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DETERMINANTS OF COMMUNITY STRUCTURE FOR CORAL REEF FISHES IN AN EXPERIMENTAL HABITAT¹

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Abstract. We examined the patterns of distribution of species of resident fishes in an experimental habitat consisting of 10 small live colonies of the coral *Acropora pulchra* (L-units), and 10 similar sized pieces of eroded coralline rock (D-units). Approximately every 4 mo for 2 yr, all fish in each unit were collected. Numbers collected were similar at all times to numbers in control units that were not disturbed.

A total of 630 fishes and 56 species were collected; most species were rare in our sample. Greater numbers of fish and of species were collected when recruitment had taken place during summer months. Greater numbers of fish and of species were collected from L- than from D-units.

Only three species were demonstrated to be seasonal in recruitment. No temporal partitioning of the habitat was demonstrated.

Five common species showed marked preferences for L-units, but most species did not make this discrimination. Comparisons of samples from L-units with samples from D-units showed somewhat less faunal similarity than comparisons between samples from the same type of unit.

There was no evidence that fishes occupying units of one type partitioned the habitat on the basis of precise microhabitat requirements that would have caused particular species to occur consistently in particular units. There was no indication that any pair of species mutually excluded each other from units.

With the exception of those few species which distinguished D- and L-units, we conclude that the distribution of species among units is a result of chance colonization, not of a systematic partitioning of the living space provided. We anticipate this conclusion to have general validity for reef fish communities. Some consequences for our understanding of the small-scale distribution of fishes on coral reefs are discussed.

Key words: *Chance; coexistence; colonisation; community structure; coral reef fish; Great Barrier Reef; living space; resource partitioning.*

INTRODUCTION

It has long been recognized that communities of fishes found on coral reefs are rich in species and diverse. It is also recognized that much of this richness is of a within-habitat type, and collections of fish from small areas of reef yield large numbers of species. For example, Smith (1973) reported that in the Bahamas, 70-80 species of fish can commonly be collected from single coral patches no more than 3 m in diameter. Goldman and Talbot (1975) have collected up to 150 species from single rotenone stations on One Tree Reef, southern Great Barrier Reef.

It is also becoming accepted that the majority of species of reef fishes are remarkably sedentary animals, and that they generally produce numerous pelagic, and hence, dispersive larvae, over extended breeding seasons (Smith and Tyler 1972, Reese 1973). Thus the groups of fishes collected from small regions of reef can be expected to be predominantly resident fishes.

What are the determinants of the diversity and

of the species composition of fishes found in such a small area of reef? There appear to be two alternative views of such communities. One is that they are interactive communities made up of species specialized in various ways, and thus effectively partitioning the resources of the environment among them. Only those potential colonists adapted to the physical environment, and to coexistence with the species already present in a site can successfully become part of such a community. The other view is that they are the result of purely chance colonization by species with broad, and largely overlapping, requirements, which do not interact with each other sufficiently for this to shape the community being formed. These can be termed (with apologies to R. M. May 1974), respectively, the order and the chaos views of community structure.

If the order view is correct, we might expect that the differences in species composition from place to place, even within quite small areas of reef, can be explained by slight differences in the places resulting in colonization by differently adapted species. Visited a number of times, a single place might be expected to support a constant assemblage of species,

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or perhaps one of a small number of distinct, but mutually exclusive sets of species.

The chaos view says that chance alone is responsible for the differences in species composition from place to place. It predicts that the species present at one site will vary randomly over time as old residents die and new colonists arrive.

It seems unlikely that either view can totally account for the distribution of species of fish on a reef. However, to the extent that the chaos view holds, the availability of the various species as colonists will be of prime importance in determining community structure. To the extent that the order view holds, the particular requirements of each species will determine community makeup.

We have attempted to determine the relative importance of patterns of colonization and degree of specialization in determining the structure of fish communities formed in one type of reef habitat—the single isolated colony of coral. To this end a series of small colonies of coral, some living and some dead, have been permitted to become colonized by fish on six successive occasions over a period of 2 yr. This paper examines the diversity, the species composition, and the species similarity of the communities formed.

METHODS

The experiment was conducted at Heron Reef (23°27'S lat., 151°55'E long.) in the Capricorn Group, at the southern end of Australia's Great Barrier Reef. In May 1972, 10 small pieces of eroded coralline limestone 25–30 cm in diameter were collected above low tide level on Heron Cay. They consisted principally of old colonies of *Acropora cuneata* (Dana). These were embedded in concrete bases, cured for 1 wk while submerged on the reef flat, and transported to the experimental site. Ten small colonies of living coral (*Acropora pulchra* [Brook]), also 25–30 cm in diameter, were collected from the reef flat, and transported, still submerged, to the experimental site. Without being removed from the water, they were tied with polypropylene rope to concrete bases 40 cm in diameter and about 10 cm thick. These bases had been poured at the same time, and cured in the same manner as those in which the pieces of coralline rock were embedded.

The colonies of living coral are subsequently referred to as L-units, those of coralline limestone, as D-units. The L- and D-units were set out in a 4 × 5 unit rectangular grid on a sand patch on the reef flat ≈ 200 m from the southern reef crest. Units were randomly allocated to grid positions. They were spaced 2 m apart, center to center. The water at the experimental site was up to 3 m deep at high

tide and about 0.7 m deep at low tide. All units were completely submerged at all times.

There has been some minor destruction during the 2-yr course of the experiment, but the majority of L-units increased markedly in size, and small colonies of living coral have developed on all of the D-units. Units were not carefully measured when first set out, but in September 1973 and again in September 1974 all units were measured. The maximum height, longest horizontal diameter, and the maximum dimension at right angles to these were each measured to the nearest 5 cm. The product of these served as a crude measure of unit volume.

We have collected fishes approximately every 4 mo for a total of six collections over 2 yr. After the first collection two L- and two D-units were randomly chosen as controls. They were not disturbed again.

Fish were collected from a unit by surrounding it with a fine-meshed net at low tide. Then the unit was lifted out of the water. All fish remaining in the unit and those trapped in the net were captured. Units were resubmerged within 2 min. Inevitably there were some escapes, but our visual censuses at high tide, before and within 24 h after the collection, indicated that few fish were missed. Control units were censused at these times.

Only the fish actually captured have been considered here. Occasionally, species which occurred in small schools in the vicinity of the grid became trapped when fish were collected. Whenever 15 or more individuals of a single schooling species were recovered from a unit, that species was not considered to be a member of the community of fish present there. Small schools of fish did not remain resident in a single unit but moved about the grid and to coral beyond the grid. All fish collected were preserved for identification.

In analyzing the data we have considered separately the collections from each L- and each D-unit at each collection time, as well as larger samples formed by pooling these collections. In particular we have examined samples formed by pooling all six collections from a single unit (termed L-over-Time and D-over-Time samples) and samples formed by pooling all collections from one type of unit at a single time (L-over-Unit and D-over-Unit samples). The total samples of fishes from all units of one type and all collections (Total-L and Total-D pooled samples) have also been examined.

