



Similarity and Diversity Among Coral Reef Fish Communities: A Comparison between Tropical Western Atlantic (Virgin Islands) and Tropical Central Pacific (Marshall Islands) Patch Reefs

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SIMILARITY AND DIVERSITY AMONG CORAL REEF FISH COMMUNITIES: A COMPARISON BETWEEN TROPICAL WESTERN ATLANTIC (VIRGIN ISLANDS) AND TROPICAL CENTRAL PACIFIC (MARSHALL ISLANDS) PATCH REEFS¹

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Abstract. The fish assemblages of groups of large natural coral patch reefs in the tropical western Atlantic and Pacific oceans were censused visually during the summers of 1976 and 1978. Thirty-one reefs were in the northeastern Caribbean Sea (25 at St. Croix and 6 at Anegada) and 15 reefs were located at the southern end of Enewetak Atoll, Marshall Islands. The degree of similarity among the faunas in each group of reefs (using a similarity index based on the log of individual abundances) was correlated with environmental parameters of the reefs in both regions (complexity of surface topography, reef height, reef area, and position with respect to the main reef, currents and grassbeds). The mean degree of similarity among all the fish faunas in each area was the same at the two major sites (0.61 at Enewetak and 0.62 at St. Croix) as was the similarity among the faunas of the most uniform subset of reefs in each area (0.68 at Enewetak and 0.73 at St. Croix). These comparable levels of similarity suggest similar levels of predictability in the composition of reef fish faunas in the two areas, in contrast to previous studies on very small natural and artificial structures, which suggested a low level of predictability among Pacific reefs (Sale 1978). The discrepancy between our results and those of previous workers in the Pacific is partly a result of differences in the sizes of the reefs studied, being several orders of magnitude larger in the present case. Reef fish diversity was greater at Enewetak (mean number of species per reef = 93; $H' = 5.38$) than at St. Croix (mean number of species per reef = 64; $H' = 4.58$) but equitability values were the same in both areas (0.82 and 0.81, respectively). At both sites fish species diversity was positively correlated with reef surface complexity, projected reef surface area and reef height, but the correlation was higher at St. Croix for all parameters. This was probably attributable to the greater structural similarity of reefs at Enewetak. At Enewetak there was also a correlation between H' and proximity to the main barrier reef. Major differences in the trophic composition of these fish faunas based on available published dietary information indicate that differences between the two sites are accounted for primarily in the proportions of diurnal planktivores and nocturnal general invertebrate feeders. These differences were probably the result of major environmental differences between the two sites: a high oceanic influence at Enewetak, resulting in abundant zooplankton, and the presence of dense grassbed (harboring abundant invertebrates; Randall 1963) surrounding the reefs at St. Croix.

Key words: community similarity; coral patch reef; Enewetak; reef fish; species diversity; Virgin Islands.

INTRODUCTION

The high diversity of coral reef fish communities includes a large within-habitat component (Goldman and Talbot 1976) wherein large numbers of species may co-occur in a very small space (Smith and Tyler 1972). It has recently been suggested by Sale (1977, 1978) that the mechanism of maintaining such great diversity may depend to a relatively large degree on stochastic processes, that is, on the chance arrival of propagules (larvae) at a particular site as well as the unpredictable production of habitable space, rather than on more deterministic factors such as habitat structure, or biological factors such as fine partitioning of food or space resources or specific predator-prey relationships. Other authors (Smith 1978) have emphasized the importance of adaptive responses to

competition or predation in structuring these communities. Sale's interpretation is based primarily on the analysis of the colonization and turnover of the fish faunas of very small structures (one or very few square metres; Russell et al. 1974, Nolan 1975, Sale and Dybdahl 1975) or the apparently random colonization of similar reef space by members of the same guild (Sale 1975). The contemporary or sequential analysis of the faunas of these structures has shown a high degree of variability among replicates. However, because these structures were of such small size and were capable of accommodating only a small fraction of the available species pool, and because the individuals on such small structures usually did not remain long enough to reach adult size (Sale and Dybdahl 1975, Talbot et al. 1978, J. C. Ogdren and W. B. Gladfelter, *personal observation*) it is likely that the unpredictable settlement of species and their relatively high turnover rate may be artifacts of the small scale

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of the habitats studied. Furthermore, these studies were carried out in the western tropical Pacific Ocean. In the western Atlantic Ocean, where the available species pool is presumably much smaller (for example, Goldman and Talbot [1976] cite figures of 398 and 850 species of coral reef fishes on reefs of comparable size in the Florida Keys and at a comparable latitude in the Great Barrier Reef system, respectively) Smith (1973) found a high degree of similarity between replicate samples of small reefs, as did Molles (1978) working in the Gulf of California (also with a small regional species pool). Gladfelter and Gladfelter (1978) also working in the western Atlantic, but with large coral patch reefs, two to four orders of magnitude larger than those used by the aforementioned authors, found a high degree of similarity among fish assemblages, and the degree of similarity of these assemblages was correlated with structural similarities of the reefs. Difficulties in making generalizations about which factors are important in determining the structure of coral reef fish communities seem to result from the fact that previous authors have worked with such small structures that the extrapolation of their results to reefs in general may not be valid, and also that different authors have worked in different oceans with species pools of apparently different magnitudes.

The principal purpose of the present study was to try to overcome these objections and to determine the degree of similarity, or predictability, between the fish faunas of groups of replicate patch reefs in the tropical western Atlantic and Pacific oceans. These groups of reefs were censused by the same workers in both oceans and were of substantial size and comparable oceanographic setting to eliminate artifacts of technique and scale. In addition to determining the similarity of fish communities on these reefs, other aspects of fish community structure were determined—in particular, species diversity and trophic composition. We then hoped to determine any correlation between fish community similarity and diversity and environmental parameters of the reefs themselves.

