coral heads (Sale & Dybdahl, 1975) or small block reefs (Russell, Talbot & Domm, 1974), and extrapolation from the results of those studies to much larger reefs may not be entirely valid.

Several major habitat types were distinguished on the reefs studied. These vary along a gradient of increasing spatial complexity from flat carbonate pavement to dense stands of the massive branched coral *Acropora palmata*, although the relationship between fish community parameters (diversity, abundance, biomass) and specific habitat was not quantified, it was quite evident that those parameters did increase as a function of increasing spatial complexity. The habitat sheltering the greatest biomass and diversity of fishes per unit area was the stands of *A. palmata*. Particularly well represented there were crepuscular and nocturnal predators (lutjanids, pomadasysids, holocentrids, serranids).

The relative uniformity of trophic composition among the fish assemblages on reefs of different structure and with quite different species composition lends further support to the idea that there is a high degree of structure and predictability in these fish communities. The actual trophic composition reflects a large degree of dietary dependence on the invertebrate fauna of the reef and surrounding grassbed areas (about 60%). This large and diverse group shows a greater degree of spatial segregation of feeding areas and times than either the herbivores or piscivores; many are nocturnal, many feed in surrounding grassbeds (Ogden & Zieman 1977; Ogden & Ehrlich, 1977), many forage in the water column.

Studies on the movements of many species of tropical reef fishes show that most species are rather sedentary in their habits, ranging over a limited area of reef (Bardach, 1958; Randall, 1962). In particular most species tend not to venture across stretches of flat habitat devoid of reef structures. It is therefore likely, that the overwhelming majority of fishes in the present study are permanent residents of particular reefs. Even species that undergo daily feeding migrations off the reef, such as pomadasysids (Ogden & Ehrlich, 1977) return to the same reef. With the exception of clearly mobile species then, most of the flux in species composition on reefs such as those in the present study is due to mortality and recruitment. Studies are currently underway to evaluate the role of random recruitment in determining the eventual composition of the reef fauna. It is felt however, on the basis of the present work that there are far fewer possibilities for the ultimate composition of the fish community on a reef of a given set of environmental parameters than is the case in the Indo-Pacific.

Fig. 1. Distribution of patch reefs censused in the present study. Reefs A, D, E, K and P are *Porites* reefs. Reefs 1 through 18 are pavement reefs. The principal influx of oceanic water into the lagoon is indicated by the arrows.



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RESUMEN

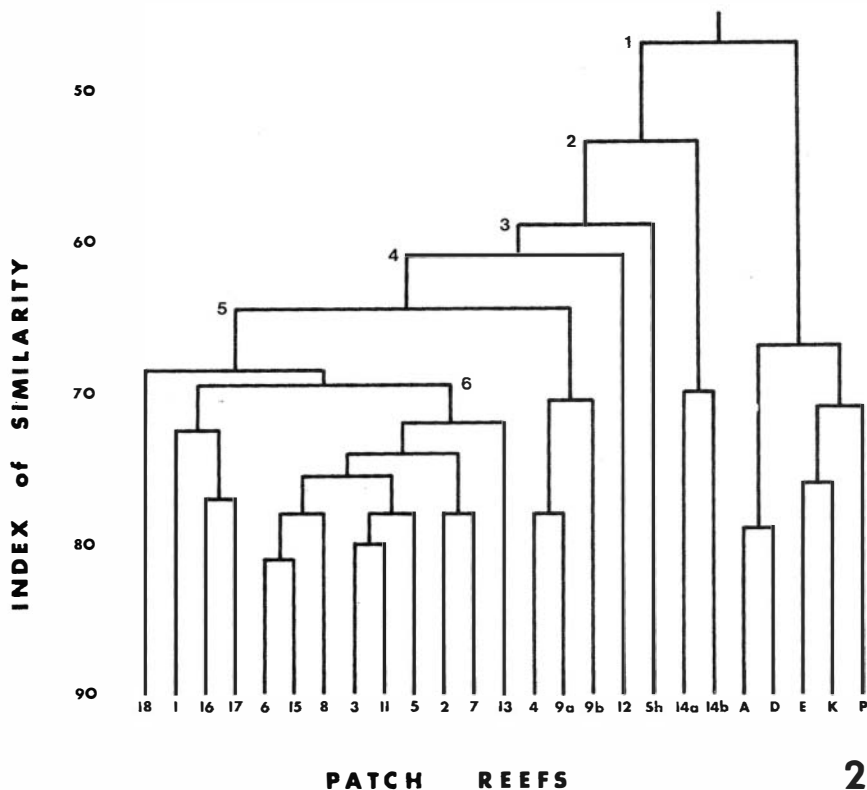
Durante el verano de 1976 se hizo un censo visual de las comunidades ictiológicas en 25 arrecifes naturales en una laguna en el sector noreste de St. Croix en las Islas Vírgenes. Estos arrecifes caen dentro de dos grupos morfológicos: los del este son de pavimentos carbonatados que alcanzan hasta casi la superficie del agua; los del oeste consisten en masas dispersas de corales (*Porites porites* y *Montastrea annularis*) separadas por arena y en aguas un poco más profundas. Los índices de similaridad de la fauna ictiológica se calcularon para todos los pares de arrecifes, basados en las comparaciones de abundancia de todas las especies encontradas. La matriz resultante se usó para construir un dendrograma de la similaridad de la fauna ictiológica que guardó una estrecha relación con las diferencias físicas de los arrecifes. La fauna ictiológica fue determinada por los caracteres estructurales de los arrecifes, encontrándose 45 especies distribuidas uniformemente en los arrecifes similares. La mayoría de las especies restantes eran escasas y poco comunes y de distribución local. La distribución de algunas de las especies tuvo una correlación con algún parámetro físico específico de los arrecifes, tales como la presencia de paredes verticales, cuevas o la proximidad de agua oceánica, o con factores biológicos tales como la abundancia de alimento. De acuerdo con la categoría trófica los omnívoros fueron muy abundantes, seguido por los herbívoros, los que se alimentan de crustáceos, los planctonívoros (en su mayoría especies nocturnas), piscívoros y especies con dietas especializadas (e. g., las esponjas). Aunque los dos grupos de arrecifes (el del este y el del oeste) son morfológicamente muy diferentes, la composición trófica de la fauna ictiológica fue en general muy similar.