We used Levins' index:

$$B = 1 / \sum p_i^2 \quad (1)$$

to measure diversity, where p_i is the proportion of individuals in the sample which belong to the i th species (Levins 1968). Many of our samples con-

tained small numbers of fish, and in analysis of both diversity and number of species, we have had to take the effects of variations in size of sample into account.

The faunal similarity of pairs of samples was determined as the Euclidian distance between them. Originally proposed as a measure of taxonomic similarity (Sokal and Sneath 1963), Euclidian distances have recently been used (Heatwole and Levins 1972) to measure community similarity. As used here, D_{ij} , the Euclidian distance between collection i and collection j , is calculated as:

$$D_{ij} = \left[\sum_{k=1}^s (p_{ik} - p_{jk})^2 \right]^{\frac{1}{2}} \quad (2)$$

where s is the total number of species considered in the calculation, p_{ik} is the proportion of individuals in collection i that belong to the k th species, and p_{jk} is the equivalent proportion of individuals in the j th collection. Using this formula, and considering only the 34 commonest species collected, we calculated two sets of Euclidian distances between samples from single D- or L-units.

First, distances between all pairs of samples collected at different times from each particular D- or L-unit were calculated. From these a mean Euclidian distance was determined between samples from that unit. There were eight such L-across-Time and eight such D-across-Time mean Euclidian distances.

Second, distances between all pairs of samples collected at a single time were calculated. For each collection time we then determined a mean Euclidian distance between samples from L-units (L-across-Units mean distance), a mean Euclidian distance between samples from D-units (D-across-Units mean distance), and a mean Euclidian distance between pairs of samples, one from each type of unit (D-L mean distance).

When samples as small as ours are compared, these Euclidian distances are strongly influenced by the sizes of samples compared. Therefore, for each mean distance, we determined the mean size of the set of samples compared in calculating it.

In a preliminary attempt to determine whether there existed pairs of species which usually excluded each other from occurring in a unit, we examined the numbers of fish of the 15 commonest species in all samples from single D- and L-units. Correlation coefficients were calculated between all pairs of these species in each type of unit.

RESULTS

Species which colonized the units

Over the 2 yr of the experiment we collected a total of 630 fishes, 193 from D-units and 437 from L-units. These belonged to 56 species. Fifty-two

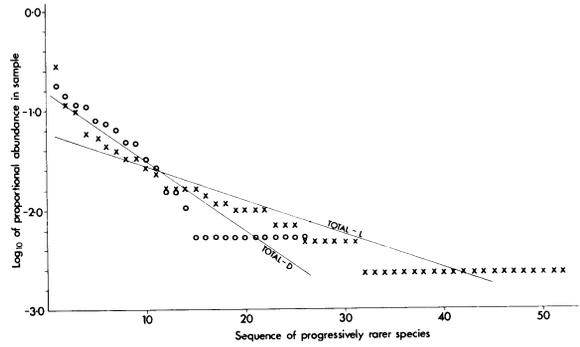


FIG. 1. Species-abundance curves for the total sample of fish collected from D-units (Total-D), and the total sample of fish from L-units (Total-L). The species are arranged along the X-axis in order of decreasing abundance. The lines shown are the linear regressions calculated for each sample.

occurred one or more times in L-units, 26 occurred in D-units. Collections from L-units consistently contained more fish and more species than those from D-units.

A considerable variation in abundance existed among the species collected. Many were very rare, 22 being represented by single individuals in our total sample. Only 15 species were represented by more than the mean of 11 individuals, and the modal number of individuals per species was only three. Figure 1 presents species-abundance curves for the Total-D, and for the Total-L samples. We roughly approximated the relationship between \log_{10} of the proportional abundance of a species, and that species' rank in abundance by a linear regression. Analysis of covariance demonstrated a highly significant difference between the two samples in the slope of this relationship ($F_{1,74} = 45.8, p < 0.005$). Regression coefficients were estimated as -0.03 for the Total-L sample, and -0.07 for the Total-D sample.

Despite the fact that all but four of the species collected from D-units also occurred in L-units,

TABLE 1. List of the most abundant species in collections from D- and from L-units (all species for which > 10 individuals were obtained from one type of unit)

| D-units | | L-units | |
|-----------------------------------|----|------------------------------------|-----|
| Species | N | Species | N |
| <i>Eviota</i> sp. | 34 | <i>Dascyllus aruanus</i> | 119 |
| <i>Ecsenius mandibularis</i> | 27 | <i>Pomacentrus sufflavus</i> | 50 |
| <i>Vauchusella</i> sp. | 22 | <i>Acanthochromis polyacanthus</i> | 33 |
| <i>Acentrogobius</i> sp. | 21 | <i>Pomacentrus wardi</i> | 25 |
| <i>Pomacentrus wardi</i> | 15 | <i>Parapercis cylindrica</i> | 23 |
| <i>Salaria fasciatus</i> | 14 | <i>Eviota</i> sp. | 19 |
| <i>Asteropteryx semipunctatus</i> | 12 | <i>Asteropteryx semipunctatus</i> | 17 |
| | | <i>Gobiodon histrio</i> | 14 |
| | | <i>Gobiodon quinquestrigata</i> | 14 |
| | | <i>Coris variegata</i> | 11 |
| | | <i>Ecsenius mandibularis</i> | 10 |

TABLE 2. Numbers of fish and of species collected from D- and from L-units at each collection time

| Date | No. in D-units | | No. in L-units | | Total No. | |
|----------|----------------|---------|----------------|---------|-----------|---------|
| | Fish | Species | Fish | Species | Fish | Species |
| Sep 1972 | 17 | 10 | 24 | 7 | 41 | 13 |
| Jan 1973 | 42 | 13 | 99 | 21 | 141 | 24 |
| May 1973 | 25 | 12 | 73 | 17 | 98 | 23 |
| Sep 1973 | 25 | 11 | 41 | 17 | 66 | 20 |
| Dec 1973 | 44 | 13 | 69 | 23 | 113 | 25 |
| May 1974 | 40 | 12 | 131 | 34 | 171 | 38 |

samples from the two kinds of unit differed markedly in the species which dominated them (Table 1). Collections from L-units were numerically dominated by four species of pomacentrid, only one of which was also common in collections from D-units. Collections from D-units consisted principally of four species, one gobiid, one eleotrid, one blenniid, and one tripterygiid. These four species were more common in collections from D-units than in collections from L-units.

Many of the commonest species in the collections are known to be sedentary enough to have restricted their activities to the immediate vicinity of the unit from which they were collected. For example, *Dascyllus aruanus*, the commonest species, spends its juvenile and adult life within a home range ≈ 1 m in radius (Sale 1971). *Pomacentrus wardi* (Low 1971, Sale 1974, 1975), *Acanthochromis polyacanthus* (Robertson 1973), and *Gobiodon histrio* and *Gobiodon quinquestrigata* (Tyler 1971) are similarly sedentary. Many other species have been classified by Russell et al. (1974) as resident on their artificial reefs. A few, such as *Thalassoma lunare*, are known to restrict their movements sufficiently to have been resident on a single D- or L-unit as juveniles—the size we collected—but to range more widely as adults (Robertson and Choat 1974). However, individuals of the majority of species, if not collected, would have passed their lives as residents of a single unit on our grid.