STUDY SITES AND METHODS

The fish communities of three sets of roughly linear assemblages of shallow-water lagoonal patch reefs were censused visually during the summers of 1976 and 1978 (Table 1). In the northeastern Caribbean Sea the main group lay off the northeastern end of St. Croix (17°45'40"N, 64°35'30"W), and a secondary site lay off the eastern end of Anegada Island (18°40'40"N, 64°17'10"W). The third group, in the western Pacific Ocean, was at the southeastern end of Enewetak Atoll, Marshall Islands (11°22'50"N, 162°21'50"E). The sites were chosen to be as similar as possible within these geographical constraints, in oceanographic setting, water depth, reef spacing, reef size and reef morphology. All three groups lay on the leeward side of barrier reefs. Those off St. Croix were the most la-

goonal due to (1) the presence of an extensive shallow marine bank (mean depth of 20 m) which dampened the amplitude of incoming waves impinging upon the barrier reef and (2) the small tidal amplitude (0.4 m) which further reduced the flow of oceanic water across the reef crest. The principal source of entry of ocean water into the lagoon was at its eastern end rather than across the reef crest. Oceanic plankton were rarely observed in the lagoon. The reefs at Anegada lay farther behind the barrier reef and partly in the lee of the island but were exposed to the prevailing southeasterly currents (B. Brown and R. Dunne, *personal communication*) and the barrier reef faced the open Atlantic Ocean and sloped directly into deep water without a shallow bank; there seemed to be a greater oceanic influence here than at St. Croix. The conditions at Enewetak were clearly oceanic. The study reefs lay close behind the windward barrier which in turn directly faced the open Pacific, without the moderating effect of a shallow bank. The mean tidal range (0.8 m) was greater than in the Atlantic and at high tide a powerful current swept across the reef crest and the study area. Frequently, typical oceanic plankton such as salps and siphonophores were observed in the study area. One subset of reefs at Enewetak lay directly inside the deep entrance to the lagoon without the interposition of a reef. At all three study sites the degree of oceanic influence was ranked on a scale of 1–5, 1 representing the greatest oceanic influence, such as at the deep entrance reefs at Enewetak, 5 being those with the least oceanic influence such as many of the lagoonal reefs at St. Croix.

Twenty-five reefs were studied at St. Croix, spanning a distance of 2.4 km, with a mean closest distance between adjacent reefs of about 0.1 km. The flat expanses between these reefs contained dense seagrass beds (primarily *Thalassia testudinum*) in the east and sparse seagrass (*Syringodium filiforme*) in the west. The depth of the lagoon ranged from 3.0 m in the southeast to 6.0 m in the west. At Anegada the six reefs spanned 2.5 km, with a mean closest inter-reef distance of 0.4 km. Flat expanses of bare sand with sparse filamentous and calcareous algae extended between the reefs. The mean water depth was 4.5 m. At Enewetak the total study area extended 12.0 km. Ten of the reefs spanned 2.6 km beginning just inside Bokandretok (Walt) Island and extending northeast. The mean closest inter-reef distance among these was 0.4 km. A cluster of four reefs lay 4.6 km north of this group inside the deep entrance. A single additional reef lay 4.8 km farther north. Bare sand extended between the reefs. The mean depth of the lagoon around the southwestern group of 10 reefs (and the single northernmost reef) was 5.6 m. The group inside the deep entrance was in deeper water (12.4 m). At Enewetak, only a minority of the reefs in the study area were censused.

The patch reefs at St. Croix were of two fundamen-

TABLE 1. Summary of patch reef parameters.

	Designation	Patch reefs	Oceanographic setting	Length of study area (km)	Mean distance between adjacent reefs (m)	Proximity to barrier reef*	Oceanic influence*	Water depth (m)	Inter-reef habitat	Projected reef area (m ²)	Maximum reef height (m)	Reef surface complexity*	Remarks
Atlantic													
St. Croix			Lagoonal	2.4									
Pavement					80				Dense seagrass				
Complex													
High													
Large	A-1	1, 16, 17				2.3	3.7	4.2		2200	3.8	1.3	
Small	A-2	18				2.0	3.0	4.2		300	4.0	1.0	
Low	A-3	2, 3, 5, 6, 7, 8, 11, 13, 15				3.6	4.7	3.1		2100	2.8	1.9	Flat-topped pavement reefs, edge zone with moderate slope and scattered coral heads and coarse rubble; <i>A. palmata</i> stands and small caves present. Steep wall usually present.
Shore	B					5.0	5.0	1.5		500	1.5	1.0	Shore-fringing reef composed mostly of <i>A. palmata</i> .
Simple													Pavement reefs without complex coral structure; heavily grazed by <i>D. antillarum</i> .
Large	C-1	4, 9a, 9b				3.3	5.0	3.6		380	3.2	5.0	
Barren	C-2	12				3.0	5.0	3.0		250	1.5	4.5	
Small	C-3	14a, 14b				2.0	5.0	2.5		10	1.0	5.0	
Rubble					200	3.8	5.0	5.6	Sparse seagrass	2100	3.0	3.0	Scattered <i>M. annularis</i> and large <i>P. porites</i> heads separated by sand channels.
Large	D-1	A, D								620	1.5	4.0	
Small	D-2	E, K, P											
Anegada		1-6	Intermediate	2.5	400	3.0	4.0	4.5	Sand	310‡	4.3	2.5	Steep-sided <i>A. palmata</i> reefs reaching water surface; numerous deep, interconnected caves; edge zone with heads and coarse rubble.
Pacific													
Enewetak			Oceanic	2.6†					Sand				High, steep-sided reefs with great small-scale surface complexity and some caves.
Lagoonal shelf					400								
Shallow													
Near reef	A-1	5, 7, 11				1.0	2.5	4.9		230	4.2	1.7	
Isolated													
Complex	A-2	1, 2, 3				3.0	3.0	5.7		180	4.0	1.3	
Moderate	A-3	4, 12, 15				3.0	3.3	5.9		150	4.0	3.3	
Simple	A-4	10				4.0	4.0	5.5		100	3.5	5.0	
Deep	B	6				5.0	4.0	12.5		160	6.5	4.0	
Deep entrance					70	3.0	1.0						
High	C-1	8, 9						14.0		170	6.7	2.0	
Low	C-2	13, 14						10.4		145	3.0	3.5	

* Ranked on a scale of 1-5 in which 1 indicates the greatest value (i.e., proximity, oceanic influence, or surface complexity). The values for complexity are not comparable between Atlantic and Pacific reefs because of qualitative differences in surface morphology.

† Excluding the deep entrance reefs and reef 15.

