

Determinants of Community Structure for Coral Reef Fishes in Isolated Coral Heads at Lagoonal and Reef Slope Sites

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Summary. Ten small isolated corals were selected as units of habitat in each of two nearby reef sites—a lagoon and a reef slope. On six occasions over two years we collected all fishes resident in each of these corals. Collections yielded 827 fishes of 64 species from the lagoon and 525 fishes of 66 species from the slope, but at each site 12 common species comprised over 80% of the fishes collected. We examined the distribution of species of fishes among units of habitat to assess the extent to which partitioning of habitat was being carried out. Results are compared with others previously reported from a reef flat site. Species discriminated among different types of habitat offered, but to a different degree in each site. Discrimination was most pronounced at the slope site where 7 of the 12 commonest species did not occur in all three types of habitat offered, and least at the lagoon site where no common species failed to occupy both types of habitat offered. No temporal partitioning of habitat could be demonstrated. Fish did not distribute themselves among units of habitat of one type by means of precise microhabitat discrimination. No pair of species in either site could be shown to mutually avoid, or exclude one another from habitat units. At all three sites, chance patterns of recruitment and loss overwhelmingly determined species composition of the groups of fishes coexisting in single habitat units. The significance of these results for our understanding of the ecology of coral reef fishes is discussed.

Introduction

The organisms found living together in a site constitute a community with a structure definable in terms of the number of species present, their relative abundances, and their identities. A question of central interest to ecology is to determine the factor or factors responsible for creating and maintaining

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this structure. In recent years a very large amount of work has been done to investigate the possible role played by competitive processes among the species present in determining community structure (see Refs., in Cody, 1974; Colwell and Fuentes, 1975; Connell, 1975; Schoener, 1974), but other determinants, involving other biotic interactions or abiotic factors may also exist.

Connell (1975) has noted that despite this considerable interest in the topic experimental investigations of community structure are rare. This is despite the fact experimental studies were done at least as long ago as Darwin's study of the species composition of a lawn before and after regular mowing was halted (cited from Connell, 1975). Recent studies have examined communities as varied as the arthropods of rotting logs (Fager, 1968), the zooplankton of small ponds (Dodson, 1974; Sprules, 1972), and the sessile invertebrates and algae of the rocky intertidal (Connell, 1974; Dayton, 1971; Paine, 1976; Underwood, 1976).

Communities of fishes on coral reefs are usually highly diverse, yet the fishes present are abundant, and easily visible when use is made of modern free-diving techniques. Many studies have confirmed that the majority of reef fish species are relatively sedentary animals (Smith and Tyler, 1972; Ehrlich, 1975; Goldman and Talbot, 1976; Sale, 1977). This fact is of particular value when experimental studies are contemplated. One feasible approach to the experimental study of reef fish communities is to work on a very local scale, so as to reduce as much as possible the complexity and the size of the group being examined. The sedentary nature of most reef fishes means that those individuals observed on a small area—such as a single patch reef, or even a single isolated coral colony—can be treated as a complete, if small, community. They are a community in the sense that the individuals are resident, and are interacting primarily with other residents.

Recently we (Sale and Dybdahl, 1975) investigated possible determinants of community structure for small assemblages of fishes living in single isolated colonies of coral on a reef flat at Heron Reef, Great Barrier Reef. Such small communities are likely to be space-limited. A single colony of coral can shelter only a certain number of fishes. Such space-limitation is probably general for many reef fish communities (Smith and Tyler, 1972, 1975; Sale, 1975, 1976, 1977; Goldman and Talbot, 1976), and we know of no convincing evidence that food, or some other resource than space is ever limiting to reef fishes.

Our experiment investigated the ways in which the species of fish present divided up the living space provided. It consisted of repeatedly denuding a series of isolated living and dead corals, and then analysing the numbers and species composition of the fishes which recolonised them. We found little pattern in the distribution of fishes among units of coral habitat, and our conclusions were that chance factors determining colonisation and loss overwhelmed any other factors determining species composition and relative abundance in this community.

This study had used corals set out as grid on a shallow reef flat. Although we believed our conclusions to have general validity, it was necessary to determine whether they would generalize to corals *in situ* in other reef environments, less physically disturbed than a reef flat. In this paper we present results of

a similar experiment using fishes in isolated corals in a shallow reef lagoon and in 8 to 10 m depth on a reef slope.

Methods

The reef slope site was on the southern edge of Heron Reef, approximately 500 m from our reef flat grid, on a gently sloping shelf of mixed sand and rubble in 8–10 m depth (low tide). The lagoon site, approximately 2 km east of Heron cay, was on fine sand, about 2 m deep at low tide. Instead of establishing grids of coral as on the reef flat, we located suitable corals in each site, mapped their locations, tagged them, and left them in situ throughout the experiment.