Evidence for seasonality of recruitment

The numbers of individuals and of species obtained at each time from all D- and from all L-units are shown in Table 2. There is apparent a seasonal fluctuation in the numbers of fish recruited to units with numbers being smallest in September each year. There is also an apparent increase in numbers recruited during the second year of the experiment. This will be considered later.

Numbers of species recruited also show a seasonal fluctuation with only 25 species collected in one or both September samples. Thirty-four species occurred in one or both of the January and the

TABLE 3. The 39 species that were absent from collections made at one or more of three times of year (September, December/January, May) are classified in terms of their abundance in the total sample of 630 fishes

| No. of fish in total sample | No. of Species | |
|-----------------------------|----------------|----|
| 1 | 22 | |
| 2 | 5 | |
| 3 | 3 | |
| 4 | 2 | |
| 5 | 3 | |
| 6 | 1 | |
| 8 | 1 | |
| 14 | 2 | |
| TOTAL | | 39 |

December sample, and 41 were collected in samples taken in May. Most species missing from collections at some season of the year were represented by very few individuals in our total of 630 fishes (Table 3). They might be expected, purely through chance, to be missing from some collections. However, three species missing from both September collections were common enough in the total collection that their absence in September samples is unlikely to be a chance event. These species were *Chromis caeruleus*, *Gobiodon histrio*, and *G. quinquestrigata* which were represented by 8, 14, and 14 specimens, respectively, in our total sample. With equal collecting effort at each of three seasons, there is a chance of $p > 0.50$ that species this common overall would be represented at least once in collections at all three seasons unless they were seasonally unavailable. Only for these three species do our data provide evidence of seasonal recruitment. All three are absent as recruits during the winter months.

Temporal changes in D- and L-units

Two kinds of change occurred during the course of the experiment which may have affected recruitment to the units. All D- and L-units were measured in September 1973 and September 1974. The results (Table 4) demonstrate that during that year a considerable increase in size occurred in L-units. D-units, as expected, did not change.

A different sort of change occurred to D-units.

TABLE 4. Mean volume (in cubic centimeters) of D- and of L-units in September 1973 and in September 1974. Change in L-units significant, $p < 0.05$, t test; change in D-units not significant

| | September 1973 | | September 1974 | |
|----------------------------|------------------|------------------|------------------|-------------------|
| | D-units | L-units | D-units | L-units |
| \bar{X} volume | 28×10^3 | 55×10^3 | 26×10^3 | 101×10^3 |
| \bar{X} change in volume | | | -2×10^3 | 47×10^3 |

All were colonized, during the course of the experiment, by one or more living corals. In September 1974 there existed 4.50 ± 0.75 SE colonies of living coral per D-unit. These colonies were each $5.0 \text{ cm}^2 \pm 1.0 \text{ cm}^2$ SE in area.

Communities of fishes in control units

Our data on the numbers of fish and of species present in control units (visual censuses) are not strictly comparable to our data on experimental units (collections). Nevertheless, we have compared (Table 5) the mean number of species and of individuals present in control units, and in experimental units of each type, at each collection time. We find only three instances when the mean number of fish or species in a control unit lies outside the 95% confidence limits of numbers collected from single experimental units. Lack of removal of fish from control units appear to have resulted on these occasions in greater numbers (of fish or of species) being present than in experimental units.

Note, however, that both the numbers of fishes and of species present in control units is, at all times, in the same range as that in experimental units. The 4-mo periods between collections have been long enough for recruitment to experimental units to be completed.

Patterns in communities of fishes in single D- or L-units

The mean number of fishes, mean number of species, and mean diversity for samples obtained from single D- and single L-units are shown in Fig. 2. The seasonal variations apparent in the total samples are mirrored in this figure. In addition some noncyclic temporal changes are also apparent. Analysis of covariance demonstrated a significant increase over time in the numbers of individuals

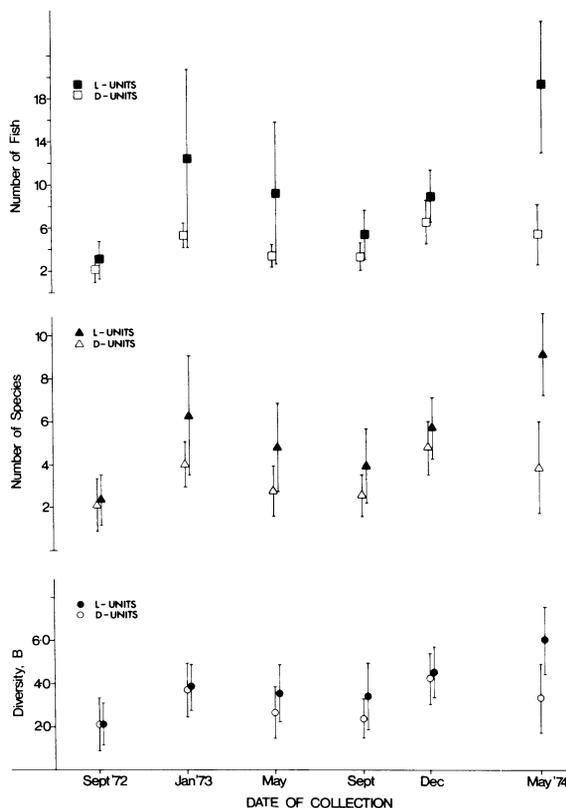


FIG. 2. Numbers of fish, numbers of species, and diversity of samples collected from single D- and L-units at each collection time. Vertical bars represent \pm one SD from \bar{X} .

present in single D- and in single L-units. The rate of increase differed in the two kinds of unit ($F_{1,92} = 5.97, p < 0.05$). The coefficient of the regression of number of individuals on time in months was $b = 0.12$ in samples from D-units (slope sig-

TABLE 5. Comparison of no. of fish and of species seen in control units, and the no. collected from experimental units

| | Sept '72 | Jan '73 | May '73 | Sept '73 | Dec '73 | May '74 | Total |
|--------------------|----------|---------|------------------|----------|------------------|---------|-------|
| No. fish | | | | | | | |
| D-units: Control | ---- | 4.5 | 5.5 ^a | 4.0 | 5.5 | 4.5 | 24 |
| Experimental | 2.1 | 5.3 | 3.3 | 3.1 | 6.3 | 5.0 | 25.1 |
| SD | 1.24 | 1.16 | 1.05 | 1.24 | 1.98 | 2.77 | |
| L-units: Control | ---- | 4.5 | 12.0 | 6.0 | 10.0 | 8.0 | 41.5 |
| Experimental | 3.0 | 12.4 | 9.1 | 5.1 | 8.6 | 18.7 | 56.9 |
| SD | 1.78 | 8.29 | 6.62 | 2.29 | 2.43 | 6.14 | |
| No. species | | | | | | | |
| D-units: Control | ---- | 3.0 | 3.5 | 3.0 | 5.0 | 3.0 | |
| Experimental | 2.1 | 4.0 | 2.8 | 2.5 | 4.9 | 3.8 | |
| SD | 1.24 | 1.07 | 1.16 | 0.93 | 1.24 | 2.12 | |
| L-units: Control | ---- | 3.5 | 9.0 ^a | 5.0 | 9.0 ^a | 7.0 | |
| Experimental | 2.4 | 6.3 | 4.8 | 3.9 | 5.6 | 9.0 | |
| SD | 1.19 | 2.77 | 2.06 | 1.73 | 1.41 | 1.83 | |

^a No. in control units lies beyond the 95% confidence limit for experimental units.