‡ Area of peripheral zone only (central portion was inaccessible).

tally different types (Table 1, Fig. 1). The main group was composed of broad, flat-topped pavement reefs with rubble-covered sloping sides (Fig. 1A). Within this group there were three categories. Thirteen of these reefs (Table 1, Group A) had stands of the very large branching coral *Acropora palmata* (Fig. 1C) and also usually small caves and one steep, vertical or overhanging side; usually >50% of the area of these reefs consisted of flat reef top. The second type was a single shore-fringing reef (B) composed largely of *A. palmata*. The remaining six pavement reefs (Group C)

lacked complex habitat and were heavily grazed by the urchin *Diadema antillarum*. All these reefs were generally of only moderate height above the surrounding substrate (3.1 m including *A. palmata* stands where present and 2.3 m where they were absent); most were comparatively large (mean projected surface area = 1350 m²). The remaining reefs at St. Croix ("head and rubble" reefs; Group D) consisted of scattered colonies of the corals *Porites porites* and *Montastrea annularis* with intervening bands of sand (Fig. 1D). Although surface complexity on coral reefs has

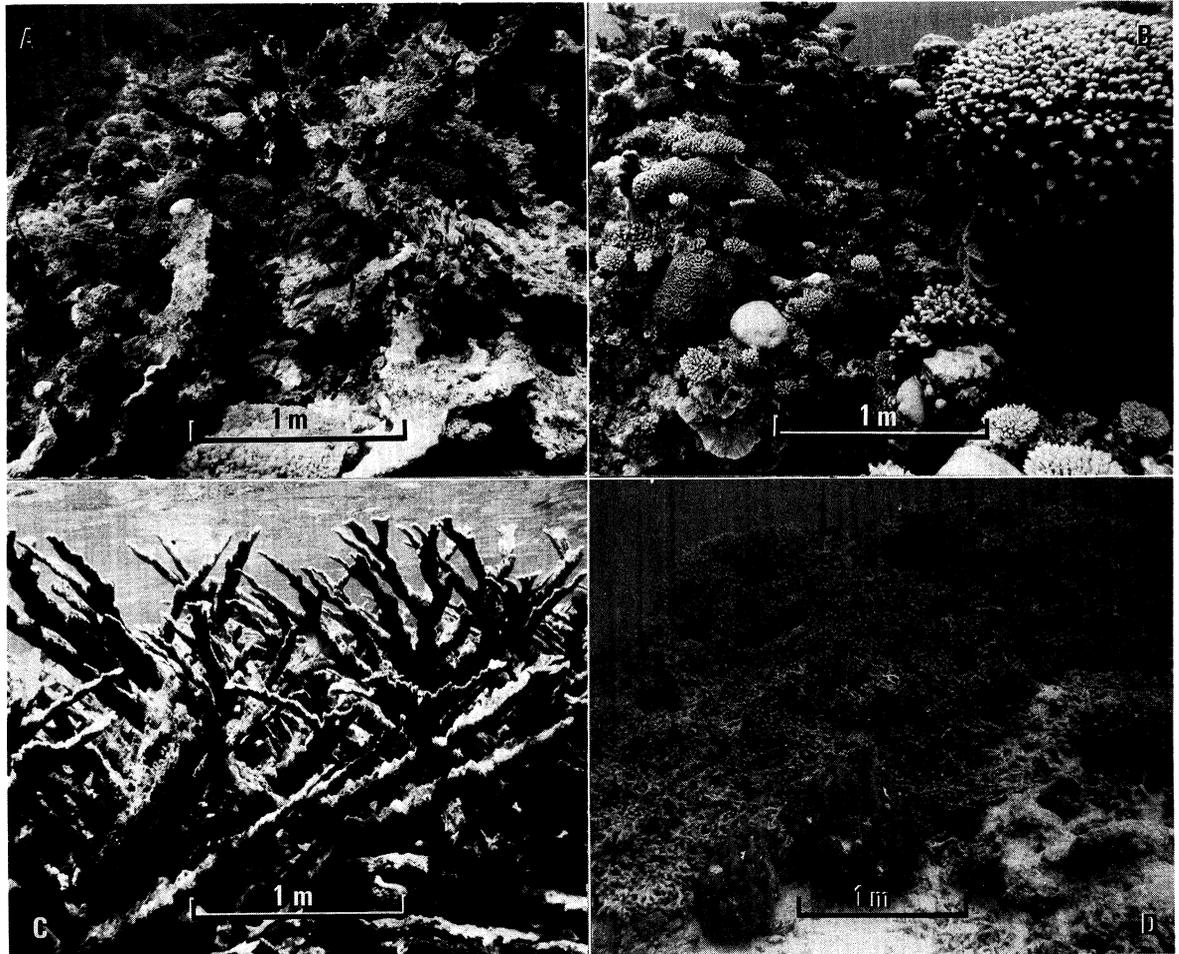


FIG. 1. Structure of principal patch reef habitats.

- A. St. Croix: Edge zone of pavement reef. Most of the structure is composed of dead and broken arms of *Acropora palmata* and small head corals. Coral diversity is low but there is a variety of small-to-moderate-sized spaces for fish refuges.
- B. Enewetak: Typical patch reef surface (reef 3). Coral diversity is high both in terms of species as well as sizes and growth forms of colonies. Refuge spaces are numerous and diverse in size and shape.
- C. St. Croix: Stand of *Acropora palmata*. Monospecific stands such as this with large-scale porosity are suitable as refuges for large fishes and small schools.
- D. St. Croix: Head and rubble reef. Porosity is small scale and relatively uniform, mainly among branches of the finger coral *Porites porites*.

been determined quantitatively by the chain-link method (Luckhurst and Luckhurst, 1978a) we felt that the overall degree of surface complexity of these reefs as well as those at other sites was judged best on a relative basis and was assigned a rank of 1 (most complex) to 5 (Table 1). The six reefs at Anegada were quite uniform in structure, composed of a framework of *A. palmata* partly fused and consolidated by crustose coralline algae, with a great amount of large-scale porosity (of the order of 0.5 m). These reefs rose high (4.2 m) and relatively steeply above the surrounding substrate to the surface (about mean low tide level). Therefore only the sloping periphery of these reefs could be censused and the surface areas presented in Table 1 are for these peripheral zones only. The lower

portions of the sloping sides had numerous coral heads and coarse rubble as at St. Croix. The reefs at Enewetak were generally similar to one another structurally at the level of the differences recognized herein. The reefs were high (4.1 m for the shallow water group and 5.3 m for those in deeper water) and steep sided (often vertical) with complex surface topography on a scale smaller than that of the Atlantic reefs (Table 1, Fig. 1B). Some of these reefs consisted of two or more separate but closely spaced major units (1–2 m apart). Caves of various sizes were usually present. These reefs fell into three groups: ten shallow-water reefs (Group A) located on the lagoonal shelf; one deeper reef on the lagoonal slope (B); and four reefs inside the principal entrance to the lagoon (Group C). Within

each of these principal subsets of reefs at each site there were secondary subsets distinguished by additional structural or other environmental parameters; these will be discussed further under Results.