Ten colonies were chosen at each site. At the lagoon site they comprised four colonies of living *Pocillopora damicornis* 40 to 60 cm diameter (to be termed L-units) and six, also 40 to 60 cm diameter, of predominantly dead coralline limestone, but each bearing 1–2 small colonies of living coral. The largest of these small live corals were a colony of *Acropora cuneata* 150 cm² in area, and one of *Pocillopora damicornis* 50 cm². These predominantly dead pieces of limestone will be termed D-units. The ten colonies were scattered over an area some 20 m in radius, and most were 3 to 5 m from other coral. Three were 1.5 m from other coral.

At the reef slope site the 10 colonies fell into three classes. Three colonies were branched *Acropora pulchra* 50 to 70 cm in diameter, termed B-units. Three others were plate-like *Acropora hyacinthus* 35 to 40 cm in diameter, termed P-units. The remaining four were complex assemblages of dead coralline limestone with some soft corals, sponges, and small colonies of living coral. Termed C-units, they were 50 to 80 cm diameter. The ten were scattered over an area about 25 m radius, containing many other corals and rocky outcrops; and coral units while never closer than 1 m from other coral were seldom more than 2 to 3 m away.

Commencing in September 1972, and continuing till May 1974, we denuded the ten units at each site of all fishes on six occasions approximately 4 months apart—Sept, 1972, Jan, May, Sept, Dec, 1973, May 1974. Removal of fish was accomplished by first enclosing the unit with a bag-shaped net, weighted at the mouth, and buoyed at the closed end. After fish were trapped in this way, we removed them using small spears, and the anaesthetic quinaldine. Visual censuses on the days before and after treatment confirmed that our methods were effective in removing all resident fishes. We rarely had to remove additional fishes the day after treating a coral unit.

The data comprise only those fish actually caught, and groups of 15 or more individuals of a single schooling species collected from a single unit have been discarded as not truly resident there. Analysis of the data from each site has generally followed the methods of Sale and Dybdahl (1975), and has been directed towards detecting patterns of distribution of species, and hence of faunal similarities, a) among collections from units of the same type, b) among units of differing type, and c) among collection times. As samples from single units at both sites have usually contained only small numbers of fish, we have used analyses of covariance to take account of variations in sizes of sample when examining patterns of species richness and faunal similarity.

Analyses of diversity of samples were carried out as for the reef flat study but are not reported as they tell nothing beyond that told by analyses of species richness and faunal similarity. We used the Euclidean distance between a pair of samples as a measure of their faunal similarity. As used here, D_{ij} , the distance between samples i and j , is calculated as:

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

where s is the total number of species considered, P_{ik} is the proportion of fish in sample i that are of the k^{th} species, and P_{jk} is the equivalent proportion of fish in sample j . Euclidean distances were calculated including all species for which two or more individuals were collected at that site.

Species may interact, positively or negatively, when distributing themselves among single coral units. Such interactions would generate patterns of species association that would be independent of factors such as unit type or time of year. To determine, for given pairs of species, if such an interaction existed, we used a Chi-square analysis to examine the independence of occurrences of each species of the pair across single units.

Table 1. Rankings in each site of those species which occurred among 12 commonest in two or more sites (in each site, the 12 commonest species accounted for over 76% of fishes collected)

| Species | Rank in site | | |
|------------------------------------|--------------|--------|------------|
| | Reef flat | Lagoon | Reef slope |
| <i>Dascyllus aruanus</i> | 1 | 4 | 3 |
| <i>Eviota</i> sp. | 2 | 1 | 4 |
| <i>Pomacentrus popei</i> | 3 | 13 | 1 |
| <i>Pomacentrus wardi</i> | 4 | 10 | 17 |
| <i>Acanthochromis polyacanthus</i> | 6 | 11 | absent |
| <i>Parapercis cylindrica</i> | 7 | 6 | 11 |
| <i>Asteropteryx semipunctatus</i> | 8 | 2 | 46 |
| <i>Coris variegata</i> | 12 | 21 | 7 |

Results

The Faunas

At the lagoon site we collected 827 fishes belonging to 64 species. Twenty-four of these species were collected only once, and only 12 were taken more often than the mean number of 13 times. The modal number of fish per species was 3. At the slope site we obtained 525 fishes of 66 species. Thirty-four of these were obtained only once, 12 species were more common than the mean number of 8 fish, and the modal number was only 1 fish per species.