TABLE 6. Effect on diversity and on number of species, of time in months and size of sample, for all samples from single D-units. Coefficient of regression on sample size alone, $b = 0.50$ and 0.64 for parts (A) and (B), respectively

| | <i>df</i> | SS | MS | <i>F</i> |
|----------------------------|-----------|--------|--------|----------|
| (A) Diversity | | | | |
| Regression: | | | | |
| Time and sample size | 2 | 52.789 | 26.394 | 37.1*** |
| Time alone | 1 | 4.628 | | |
| Sample size after time | 1 | 48.160 | 48.160 | 67.7*** |
| Sample size alone | 1 | 52.440 | | |
| Time after sample size | 1 | 9.349 | 0.349 | 0.5 |
| Deviations from regression | 44 | 31.286 | 0.711 | |
| (B) No. species | | | | |
| Regression: | | | | |
| Time and sample size | 2 | 86.366 | 43.183 | 67.4*** |
| Time alone | 1 | 9.688 | | |
| Sample size after time | 1 | 76.678 | 76.678 | 119.7*** |
| Sample size alone | 1 | 86.224 | | |
| Time after sample size | 1 | 0.141 | 0.141 | 0.2 |
| Deviations from regression | 44 | 28.187 | 0.641 | |

*** Regression significant at $p < 0.001$.

nificant at $p < 0.01$, t -test), and $b = 0.47$ in samples from L-units (slope significant at $p < 0.005$, t -test).

Because the samples obtained from single units were small, diversity (B), and number of species can be expected to be strongly affected by sample size variation. Since size of samples varied over time,

TABLE 7. Effect on diversity and on number of species, of time in months and size of sample, for all samples from single L-units. Coefficients of regression on time and sample size: (A)

| | <i>df</i> | SS | MS | <i>F</i> |
|----------------------------|-----------|---------|---------|----------|
| (A) Diversity: | | | | |
| Regression: | | | | |
| Time and sample size | 2 | 74.324 | 37.162 | 30.9*** |
| Time alone | 1 | 47.839 | | |
| Sample size after time | 1 | 26.485 | 26.485 | 22.0*** |
| Sample size alone | 1 | 58.004 | | |
| Time after sample size | 1 | 16.319 | 16.319 | 13.6*** |
| Deviations from regression | 44 | 52.982 | 1.204 | |
| (B) No. species: | | | | |
| Regression: | | | | |
| Time and sample size | 2 | 287.109 | 143.555 | 123.1*** |
| Time alone | 1 | 96.921 | | |
| Sample size after time | 1 | 190.188 | 190.188 | 163.1*** |
| Sample size alone | 1 | 278.252 | | |
| Time after sample size | 1 | 8.857 | 8.857 | 7.6** |
| Deviations from regression | 44 | 51.316 | 1.166 | |

*** Regression significant at $p < 0.001$.

** Regression significant at $p < 0.01$.

TABLE 8. Covariance analysis for the relationship between diversity and size of sample in four types of pooled sample: D-over-Time, D-over-Unit, L-over-Time, and L-over-Unit samples. Comparison of slopes: $F_{3,20} = 1.317$ ns; comparison of elevations: $F_{3,23} = 1.663$ ns; test of pooled regression coefficient: $t = 1.58$, ns

| | Total SS | <i>b</i> | Deviations from regression | | |
|------------------------------|----------|----------|----------------------------|--------|-------|
| | | | <i>df</i> | SS | MS |
| Within | | | | | |
| D-over-Time | 16.177 | -0.04 | 6 | 15.796 | 2.633 |
| D-over-Unit | 4.941 | -0.01 | 4 | 4.835 | 1.209 |
| L-over-Time | 10.019 | -0.04 | 6 | 8.039 | 1.340 |
| L-over-Unit | 36.340 | +0.04 | 4 | 22.266 | 5.566 |
| | | | 20 | 50.936 | 2.547 |
| Pooled within | 67.477 | +0.03 | 23 | 60.997 | 2.652 |
| Differences among slopes | | | 3 | 10.061 | 3.354 |
| Total | 74.318 | | 26 | 74.227 | 2.855 |
| Differences among elevations | | | 3 | 13.230 | 4.410 |

we used multiple regression analysis in examining temporal change in these indices.

Changes in diversity of samples from single D-units, and changes in number of species present in samples from single D-units were accounted for solely by the variations in sizes of samples (Table 6). A significant effect of time independent of that of sample size did not exist.

In single L-units, however, significant temporal effects remained after the removal of the effects of sample size in diversity and in the number of species represented (Table 7).

In an attempt to analyze the differences between samples taken from different D- or L-units, while avoiding the problems resulting from using samples of such small sizes, we examined samples pooled over time for each unit (the D-over-Time and L-over-Time pooled samples). These samples were

TABLE 9. Covariance analysis for the relationship between the number of species present and size of sample, in four types of pooled samples: D-over-Time, D-over-Unit, L-over-Time, and L-over-Unit samples. Comparison of slopes: $F_{3,20} = 0.621$ ns; comparison of elevations: $F_{3,23} = 2.074$ ns; test of pooled regression coefficient: $t = 8.04$, $p < 0.001$

| | Total SS | <i>b</i> | Deviations from regression | | |
|------------------------------|----------|----------|----------------------------|---------|--------|
| | | | <i>df</i> | SS | MS |
| Within | | | | | |
| D-over-Time | 25.875 | 0.23 | 6 | 9.685 | 1.614 |
| D-over-Unit | 6.833 | 0.09 | 4 | 1.284 | 0.321 |
| L-over-Time | 71.500 | 0.15 | 6 | 40.444 | 6.741 |
| L-over-Unit | 392.830 | 0.21 | 4 | 68.008 | 17.002 |
| | | | 20 | 119.421 | 5.971 |
| Pooled within | 497.042 | 0.19 | 23 | 130.547 | 5.677 |
| Differences among slopes | | | 3 | 11.126 | 3.709 |
| Total | 852.107 | | 26 | 165.866 | 6.379 |
| Differences among elevations | | | 3 | 35.319 | 11.773 |

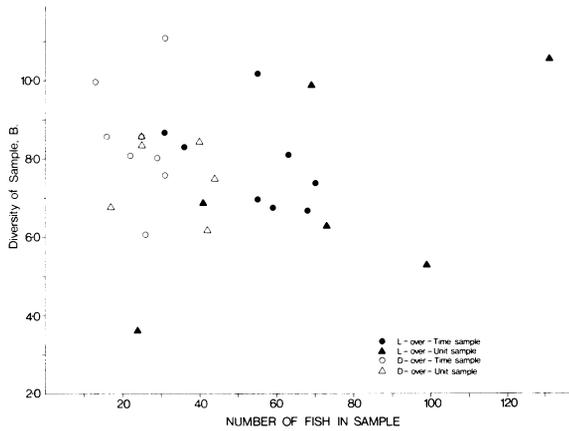


FIG. 3. Relationship between the diversities of pooled samples and number of individuals in pooled samples. There is no overall regression of diversity on sample size, and no significant differences in mean diversity among pooled samples of the four types.

compared with the samples pooled across similar units at single collection times (the D-over-Unit and L-over-Unit pooled samples).