All reefs were censused visually using SCUBA. Each reef was censused simultaneously by the authors using a standardized census form. Two sets of censuses, usually more than a week apart, were made on nearly all the reefs (except those at Anegada), yielding a total of six censuses per reef (four at Anegada). A total of 140 man-h was spent censusing: St. Croix, 54 h; Anegada, 13 h; Enewetak, 72 h. Individual abundances were summarized in the following categories for each species: I = 1 individual per species per census (≈ 1 h); II = 2–5 individuals; III = 6–10 individuals; IV = 11–25 individuals; V = 26–50 individuals; VI = ≥ 50 individuals. Other techniques such as rotenone stations (Smith 1973) or explosive charges (Talbot and Goldman 1972) may yield quantitatively more accurate data on fish community composition but are considerably more destructive and impractical on the scale used in this study. Of the visually censusable species, there were very few that could not be accurately identified in the field. The main shortcomings of visual censusing in a study of this nature are: (1) Cryptic or nocturnal species are generally underrepresented or not represented in daytime counts. (Nocturnal censuses were carried out on some of the reefs at all three sites and showed that nearly all nocturnal species were censused by day but were numerically underrepresented.) (2) Accurate counts of individuals are difficult, especially in mobile species. However, despite these disadvantages, there was a high degree of consistency in the six (only four at Anegada) replicate censuses made on each reef in this study, and when several visual censuses had been carried out, those species which remained undetected were a predictably highly cryptic group and their absence did not invalidate the comparisons made herein. The great majority of fishes censused on a patch reef at any one time belonged to a sedentary resident reef fauna which either did not move between reefs once they had settled as larvae, or underwent diel feeding migrations to return daily (Bardach 1958, Randall 1961, Hobson 1973, Ogden and Ehrlich 1977). A small fraction, however, belonged to a transient group (roving fish assemblage of Nolan 1975) which appeared to move freely between reefs. Because of the relatively small numerical contribution made by these species it is felt that their inclusion in the analyses did not significantly affect the comparisons.

The analysis of similarity between all pairs of patch reef fish faunas within each of the three study areas was carried out by applying a modified version of Schoener's (1968) index of niche overlap:

$$d = 1 - \frac{\sum |x_i - y_i|}{\sum |x_i + y_i|}$$

where x_i and y_i represent the abundance values for each species i for a total of n species on all pairs of reefs. 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 abundance categories. The advantage of this index is that it considers general level of abundance (roughly on a log scale; see abundance categories above) as well as species presence or absence. The resulting indices of similarity were combined into a matrix and were further reduced by constructing a dendrogram based on the matrix values (Cody 1974).

RESULTS

The mean degree of similarity among the fish faunas of the reefs at St. Croix (0.62) was the same as the mean similarity among those of the reefs at Enewetak (0.61). There was the same mean similarity among the assemblages of the principal subset of 13 pavement reefs with *Acropora palmata* (Group A) at St. Croix (0.73) as among the 6 reefs at Anegada (0.74), but the main subset of 10 shallow reefs (Group A) at Enewetak had a slightly lower mean similarity (0.68; $P < .1$, Student's t test).

The degree of similarity among the fish assemblages of the 25 reefs at St. Croix was a general function of reef structure (Table 1, Fig. 2). The major dichotomies in fish faunal similarity (Fig. 2, St. Croix: I–VII) reflected obvious differences in the structure and to a lesser degree other environmental parameters of the reefs on each side of the dichotomy. The first major division (I) occurred between the fish faunas of the 19 pavement reefs and those of the "head and rubble" reefs (Group D). The second dichotomy, within the group of pavement reefs, set off the faunas of the two very small simple pavement reefs (14a, 14b) from the remaining larger reefs. The third dichotomy was between the remaining pavement reefs and the small shore-fringing reef, which differed in lying along the shore in shallow water and in consisting largely of *Acropora palmata*. The fauna of patch reef 12 (dichotomy IV) was distinguished from those of the remaining reefs probably because it was a barren reef, heavily overgrazed due to the introduction of large numbers of the urchin *Diadema antillarum* 3 yr previous to this study. The next dichotomy (V) separated the faunas of all those pavement reefs having complex habitat (*A. palmata* stands and usually small caves) from the remaining pavement reefs lacking such habitat (4, 9a, 9b). Among those 13 reefs, numbers 1, 16, 17 (and 18) were all high reefs with much greater vertical relief than the others (VI) and were in deeper water; three of these were just inside the entrance to the lagoon. Of these, reef 18 was considerably smaller than the others. A seventh dichotomy divided the faunas of the "head and rubble" reefs into those of the large reefs (A, D) and those of the small reefs (E, P, K). Major differences in fish faunal similarity were

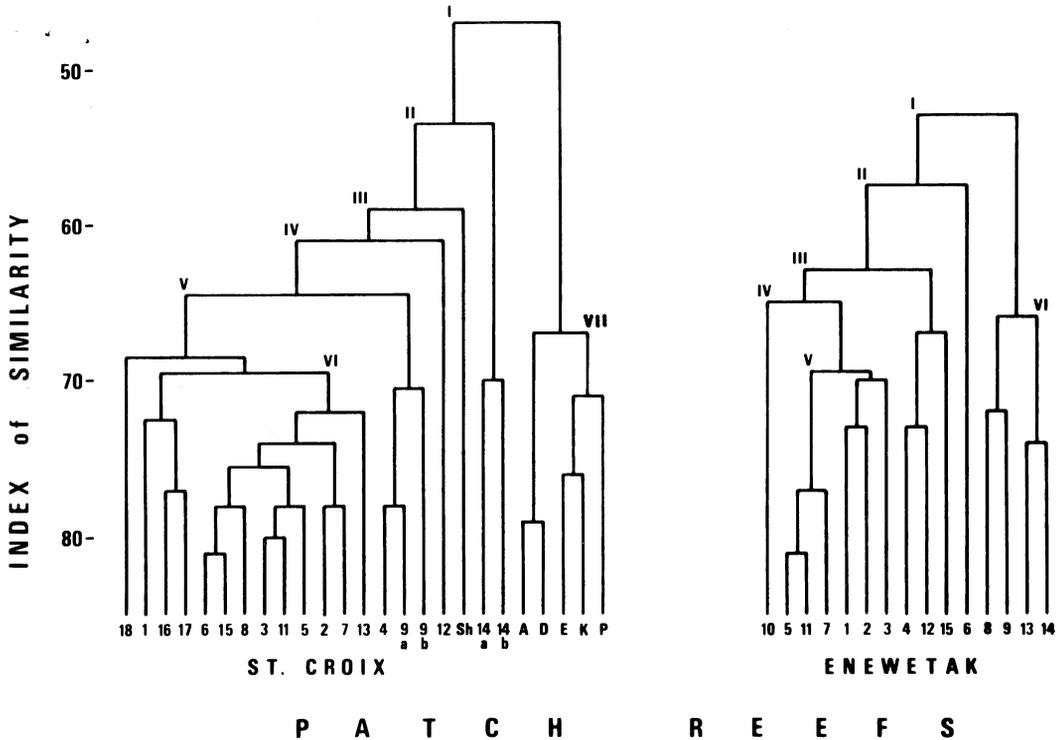


FIG. 2. Similarity among the fish faunas of natural coral patch reefs at St. Croix and Enewetak. Similarity between reefs or groups of reefs theoretically ranges from a minimum of 0 (no fish species in common) to a maximum of 1 (all species present in the same abundance categories). Thus, the uppermost linkages (I) connect groups of least similarity.