The three faunas represented by our collections at the lagoon, slope, and reef flat sites were not identical, although they did contain many species in common. In many instances, species present at all three differed from site to site in relative abundance. Only three of the 12 commonest species at the reef flat were among the 12 commonest at both other sites, and in general each pair of sites shared only half their twelve commonest species (Table 1).

Changes in Coral Units with Time

All units were measured in September 1973 and September 1974. The maximum height, longest horizontal diameter, and the maximum dimension at right angles to these were measured to the nearest 5 cm. The product of these served as a crude measure of unit volume. In contrast to the situation on the reef flat grid (Sale and Dybdahl, 1975), significant change in size was not recorded for any class of unit in either site. While some individual colonies grew, others decreased in size during the same time period. None of the colonies showed the extent of growth recorded for many L-units on the reef flat grid. This lack of increase in size of the units during the course of the experiment has facilitated our analysis of the patterns of distribution of species of fish.

Table 2. Classification, in terms of number of individuals collected, of the species at each site that were absent from at least one type of coral unit

| Number of fish in total sample at site | Number of species | |
|--|-------------------|-------|
| | Lagoon | Slope |
| 1 | 24 | 34 |
| 2 | 6 | 9 |
| 3 | 4 | 4 |
| 4 | 1 | 1 |
| 5 | — | 2 |
| 7 | — | 1 |
| 8 | 1 | 1 |
| 10 | — | 1 |
| 11 | — | 1 |
| 19 | — | 1 |
| 21 | — | 1 |
| 38 | — | 1 |
| 55 | — | 1 |

Discrimination among Coral Units by Species of Fish

At the lagoon site there was little evidence that any species of fish completely avoided units of one type in favour of units of the other. This was so despite the fact that 18 species occurred only in D-units and 18 other species only in L-units. Twenty-four of these 36 species were collected only once, and for only one of the 36 were more than 4 individuals collected (Table 2). This was a *Chromis* sp. of which 8 juveniles in a single group were taken from one L-unit in September 1973. All of the commoner species at the lagoon site occupied both classes of unit. Although many of them showed a preference for units of one or other type, 5 of the 7 commonest species in L-units were among the 7 commonest in D-units also.

At the slope site, by contrast, many species of fish did discriminate among units to the extent that they completely avoided units of certain types. Of the total of fish collected, the three B-units yielded 183 fish of 40 species, the four C-units yielded 166 fish of 37 species, but the three P-units produced 176 fish of only 21 species.

As in the lagoon site many of the species absent from one or more types were rare in the total collection (Table 2). However, 15 of the 23 species collected more than three times did not occur in all three classes of unit. Of these, 7 were common enough and distributed in such a way that their complete absence from units of one type is unlikely to have been a chance event ($P < 0.05$, Chi square). These seven species were among the 12 commonest species at the slope site.

Temporal Partitioning of Habitat by Fish

The three collections each year of the experiment were spaced to permit assessing which species recruited in the winter, the spring/summer, and the summer/au-

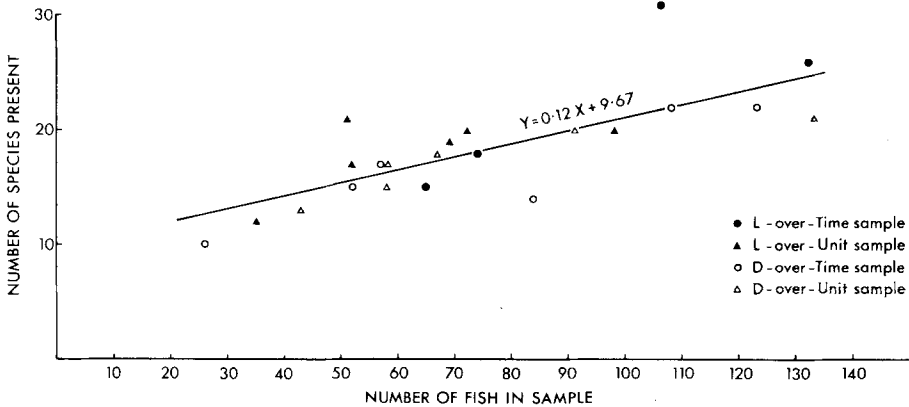


Fig. 1. Four different types of pooled sample of fishes from the lagoon site yield a single positive linear relationship between the number of species present in a sample and the number of fishes in that sample. The regression coefficient is significant ($t_{17} = 5.17$, $P < 0.01$)

tumn months (Sept, Dec/Jan, and May collections respectively). They provide evidence indicating that only 5 species were seasonally unavailable as recruits, although many species, rare in the total collections, were missing at one or more seasons.