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Fig. 2. Dendrogram of the similarity of the fish faunas of twenty-five lagoonal patch reefs. Index of similarity between the various (groups of) reefs is shown on the left. The higher order the dichotomy between two groups of reefs, the less similar the fish faunas of those groups of reefs; e. g. the greatest difference between fish faunas is shown between the faunas of the *Porites* reefs and those of the pavement reefs. At the fifth main dichotomy, a great deal of similarity is shown among the thirteen pavement reefs with complex habitat (primarily *Acropora palmata* stands)



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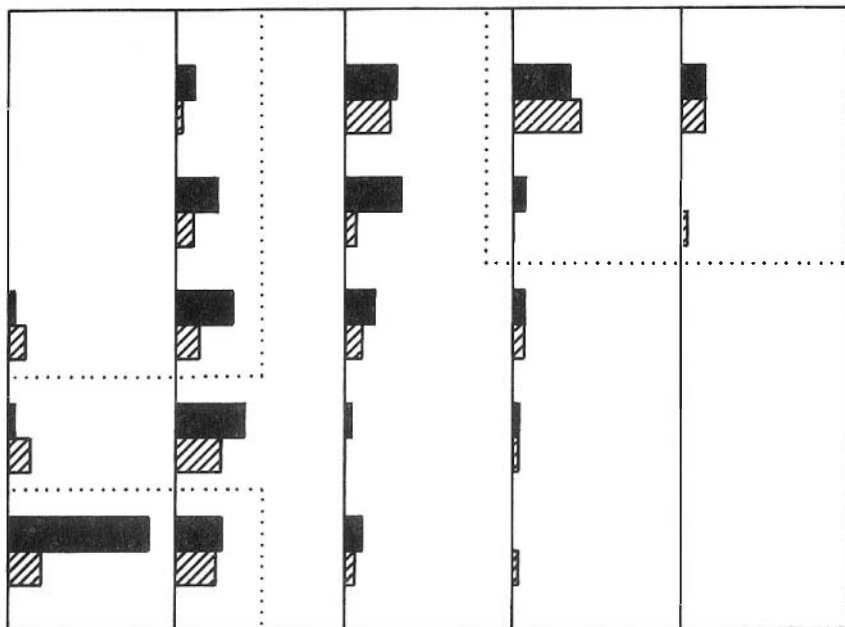
Fig. 3. Fish species distribution and abundance on twenty-five lagoonal patch reefs. Black bars represent numbers of species on pavement reefs (number of reefs indicated on the left), and hatched bars represent numbers of species on *Porites* (rubble) reefs (numbers of reefs indicated on the left). Thus the largest category is species occurring on only 1-3 pavement reefs in abundance category 1 (one individual only).

MEAN ABUNDANCE RANK

1.0 1.1 - 2.0 2.1 - 3.0 3.1 - 4.0 4.1 - 5.0

NUMBER OF REEFS

16-19
(5)
12-15
(4)
8-11
(3)
4-7
(2)
1-3
(1)



correlation coeff = 0.919 (P < 0.001)
0.614 (P < 0.001)

■ pavement reefs

▨ rubble reefs

3

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