thus correlated with gross structural differences of the reefs. Groups of reefs with faunas of increasing degrees of similarity are depicted to scale within contours of similarity in Fig. 3. Although there was some correlation between faunal similarity and position of the reefs, it was probably coincidental to the fact that some of the structurally similar reefs were close together; however, others were not, for example reefs 1, 16 and 17 or 4, 9a and 9b. Furthermore, the study area was environmentally uniform and small (2.5 km) in relation to the larval dispersal range of most of the species present. The high degree of similarity of the faunas of the reefs at Anegada (0.74) reflected the great structural homogeneity among them, as well as the uniformity of other obvious environmental parameters such as position with respect to oceanic influx, depth and sparseness of seagrass surrounding the reefs.

Structurally, the reefs at Enewetak did not show such conspicuous differences as the groups of reefs at St. Croix, but the faunal similarities covered about the same range (Fig. 2). In addition to structural parameters, position of the reefs, especially with respect to the degree of exposure to ocean current, water depth and proximity to the main barrier reef played a role in determining fish community composition as reflected in faunal similarity. The least similarity occurred between the faunas of the group of deep reefs lying inside

the main entrance to the lagoon and all the others (Fig. 2, dichotomy I). The second dichotomy was between the remaining deep reef (6), which lay on the lagoon slope near the southern shallow reefs, and all the shallow reefs. Reefs 4, 12 and 15 (dichotomy III) all had a low proportion of live coral and only moderate surface complexity (Table 1) relative to most of the remaining reefs. The next dichotomy (IV) distinguished the fauna of reef 10 which was in the lee of Bokandretok (Walt) Island and had a low proportion of live coral and low surface complexity. The fifth dichotomy separated the faunas of those reefs which were close to the main barrier reef and were connected to it by rubble zones rather than by sand (5, 7, 11) from the remainder (1, 2, 3). Among the group of reefs inside the deep lagoon entrance the faunas of the two high reefs and the two low reefs could be distinguished (dichotomy VI).

The relative degrees of similarity between the faunas of groups of reefs at various levels in the hierarchy reflected the relative number of species which differed significantly in their distribution between these two groups of reefs. Thus, if we consider the two principal subsets of reefs at each site, at St. Croix 42 (36%) of the fish species censused differed significantly in distribution between the 13 complex pavement reefs and the 5 "head and rubble" reefs (Table 2); at Enewetak

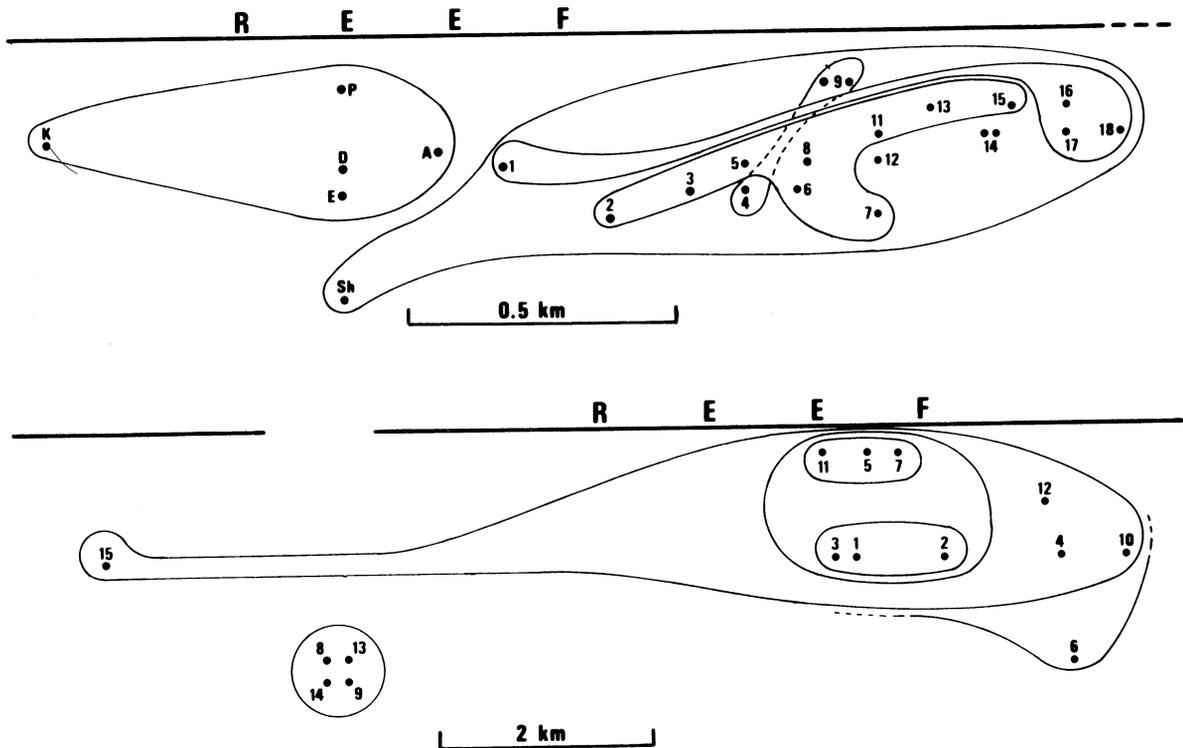


FIG. 3. Spatial arrangement of patch reefs at St. Croix (above) and Enewetak (below). Groups of reefs with similar fish faunas are nested within lines corresponding to the major linkages in Fig. 2. Similarity is correlated less with proximity of reefs than with environmental parameters such as reef structure and position with respect to depth and currents.

52 (29%) of the species differed significantly between the 10 shallow reefs and the 4 deep entrance reefs. Thus at both sites environmental parameters of the reefs determined the distribution and abundance of a large proportion of the species. Those species which were represented only on one subset of reefs at a high

significance level (<.01) clearly were highly specific in their habitat requirements; there were nine such species at each study site (7% and 5% of the faunas, respectively).

TABLE 2. Number of species with significantly* greater abundance on one major subset of patch reefs at each study site.