The diversities, B , for all pooled samples of each of the four types are plotted against sample size in Fig. 3. Analysis of covariance of these data (Table 8) showed no overall effect of sample size on diversity, and no differences between the four types of pooled sample. Mean diversities for samples of all four types do not differ ($F_{3,24} = 0.881, p > 0.05$), and are estimated as $B = 7.83 \pm 1.68$ SD.

By contrast, if possible effects of sample size are not taken into account, a test of differences among mean numbers of species in pooled samples of the four types is highly significant ($F_{3,24} = 5.71, p < 0.01$). The relationship between number of species and sample size, for pooled samples of each type is shown in Fig. 4. Analysis of covariance of these data (Table 9) showed a highly significant overall positive regression of number of species on sample size ($b = 0.19, p < 0.001, t$ -test), and no differences in the relationship among the four types of sample. This relationship accounts completely for the apparent differences in numbers of species in the four types of pooled samples.

A Bartlett's test showed some heterogeneity of variance in these data, and attempts to eliminate it by using standard transformations of the data (square root, logarithmic) were unsuccessful. The lack of significant differences in slope or elevation of the calculated regression lines, despite this heterogeneity, remains a secure finding because such heterogeneity tends to overestimate significant differences (Snedecor and Cochran 1967).

The best estimate of the relationship between size

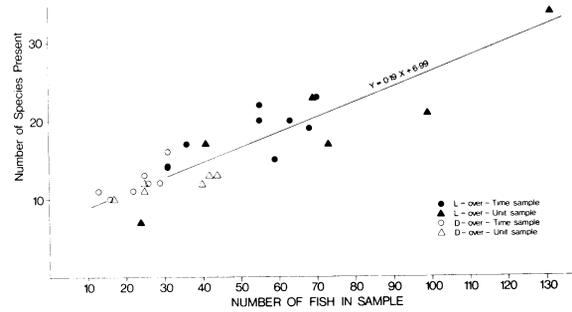


FIG. 4. Relationship between numbers of species present in pooled samples of four types, and numbers of individuals present in the samples. The regression, $Y = 0.19X + 6.99$, is highly significant ($p < 0.001$) and no significant differences exist among the four types of sample.

of sample and number of species present for pooled samples of any of these four types is:

$$Y = 0.19X + 6.99$$

where Y is the number of species present and X is the size of the sample.

In the smaller samples derived from single units at single times the regression of species number on sample size is steeper than this ($b = 0.64$ for samples from D-units, $b = 0.32$ for samples from L-units), even after independent effects of time have been removed.

Faunal similarity of communities formed in single D- or L-units

In assessing faunal similarity of samples, we examined mean Euclidian distances in two ways. First, to quantify the degree of faunal differences between samples from the two kinds of units, we compared D-across-Units and L-across-Units mean distances with D-L mean distances. These data are plotted in Fig. 5 against the mean size of samples compared in determining each mean Euclidian distance. Analysis of covariance following square root transformation of the data showed significant differences among the three sets of distances. The relationship between mean distance and mean sample size is steeper for D-across-Units comparisons than for the others, and for any mean sample size, D-L mean distances are greater than are L-across-Units distances (Table 10). As Fig. 5 shows, D-L mean distances are greater than either of the other types of distance over most of the range of sample sizes represented in our data.

Second, to assess the degree of faunal similarity in samples from a single unit, we compared D-across-Time and L-across-Time mean Euclidian distances with D-across-Units and L-across-Units mean dis-

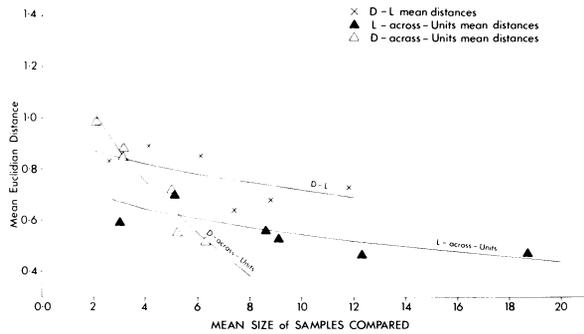


FIG. 5. Relationship between mean Euclidian distance, and mean size of samples compared in calculating the Euclidian distances, for three sets of comparisons between samples from single units. Curves shown are those obtained from the analysis shown in Table 10. D-L mean Euclidian distances are greater for any size of sample than are L-across-Units mean distances, and greater, over most of the range of sample sizes than D-across-Units mean distances. Thus, except for very small samples, there is less faunal similarity between single samples from D- and single samples from L-units, than between pairs of samples from either D- or L-units.

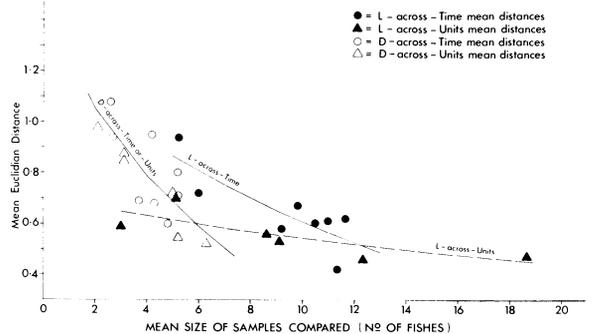


FIG. 6. Relationship between mean Euclidian distances, and mean size of samples compared in calculating the Euclidian distances, for four sets of comparisons between samples from single units. Curves shown are those obtained from the analysis in Tables 11 and 12. The slope of the relationship in L-across-Units comparisons is not significantly different from zero. The L-across-Time comparisons yield significantly greater mean distances than L-across-Units comparisons over most of the range of sample sizes in our data.

tances. These data are plotted in Fig. 6 against mean size of samples compared in determining each mean distance. Analysis of covariance after square root transformation showed no differences between the set of D-across-Time and the set of D-across-Unit mean distances (Table 11). L-across-Time mean Euclidian distances showed a significant nega-

tive relationship with size of samples (Table 12), in contrast to L-across-Units distances. Significantly, (Fig. 6) the L-across-Time mean distances were greater for a given size of sample than were L-across-Units mean distances over most of the range of sample sizes covered by our data.

Correlation in occurrence of species of fish

The results of the correlation analysis are summarized in Table 13. The distribution of species among samples from D-units yielded only one significant correlation. *Vauclusella* sp., a tripterygiid, was positively associated with the blenniid, *Salarius fasciatus* ($r = +0.35$). Both species tended to be commonest in the same D-unit samples.

Analysis of samples from L-units yielded 15 sig-

TABLE 10. Covariance analysis of the relationship between mean Euclidian distance, and mean size of samples compared, for three types of comparison among samples from single units: D-across-Units, L-across-Units, and D-L comparisons. Comparison of slopes: $F_{2,12} = 11.16, p < 0.005$; test of regression coefficient, D-across-Unit: $t = 7.46, p < 0.005$. Comparison of L-across-Unit and D-L yields a comparison of slopes: $F_{1,8} = 4.32, ns$; comparison of elevations: $F_{1,9} = 20.14, p < 0.005$; test of pooled regression coefficient: $t = 3.56, p < 0.01$. The analysis was carried out on data transformed as: $X = (\text{mean sample size} + 1)^{1/2}$ $Y = (\text{mean Euclidian distance} + 1)^{1/2}$

| | Total SS | b | df | Deviations from regression | |
|---------------------------------|----------|-------|----|----------------------------|---------|
| | | | | SS | MS |
| Within | | | | | |
| D-across-Unit | 0.02522 | -0.19 | 4 | 0.00169 | 0.00042 |
| L-across-Unit | 0.00615 | -0.03 | 4 | 0.00224 | 0.00056 |
| D-L | 0.00683 | -0.04 | 4 | 0.00368 | 0.00092 |
| | | | 12 | 0.00761 | 0.00064 |
| Pooled within | 0.03820 | -0.05 | 14 | 0.02179 | 0.00156 |
| Differences among slopes | | | 2 | 0.01417 | 0.00709 |
| Total | 0.06381 | | 16 | 0.03330 | 0.00208 |
| Differences among elevations | | | 2 | 0.01152 | 0.00576 |
| Comparing L-across-Unit and D-L | | | | | |
| Pooled within | 0.01298 | -0.04 | 9 | 0.00601 | 0.00067 |
| Differences among slopes | | | 1 | 0.00211 | 0.00211 |
| Total | 0.03408 | | 10 | 0.01947 | 0.00195 |
| Differences among elevations | | | 1 | 0.01346 | 0.01346 |

TABLE 11. Covariance analysis of the relationship between mean Euclidian distance and mean size of samples compared, for two types of comparisons of samples from D-units. Analysis was carried out on data transformed as: $X = (\text{mean sample size} + 1)^{1/2}$ $Y = (\text{mean Euclidian distance} + 1)^{1/2}$. Comparison of slopes: $F_{1,10} = 0.009, ns$; comparison of elevations: $F_{1,11} = 1.06, ns$; test of pooled regression coefficient: $t = 5.13, p < 0.001$

| | Total SS | b | df | Deviations from regression | |
|------------------------------|----------|-------|----|----------------------------|---------|
| | | | | SS | MS |
| Within | | | | | |
| D-across-Time | 0.02676 | -0.19 | 6 | 0.01360 | 0.00227 |
| D-across-Unit | 0.02522 | -0.19 | 4 | 0.00169 | 0.00042 |
| | | | 10 | 0.01529 | 0.00153 |
| Pooled within | 0.05198 | -0.19 | 11 | 0.01530 | 0.00139 |
| Differences among slopes | | | 1 | 0.00001 | 0.00001 |
| Total | 0.05357 | | 12 | 0.01678 | 0.00140 |
| Differences among elevations | | | 1 | 0.00148 | 0.00148 |

TABLE 12. Covariance analysis of the relationship between mean Euclidian distance and mean size of samples compared, for two types of comparisons of samples from L-units. Analysis was carried out on data transformed as: $X = (\text{mean sample size} + 1)^{1/2}$, $Y = (\text{mean Euclidian distance} + 1)^{1/2}$. Comparison of slopes: $F_{1,10} = 6.17, p < 0.05$; test of regression coefficient for L-across-Unit sample: $t = 2.60, ns$

| | Total SS | b | Deviations from regression | | |
|------------------------------|----------|-------|----------------------------|---------|---------|
| | | | df | SS | MS |
| Within | | | | | |
| L-across-Time | 0.02234 | -0.11 | 6 | 0.00727 | 0.00121 |
| L-across-Unit | 0.00615 | -0.03 | 4 | 0.00224 | 0.00056 |
| Pooled within | | | | | |
| | 0.02849 | -0.05 | 10 | 0.00951 | 0.00095 |
| | | | 11 | 0.01537 | 0.00140 |
| Differences among slopes | | | | | |
| Total | 0.03267 | | 1 | 0.00586 | 0.00586 |
| | | | 12 | 0.02018 | 0.00168 |
| Differences among elevations | | | | | |
| | | | 1 | 0.00481 | 0.00481 |

nificant correlations in occurrence. All 15 were positive associations of pairs of species of fish.

DISCUSSION

It is helpful to view our grid of D- and L-units as a small area of reef composed of patches of two habitat types. The experiment has demonstrated the occurrence there of 56 species of fish, and our primary interest is to explain the mechanisms whereby these 56 species are able to share this small area of reef. Our attention, therefore, has been directed principally to the patterns with which these fish have distributed themselves among the individual D- and L-units.

There are two reasons for arguing that the groups of fishes collected at one time from single D- or L-units represent communities of fishes such as one might find in a natural, isolated patch of living or dead coral on the reef flat. Many of the species collected are known to be sedentary enough to have restricted their activities to the vicinity of a single unit. To this extent they would be interacting primarily with other fishes occupying that unit. Secondly, sufficient time was allowed between collections for the recruitment of fishes to units to be completed. The units held, at the time of collection, a number of fishes and of species comparable to that in uncollected control units, and in similarly sized, naturally occurring isolated corals on the reef flat. Russell et al. (1974) demonstrated similar rates of recruitment to much larger artificial reefs of concrete blocks. Their results are particularly relevant to our work because they worked at One Tree Reef, just 20 km from our experimental site. They found that a group of artificial reefs established in mid-summer were colonized rapidly, and had reached a stable number of species of fish in 4 wk. A similar

TABLE 13. Numbers of positive and of negative associations among all pairs of the 15 commonest species, as determined from their occurrence in single samples from D-units, and in single samples from L-units. Four of the 15 species did not occur in D-units

| | Positively associated | | Negatively associated | |
|---------|-----------------------|------------------|-----------------------|------------------|
| | No. pairs | No. significant* | No. pairs | No. significant* |
| D-units | 27 | 1 | 28 | 0 |
| L-units | 55 | 15 | 50 | 0 |

* if $|r| \geq 0.288$, significant at $p < 0.05$.

group of reefs established in midwinter required 3 mo to reach the same number of species of fish. We allowed longer than this between successive collections.