	Number of species Unique to one subset of reefs			Number of species present on both subsets of reefs		
	P* < .01	.05	.1	.01	.05	.1
Enewetak						
10 shallow reefs	4	5	0	4	9	5
4 deep entrance reefs	5	2	0	9	4	5
St. Croix						
13 complex pavement reefs	8	3	2	6	7	4
5 head and rubble reefs	1	2	0	5	3	1

* Level of significance was determined by applying Student's t test to the mean abundance (by category) of each species on each group of reefs.

Species diversity was clearly greater at the Pacific site than either Atlantic site and this was principally in the species richness component of diversity (Table 3). This was true for the entire study site (Enewetak: 178 species; St. Croix: 122 species; Anegada: 76 species) as well as for individual patch reefs (Enewetak: 93 species per reef, $H' = 5.38$, $J' = 0.81$; St. Croix: 64 species per reef, $H' = 4.58$, $J' = 0.81$; Anegada: 51 species per reef, $H' = 4.82$, $J' = 0.86$). The ratio of the mean number of species per reef to the number of species censused in the entire study area was roughly the same at Enewetak (0.52) and St. Croix (0.55).

The diversities (H') of the groups of patch reef fish faunas distinguished on the basis of their similarities are arranged by rank in Table 3. At Enewetak the mean diversity for the shallow reefs of Group A was significantly higher than for the deep entrance reefs (Group C) which in turn had a greater mean diversity than the deep slope reef (6). Among St. Croix reefs the complex pavement reefs (Group A) had greater diversity than the remainder and the "head and rubble" reefs (Group D) had slightly higher diversity than

TABLE 3. Mean fish species diversities of principal subsets of patch reefs (based on Fig. 2). groups of patch reef fish faunas at each study site are listed in sequence of decreasing diversity (H'). Values are mean \pm standard deviation. Levels of significance (P) are presented only where H' values between adjacent entries differ.

	Patch reef groups	Reefs	H'	P	Number of species per reef	J'	Number of individuals
Major study sites	Enewetak ($N = 15$)		5.379 \pm .240	.001	93 \pm 12	.824 \pm .029	611 \pm 132
	St. Croix ($N = 25$)		4.581 \pm .349	.1	64 \pm 8	.810 \pm .036	848 \pm 309
	Anegada ($N = 6$)		4.819 \pm .120		51 \pm 7	.855 \pm .028	370 \pm 93
Primary subsets of patch reef fish assemblages	Enewetak						
	A ($N = 10$)		5.481 \pm .199	.05	94 \pm 9	.836 \pm .022	619 \pm 79
	C ($N = 4$)		5.236 \pm .153	.2	92 \pm 19	.807 \pm .017	738 \pm 221
	B ($N = 1$)		4.930		87	.765	621
	St. Croix						
	A ($N = 13$)		4.818 \pm .172	.01	64 \pm 8	.805 \pm .015	954 \pm 151
	B ($N = 1$)		4.463		49	.795	539
	D ($N = 5$)		4.426 \pm .332	.4	45 \pm 11	.814 \pm .019	722 \pm 236
	C ($N = 6$)		4.215 \pm .303		36 \pm 7	.822 \pm .072	312 \pm 125
	Secondary subsets of patch reef fish assemblages	Enewetak					
A-1		5, 7, 11	5.627 \pm .042	.2	104 \pm 6	.840 \pm .010	641 \pm 122
A-2		1, 2, 3	5.502 \pm .103		92 \pm 7	.844 \pm .006	599 \pm 99
A-3		4, 12, 15	5.456 \pm .203		90 \pm 3	.840 \pm .029	611 \pm 41
C-1		8, 9	5.369 \pm .005	.001	109 \pm 2	.794 \pm .004	901 \pm 49
C-2		13, 14	5.104 \pm .003		76 \pm 6	.819 \pm .016	574 \pm 194
A-4		10	5.056		84	.789	639
B		6	4.930				
St. Croix							
A-1		1, 16, 17	5.044 \pm .161	.01	74 \pm 10	.813 \pm .004	998 \pm 81
A-3		2, 3, 5, 6, 7, 8, 11, 13, 15	4.757 \pm .113		61 \pm 5	.803 \pm .017	924 \pm 170
D-1		A, D	4.753 \pm .040		56 \pm 6	.825 \pm .025	944 \pm 22
A-2		18	4.691		59	.797	1061
B		Shore	4.463				
C-1		4, 9a, 9b	4.315 \pm .090		41 \pm 5	.805 \pm .019	396 \pm 35
C-3		14a, 14b	4.299 \pm .428		29 \pm 1	.886 \pm .101	158 \pm 67
D-2	E, P, K	4.207 \pm .202	.5	37 \pm 5	.807 \pm .014	574 \pm 172	
C-2	12	3.750		33	.744	365	

the simple pavement reefs (Group C). Among the secondary subsets of reefs, at Enewetak those closest to the main barrier reef had higher diversity than the remainder; among the deep entrance reefs, the high reefs had greater diversity than the low. At St. Croix, among the complex pavement reefs the high reefs were most diverse; differences between other adjacent subsets were nonsignificant. In terms of species numbers, the patterns were similar, with the most notable exception, at Enewetak, of the high deep entrance reefs which had the highest mean number of species but were intermediate in rank in terms of H' .

Species diversities (both H' and species number) were ranked at each study site and showed significant correlations (Spearman Rank Correlation Coefficient) with some of the principal environmental factors (Table 4). At St. Croix there was a high correlation of both H' and species number with reef surface area, reef surface complexity and reef height (in that order).

At Enewetak both H' and species number were significantly ($P < .05$) correlated only with surface complexity. Species number was correlated with both reef area and height and H' was also correlated with proximity to the main reef.

Of the 42 families of teleosts represented in these two study areas, 26 were shared between the two sites (Table 5). Of the remaining 16 (9 at St. Croix, 7 at Enewetak) only 1 (Pomadasyidae, St. Croix) was present in large numbers. The species distributions within some of the families present were greatly unequal between the two sites, especially in the case of the Labridae (Pacific: 40 species; Atlantic: 7 species), Chaetodontidae (Pacific: 20 species; Atlantic: 5 species), Acanthuridae (Pacific: 14 species; Atlantic: 3 species), Pomacentridae (Pacific: 22 species; Atlantic: 11 species), and Pomadasyidae (Pacific: none; Atlantic: 8 species). A similar pattern was seen in terms of the total abundances within families, a few families show-

TABLE 4. Spearman rank correlation coefficients (r_s) between fish species number and diversity and environmental parameters of patch reefs; z = coefficient of determination.

	Reef surface complexity (rank)		Reef surface area (m ²)		Reef height (m)		Proximity to main reef (rank)		Oceanic influence (rank)	
	H'	No. species	H'	No. species	H'	No. species	H'	No. species	H'	No. species
St. Croix ($N = 25$)										
r	.70	.70	.78	.76	.54	.57	-.06	-.18	.12	.14
z	3.43	3.44	3.82	3.73	2.66	2.77	-.32	-.90	.60	.68
P	<.001	<.001	<.001	<.001	<.01	<.01	NS	NS	NS	NS
Enewetak ($N = 15$)										
r	.60	.67	.25	.72	.04	.66	.81	.37	.10	.23
z	2.23	2.50	.95	2.70	.16	2.49	3.05	1.38	.39	.86
P	<.05	<.05	NS	<.01	NS	<.05	<.01	NS	NS	NS

ing very large differences in individual abundances between Atlantic and Pacific sites, especially Lutjanidae, Pomadasysidae and Scaridae (Table 5). The standard deviations of abundances (Table 5) provide a general measure of the evenness of distribution of families among the reefs of the two areas. In general a standard deviation less than the mean indicates a relatively even distribution among patch reefs; a standard deviation of <50% of the mean indicates a very uniform distribution among patch reefs; a standard deviation more than twice the mean indicates a very patchy distribution.

Many families of tropical reef fishes show trophic homogeneity within broad limits. Using the available data on the food habits of reef fishes (Hiatt and Strasburg 1960, Randall 1967, Vivien 1973, Hobson 1974) along with behavioral observations it was possible to categorize nearly all the families of fishes censused by general food types: plants (H), plankton (P), other invertebrates (I), crustacea (C) or fishes (F). Because of the incompleteness of the food data for Pacific species, the proportional breakdown of food categories in some of the families which fell into more than one group was difficult. Herbivores and plankton feeders (planktivores) formed relatively distinct and readily recognized groups because of their specialized mode of feeding or processing food (Davis and Birdsong 1973, Ogden and Lobel 1978). The distribution of fishes at the two major study sites among the five general trophic categories is presented on the basis of individual abundances in Table 6. The abundance of individual herbivores was greater at St. Croix, although more species were present at Enewetak. Diurnal planktivores were clearly greater at Enewetak and reflected the greater abundance of plankton visible in the water column by day. Nocturnal (N) plankton feeders (based on diurnal censuses in both areas) were slightly more abundant at Enewetak. Of the fishes feeding primarily on benthic invertebrates, there was a much higher degree of utilization of crustacea at Enewetak. Noctur-

nally active invertebrate generalists comprised nearly one-fourth of the fauna at St. Croix and consisted primarily of pomadasysids, which foraged in surrounding grassbeds. Piscivores were slightly more abundant at Enewetak.

DISCUSSION

Studies of the colonization patterns and sequential changes of the fish faunas of very small replicate reefs or reef-like structures have shown that the fish communities of such structures have a high species turnover rate and do not appear to reach species equilibrium. Moreover, identical structures supported faunas which were unpredictable, insofar as replicates showed very low similarity (Russell et al. 1974, Nolan 1975, Sale and Dybdahl 1975, Talbot et al. 1978). Based on such studies, all carried out in the tropical western Pacific Ocean, Sale has embraced the view that the structure and high diversity of reef fish communities is largely determined by stochastic factors, namely the chance recruitment of larvae to unpredictably available habitat. Studies carried out in other areas, however, have suggested that species equilibrium is indeed achieved in coral reef fish communities and that stochastic factors are less important in the determination of these communities. A high degree of similarity of the fish faunas of small replicate reefs was found by Smith (1973) in the tropical western Atlantic and by Molles (1978) in the eastern tropical Pacific. Smith and Tyler (1975) found the fish faunas of two large coral heads in the Virgin Islands and the Bahamas to be very similar after periods of 1 and 3 yr, respectively. Gundermann and Popper (1975) found that the fish faunas that developed on coral heads in the Red Sea after their defaunation by poisoning were very similar to those existing beforehand. Our present analysis of the fish communities of very large (compared to previous studies) natural patch reefs has shown a high degree of similarity among similar reefs at sites in both oceans. Since the faunas of the reefs

TABLE 5. Composition of patch reef fish communities.

	Trophic category*	St. Croix				Enewetak		
		No. species	No. individuals		No. Species	No. individuals		
			Mean	SD		Mean	SD	
Synodontidae	F	1	.8	1.0	2	3.1	1.8	
Muraenidae	CF	6	2.1	2.6	1	.1	.4	
Aulostomidae	FC	1	2.9	3.0	1	.1	.4	
Syngnathidae	C	0			1	2.4	1.8	
Holocentridae	C(N)	5	47.1	31.6	7	11.6	9.9	
	P(N)	1	14.1	10.3	4	27.6	22.3	
Serranidae	FC	14	14.3	13.1	12	19.0	10.5	
	P	0			1	13.9	26.6	
Grammidae	P	1	5.8	15.4	0			
Grammistidae	C(N)	1	1.0	1.9	0			
Priacanthidae	P(N)	1	3.4	5.8	1			
Apogonidae	C(N)	5	19.3	24.8	4	12.6	23.2	
	P(N)	1	10.7	20.6	1	20.5	24.6	
Cirrhitidae	C	0			2	3.9	2.7	
Parapercidae	C	0			1	1.1	.7	
Carangidae	F	3	4.5	7.6	1	1.1	1.9	
Lutjanidae	FCI	3	2.9	6.8	9	29.1	32.3	
	P	1	4.0	3.3	1	29.7	34.3	
Lethrinidae	F	0			2	1.7	1.9	
Pomadasyidae	I(N)	8	≈200	≈100	0			
Sparidae	I	1	.2	.4	1	10.2	18.6	
Sciaenidae	P(N)	3	1.8	2.5	0			
Mullidae	I	2	18.8	16.9	5	22.3	22.4	
Pempheridae	P(N)	1	2.9	7.3	1	.1	.3	
Gerreidae	I	1	4.3	5.5	0			
Kyphosidae	H	1	.9	3.0	1	.1	.4	
Chaetodontidae	IH	5	13.1	11.4	15	17.7	9.2	
	H	0			5	16.8	8.6	
Pomacentridae	HI	9	106.9	68.7	8	69.5	34.4	
	P	2	.2	.4	14	102.4	77.8	
Labridae	IC	7	90.2	63.4	40	88.1	28.9	
Scaridae	H	9	≈200	≈75	10	31.9	13.2	
Dactyloscopidae	P(N)	1	.1	.4	0			
Acanthuridae	H	3	24.7	16.4	11	53.2	18.4	
	P	0			3	5.4	12.3	
Zanclidae	I	0			1	1.5	1.4	
Siganidae	H	0			1	.5	.8	
Gobiidae & Eleotriidae	HP	3	39.4	42.2	1	1.5	2.5	
Blenniidae & Clinidae	HC	3	3.8	6.5	4	8.1	8.3	
Sphyrnaeidae	F	1	.1	.3	0			
Scorpaenidae	FC(N)	2	.2	.8	2	.2	.4	
Bothidae	FC	1	.1	.3	1	.1	.4	
Balistidae	I	1	.1	.3	2	1.2	2.2	
Monacanthidae	C	2	.6	1.2	3	1.3	2.2	
Ostraciontidae	I	4	1.8	3.4	1	.1	.3	
Tetraodontidae	I	1	3.5	5.4	3	1.1	1.7	
Diodontidae	I	2	1.5	1.3	0			
Total		116	848		178	611		