One disadvantage we faced in analyzing our data is that the collections have been of generally small size. The maximum number of fish removed from a single unit was only 29. Because of this, and because the sizes of collections varied from time to time and from unit to unit, assessment of the richness of communities found has had to take account of the numbers of fishes present. The diversity index and the simpler count of species have been shown to be strongly influenced by numbers of fish in samples. Although we have presented data using diversity as well as number of species, we believe the latter may be the more appropriate measure for samples of this type. May (1975) has recently discussed the virtues of the several measures of diversity available in the literature.

The 56 species of fish collected have used the units primarily as shelters. One dominant group, typified by the pomacentrids, feeds principally in midwater and shelters within the units. To some extent these fishes might feed off the surface of the unit (particularly D-units) or from the sand near its base. The other major group of fishes, typified by the gobiids and blenniids, is physically much more closely associated with the unit. These fish rarely feed in midwater, and in the case of species of *Gobiodon*, for example, are rarely seen outside the interstices of the unit's surface.

There appear to be three ways in which the various species of fish might partition the space resources of our experimental environment. First, they might have been present at different times, with one group of species coexisting on the grid at one time of year, and other groups of species at other times. For this reason we looked for seasonal variations in recruitment to the grid.

Second, the species present may all be extreme habitat specialists, each being precisely adapted to one particular kind of shelter space. The units provided for them were of two classes, L- and D-units,

but within these classes the units inevitably varied slightly, and thus provided slightly different kinds of spaces to the fishes. If the species of fish are extreme space specialists then certain species should occur principally in certain particular units, while other species occur in other units.

A third possibility is that while the species involved might be capable of using space in any unit, they might be particularly sensitive to the presence of other species. Certain pairs of species might consistently occur together, and certain other pairs might consistently avoid each other. Priority of colonization would determine which of several possible species groups was likely to occupy any particular D- or L-unit.

Partitioning of the grid habitat might involve any of the above in conjunction with one another. In addition, the possibility remains that the species do not partition space on the grid, but that colonists of any species are added to a unit until that unit is filled and recruitment ceases. Under these circumstances, the particular mix of species in a unit is entirely due to chance priority of colonization.

Temporal variation

Samples of fish obtained at the six collection times differed. There was an overall increase in the numbers of fish per unit, and in L-units there was a significant increase in the numbers of species and the diversity of communities in units (Fig. 2). These tendencies towards an increase in size and complexity of communities, although significant, were of minor extent. Furthermore, they could be accounted for by changes that took place in the units. All D-units were colonized by one or more colonies of living coral during the experiment and L-units doubled in size.

In addition to these trends there was evident a seasonal periodicity in numbers of fish, in diversity, and in numbers of species present in both kinds of unit (Fig. 2). Winter collections gave the smallest and least diverse samples. But there was little evidence in our data of a seasonal nonavailability of any particular species. Only three species, *Chromis caeruleus*, *Gobiodon histrio*, and *G. quinquestrigata*, were sufficiently abundant overall that their absence from one season could be taken as indicative that they do not produce recruits throughout the year. But these species were simultaneously absent from winter collections, and there is thus no indication that they have partitioned the environment temporally. Since none of the 56 species collected are known to be able to complete their life-cycles in less than a year, temporal partitioning of the environment seems an unlikely possibility in any event.

Variation between communities in single units

There remain the possibilities that the 56 species are predominantly microhabitat specialists, that they are habitat generalists but interact so strongly that certain species combinations are prohibited, or that chance alone determines their distribution among the units of habitat. To examine these possibilities we turned to the variability which existed among communities in single units.

Differences were apparent between communities in D- and those in L-units. Those in D-units contained fewer fish and fewer species. We expected fewer fish in these units—D-units provided fewer topographic irregularities, and thus, fewer living sites than did L-units.

More importantly, different species dominated D- and L-units, and some common ones avoided D-units. For example, the commonest species on the grid, *Dascyllus aruanus*, was collected 119 times from L- but never from D-units (this confirms a preference for living coral reported earlier [Sale 1971]). Similarly, *Pomacentrus sufflavus* occurred 50 times in L- but only once in a D-unit. *Acanthochromis polyacanthus*, *Gobiodon histrio*, and *Gobiodon quinquestrigata* occurred 33, 14, and 14 times, respectively, in L-units and never in D-units. The three former species are planktivores using the units only for shelter. It is not clear why they avoid D-units. The latter two are gobies which feed upon the invertebrates found among the interstices of living coral. All five species have demonstrated conclusive preferences for L-units, and, to this extent, there is a partitioning of the grid by species showing habitat preferences. This point can be overstated, however, as no species showed a similarly strong preference for D-units, and all other species absent from D-units were rare on the grid. Remarkably, species of fish do not appear to have distinguished between the D- and the L-units, and we are surprised at the degree to which samples from these two rather different kinds of unit are similar to one another.

Our data strongly refute the possibility that the 56 species have partitioned the habitat available to them by means of precise microhabitat preferences. As noted above, the majority of species are available as recruits throughout the year, though in reduced numbers during the winter months. This being so, if species were habitat specialists, a sample formed by pooling successive collections from a single unit (a D- or L-over-Time sample) would contain fewer species, for a given size of sample, than one obtained by pooling across collections from several units (the D- or L-over-Unit samples).

Our analysis of the relationship between number of species and sample size for these pooled samples (Fig. 4) convincingly demonstrates that no such

difference in this relationship occurs, either for samples from D- or those from L-units. In fact, samples from D-units and those from L-units appear to show the same relationship. There is thus no evidence that particular ones of the 56 species occur in particular units, and there is the suggestion that given enough D-units to support equivalent numbers of individuals we could have obtained the same number of species as in L-units. Diversities of these pooled samples (Fig. 3) also did not differ.

Note that points obtained from September collections (Table 2) with one exception fall very close to the regression line in Fig. 4. This indicates once more that the low numbers of species recruited to the grid during the winters was due to the small numbers of individuals recruited at that time.

Our analysis of Euclidian distances between selected pairs of samples served as an independent approach to the question of whether there existed partitioning of the grid habitat by means of the maintenance of differing habitat specializations. The results strongly support the conclusions reached through the analysis of numbers of species in samples.

Comparisons of single samples from L-units with single samples from D-units averaged only slightly larger Euclidian distances (and hence less faunal similarity) than did comparisons between samples from units of the same type, whether from L- or D-units (Fig. 5). Thus the groups of fishes occupying neighboring units of the same type are but little more similar to one another in faunal composition than are those in D-units to those in L-units.

Comparisons of successive samples from the same unit did not yield greater faunal similarity (smaller Euclidian distances) than did comparisons of samples from different units of the same kind (Fig. 6). In samples from D-units no significant differences existed between these two kinds of comparisons, and in L-units there was a greater faunal similarity among samples collected from different units at the same time, than among successive samples from a single unit. Considering the rather slight seasonal variation in availability of species on the grid, this latter result is particularly remarkable. Overall there is no detectable tendency for single L- or D-units to be repeatedly colonized by the same species of fish.

Once more, we conclude that there is no evidence for the existence of fine microhabitat specializations held by particular species, nor for a concomitant partitioning of the grid by the species present. At best, a few species distinguish between D- and L-units as habitats. Most species do not make this distinction. Overwhelmingly, most D- or L-units can be occupied by most species at most times of year.