* N = nocturnal. Food types: H = plants; P = plankton; I = other invertebrates; C = crustacea; F = fishes.

in both areas have presumably had the benefit of long periods of time (relative to previous studies) to develop, we feel that the high degree of similarity among similar reefs reflects the attainment of species equilibrium and indicates a constancy of composition not explainable by stochastic factors alone. The apparent discrepancies among previous studies in results and interpretation of the factors most important in structuring reef fish communities are undoubtedly a result of the relative sizes of the reefs studied and also the relative sizes of the available species pools supplying those reefs.

Although the random settlement of larvae on reefs undoubtedly plays a role in determining which species ultimately occupy a particular reef, for example among similar species of a particular feeding guild (Sale 1975), other determinants are clearly at work. In the present study we have shown that overall habitat structure as well as location with respect to currents, depth and grassbeds play an important role in determining fish community structure.

At St. Croix in particular, the high correlation between fish community similarity and patch reef structure has indicated the importance of reef structure as

TABLE 6. Summary of major trophic categories of patch reef fishes.*

Principal food category	Principal activity period	St. Croix			Enewetak		
		Mean no. individuals per reef	% of total individuals	Approximate no. species	Mean no. individuals per reef	% of total individuals	Approximate no. species
Plants	Diurnal	329	38.8	22	156	25.5	37
Plankton	Diurnal	10	1.2	4	151	24.7	20
	Nocturnal	30	3.5	8	48	7.9	8
Crustacea	Diurnal	11	1.3	8	100	16.4	34
	Nocturnal	69	8.1	21	24	4.0	11
Other invertebrates	Diurnal	180	21.5	28	108	17.7	49
	Nocturnal	200	23.3	8
Fish	Diurnal and nocturnal	18	2.1	17	31	5.0	19

* Based on data in Hiatt and Strasburg (1960), Randall (1967), Vivien (1973) and Hobson (1974) and personal observations.

a determinant of fish community structure. A number of authors have stressed the importance of particular types of refuge space on reefs in determining fish community composition (Smith and Tyler 1972, Nagelkerken 1974, Luckhurst and Luckhurst 1978b). Talbot et al. (1978) have shown significant differences in the fish communities of some groups of small block structures with different pore sizes. In the present study we showed that a large number of species (36%) at St. Croix differed significantly in their distribution and abundances between the two major types of reefs. A certain amount of habitat specificity is implied in these results. In the only detailed quantitative study of habitat specificity among reef fishes, Clarke (1977) showed varying degrees of specificity among the chaetodontids and pomacentrids of Bimini (Bahamas); however, factors in addition to substrate morphology (such as depth) were involved in that study.

The correlation of fish community composition with the proximity of patch reefs to currents and grassbeds and possibly water depth as well was related to the trophic importance of these variables. The correlation between fish community composition and the proximity of a particular foraging grounds was most evident between the shallow and deep entrance reefs at Enewetak. Planktivores (and water column piscivores) constituted the most obvious ecological group which differed significantly between these two sets of reefs; half the species occurring significantly more abundantly on the deep entrance reefs (Table 2) belonged to this guild (Hobson and Chess 1978, working at approximately the same sites as we did, have pointed out these differences). Other differences were not so obvious. At the Atlantic sites the density of seagrass beds around the patch reefs had an effect on the composition of the fish fauna, as pointed out by Randall (1963) in his comparison of the fish communities of a large artificial reef in a grassbed and a shore-fringing reef in the Virgin Islands. In our study, the abundance and diversity of grassbed-foraging pomadasysids (see

Randall 1963, Ogden and Ehrlich 1977) was positively correlated with seagrass density: highest on the pavement reefs at St. Croix, intermediate on the rubble reefs at St. Croix, and lowest on the Anegada reefs where seagrass was absent. The low individual abundance value of nocturnal general invertebrate feeders on the Enewetak reefs may be due to the absence of this important category of foraging ground.

The diversities of patch reef fish communities at both Enewetak and St. Croix showed a high correlation with obvious structural parameters of the reefs, particularly surface complexity, reef area and reef height. These parameters are analogous to those that have been shown to be important correlates of species diversity of island and other terrestrial communities (MacArthur 1972, Lack 1976). Surface complexity (or small scale spatial heterogeneity) has been shown to be positively correlated with species diversity in a number of communities including coral reef gastropods (Kohn 1967) and birds (MacArthur 1964). In studies of the fish communities of natural reefs it has also been clearly demonstrated that species diversity is a function of substrate complexity (Risk 1972, Luckhurst and Luckhurst 1978a). Molles (1978) has shown a correlation between the height and area of small natural and artificial reefs in the Gulf of California and species diversity at most times of the year. At Enewetak the correlation between species diversity and these structural parameters of the reefs was not as great as at St. Croix; Enewetak reefs were not as variable in their range of size or morphology, even though they covered a greater range of height. Although there was no correlation between diversity and position with respect to environmental variables at St. Croix, there was a correlation between H' and proximity to the main barrier reef at Enewetak, suggesting that patch reefs closer to the main reef received (more) immigrants from the larger source.

On the basis of the correlation between fish community similarity and the similarity of patch reef pa-

rameters, as well as the correlation between species diversity and structural parameters of the reefs, we conclude that the high diversity of coral reef fish communities is permitted by a variety of factors other than random recruitment of larvae alone; of these, habitat structure is the most evident. Furthermore, the same factors are operating in both oceans, although their proportional roles may differ. Differences in within-habitat diversity between Atlantic and Pacific sites can be explained partly by the greater availability of resources (e.g., plankton or greater spatial heterogeneity) at the latter, but undoubtedly other factors, as yet not clarified, are operating.

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