There remains the possibility that, although habitat

generalists, the species of fish interacted strongly, so that single units came to be occupied by one or other particular subset of fishes. No such partitioning was apparent from a casual inspection of the data, but our search for correlations in occurrence among the commonest species of fish served as a further check of this possibility.

If our units had yielded identical numbers of fishes, then, in the absence of any interaction among the species, we would expect all correlation coefficients to be close to zero. However, the units (particularly L-units) supported variable numbers of fish. This, in the absence of any interactions among the fishes, might lead to the occurrence of some positive correlations in occurrence. Several species might all be most abundant in the units supporting the greatest numbers of fishes. Only if species excluded each other from units, or if particular species had markedly different habitat preferences, would we expect to find negative associations between species. We have shown above that differences in habitat requirements were minor.

The results of our correlation analysis provided no evidence of the mutual exclusion from units by any pair of species. Only 16 significant correlations were detected, and all were positive associations between pairs of species. Even those species expected to have particularly similar ecological requirements showed some significant positive associations. For example, in D-units the only significant association found was between a blennioid and a tripterygiid. The four commonest pomacentrids in L-units included two pairs that were significantly positively associated with each other.

Conclusions and broader implications

On a coarse scale, reef fishes partition their habitat spatially. Hiatt and Strasburg (1960), and later Jones (1968), were able to recognize, primarily on the basis of field observation, groupings of reef fishes that were associated with particular reef habitats such as reef crest, surge channel, and reef flat. Talbot and Goldman (1972) made a series of explosive collections of fishes on One Tree Reef and demonstrated that from 39% to 60% of the species collected in any one of their broad habitat zones were present only in that zone. Only 13% of species were found in all zones.

However, on a smaller scale, numerous species of reef fishes coexist. Smith and Tyler (1972), for example, recorded the presence of 75 species on a single patch reef about 3 m in diameter and 1.6 m high. Of these, 53 species were recorded as residents of the patch, and the same individuals were seen each day over a 2-wk period.

In the present experiment, we have searched for

patterns of distribution of species on this smaller scale. Our data demonstrate that a diverse pool of species was available to colonize the units of habitat we provided, but the variation in the communities of fish that formed within units was remarkably unpatterned. Diversity and species composition of these communities was more readily explained by how many individuals they contained than by what type of unit they occupied, although five species did exhibit a strong preference for L- over D-units. The faunal similarity of communities was only slightly greater if the communities had formed in units of the same type than in units of differing type.

We found that most species available could be recruited to our grid at any time of year, although numbers of recruits of all species fell off during the winter months. We predict that on more equatorial reefs even this degree of seasonality in recruitment would not be found. In any event, a temporal partitioning of occupancy of the habitat did not occur.

Using several approaches we have eliminated the possibility that these species of fish partitioned the grid habitat by maintaining subtly different, specialized habitat requirements. Finally, by means of a correlation analysis, we failed to find any pair of species negatively associated with each other in units of the same type. We conclude that chance colonization has overwhelmingly determined the small-scale distribution of species of fish in this experimental habitat. It follows that the chaos view of community structure comes closer to reality for communities of fish in isolated colonies of coral than does the order view. We anticipate that further research will demonstrate the generality of our conclusions for most kinds of assemblages of fish on small patches of reef. This being so, there are the following important consequences for our understanding of reef fish communities.

The species composition of the fishes occupying small areas on a reef will be best understood in terms of chance colonization and chance mortality. Competitive interactions between residents seem likely to be important only in so far as they affect either of these processes. This certainly appears to be true for one other kind of reef fish community—the multispecies group of territorial pomacentrids which occupies a patch of rubble (Low 1971, Sale 1974).

On Heron Reef, eight species of this guild occur, and while to some extent they occupy different parts of the reef, any suitable patch of rubble can be occupied by three to six species. In rubble patches on the upper reef slope three species, *Pomacentrus apicalis*, *Pomacentrus wardi*, and *Abudefduf lacrymatus*, occur together. The three do not differ in their requirements for space on rubble patches yet

they are in competition for a short supply of such space. *Pomacentrus wardi* operates as a fugitive using other kinds of space as well. The three species persist because the competition between them is principally a competition by colonists for vacant spaces which randomly appear on rubble patches (Sale 1974, 1975).

An analysis of niche breadth and resource partitioning will not be able to tell us much concerning the diversity of communities of reef fishes. There is much circumstantial evidence that in the kind of habitat we used in our experiment, living space is the one resource most likely to be in short supply. Yet our experiment disclosed little partitioning of this resource. Many reef fishes show considerable overlap in their food requirements as well as in their habitat requirements (Jones 1968, Choat 1969) yet coexist successfully. This is in marked contrast to communities of birds. In the latter, analyses of resource partitioning appear to have been very effective in explaining and in predicting the diversity of species present (reviews in MacArthur 1969, 1972, Cody 1973). Considering their very different environments and life histories, we should not be surprised at there being differences in the organization of fish and bird communities. Yet in the past there has been a perhaps unwritten assumption that the fishes are to a coral reef what birds are to a forest.

In fact there are reasons to expect that the particular characteristics of reef fish life histories that distinguish them from birds (their long reproductive seasons, and their numerous dispersive larvae) coupled with their notably patchy environment will result in communities of fish that are consistently more diverse than one would predict from an analysis of niche breadth and resource overlap among the species present (Sale 1974). Recently, the coexistence of species in a patchy environment has been the subject of theoretical investigation by several authors (Levins and Culver 1971, Horn and MacArthur 1972, Levin 1974). They have all concluded that the possibility of migration between or repeated recolonization of small patches of habitat enhances the likelihood of coexistence of similar species. Their models seem readily applicable to the reef environment.

Communities of reef fishes are likely to demonstrate only weak stability. (Perhaps, at last, the equation "diversity = stability" can be laid to rest.) At the level of the single patch of habitat, species composition is a result of chance patterns of colonization and represents but one of a number of possibilities for that place. The species composition of a number of adjacent patches will be a reflection of the relative abundance of colonists of different species. Any fluctuation in physical or biotic con-

ditions which favors one species more than others will lead to a shift in species composition as greater numbers of this species are recruited to patches. Nothing other than further chance fluctuations in conditions will return the structure to its previous state. The magnitude of such fluctuations in community structure will depend upon the size of the area of reef from which colonists to a patch are derived. If adjacent patches are colonized by fish produced in a small area of reef, fluctuations in species abundance there will be larger, for a given degree of variation in conditions, than if they are colonized by fish produced over a much larger area of reef. If source areas are large enough there may be considerable inertia to change in species composition. This inertia will give the (false) impression that the community is stable. A fuller understanding of community structure will urgently require far greater information than we now have concerning reproductive seasons, fecundity, larval survival and behavior, and longevity of reef fishes. Certainly, information on events at the moment of larval settlement on the reef, though difficult to obtain, and long neglected, will be crucial to our further understanding of reef fish communities.

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