At the lagoon site, 4 of 17 species common enough to test (i.e. at least 7 fish collected) failed to be recruited at all three seasons. *Stethojulis axillaris* (8 fish collected) missed May samples, *Pomacentrus popei* (= *sufflavus*) (12 specimens) missed September samples, and a group of 8 juvenile *Chromis* sp. and one of 11 juvenile *Cheilodipterus* sp. were each collected in September 1973.

At the reef slope site, one of 12 species common enough to test was seasonally unavailable. *Pseudochromis polyacanthus* (8 specimens) did not occur in May samples.

Species/Numbers Test for Microhabitat Partitioning

In samples small enough that the entire species pool is not likely to be represented in each, a positive relationship between the number of species present and the number of individuals in the sample is expected. We used this relationship in a test for microhabitat partitioning among the species of fish collected from each class of unit. Following our earlier procedure (Sale and Dybdahl, 1975) we pooled samples taken from each class of unit in two ways. All samples from units of one class at one time were pooled as a sample 'over-Units'. All six samples from a single unit over the six collection times became a sample 'over-Time'. For each class of unit we used covariance analysis to compare the species/number curves generated by the two sets of pooled samples.

In none of the 5 classes of unit did significant differences exist between the species/number curves generated from samples pooled over units and samples pooled over time. Lagoon results are very straightforward with no significant differences in slope ($F_{3, 14} = 0.881$, n.s.) or in elevation ($F_{3, 17} = 1.832$, n.s.) of the species/number curve derived from any of the four sets of pooled samples (Fig. 1).

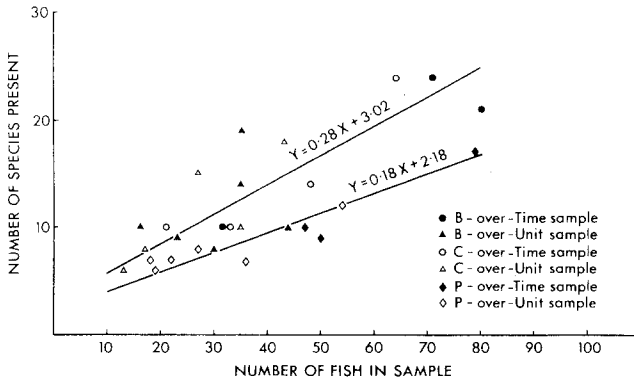


Fig. 2. Samples pooled from the reef slope site yield two different positive linear relationships between the number of species and the number of fishes in a sample. Pooled samples from B-units or from C-units (*upper line*) are richer in species than pooled samples from P-units (*lower line*). Both regression coefficients are significant (upper line, $t_{14}=4.78$, $P<0.001$; lower line, $t_6=5.49$, $P<0.005$)

The situation at the slope site is more complex (Fig. 2). When all six sets of pooled samples were compared, significant differences in the elevation of the species/number curves were present ($F_{5, 21}=3.12$, $P<0.05$). Subsequent analyses of covariance showed that a single species/number curve was generated by B-over-Time, B-over-Unit, C-over-Time, and C-over-Unit samples (for slope, $F_{3, 11}=0.33$, n.s., for elevation, $F_{3, 14}=0.15$, n.s.). A separate species/number curve was produced by P-over-Time and P-over-Unit samples (for slope, $F_{1, 5}=3.27$, n.s., for elevation $F_{1, 6}=0.69$, n.s.).

Faunal Similarities among Samples from Single Units

Euclidean distances calculated among pairs of single samples were analysed with reference to three questions as follows:

1. Similarity of Samples from Similar and Dissimilar Units. We first addressed the question of whether samples from units of one type were more similar to each other than to samples from units of different type, obtained at the same site and collection time. A simple picture was obtained for lagoon data. Using covariance analysis we examined the relationship between Euclidean distance obtained and the mean size of the set of samples being compared, for three classes of comparison: a) among samples from L-units (L-across-Units), b) among samples from D-units (D-across-Units), and c) among samples from units of opposite type (L-D).

Analysis showed a significant regression of Euclidean distance on size of samples being compared ($t_{14}=2.37$, $P<0.05$), but no significant differences among the three classes of comparison (for slope, $F_{2, 12}=0.30$, n.s., for elevation, $F_{2, 14}=2.11$, n.s.). The mean Euclidean distance between samples collected at any one time is independent of whether the samples being compared come from L- or from D-units.

Table 3. Covariance analysis of the relationship between mean Euclidean distance and mean size of samples compared for six classes of comparison of pairs of samples from the reef slope site

| Test ^a | Pooled regression | Differences in | |
|-------------------|------------------------|---------------------------|------------------------------|
| | | Slope | Elevation |
| A | $b = -0.03, P < 0.001$ | $F_{5, 24} = 0.31, n. s.$ | $F_{5, 29} = 6.97, P < 0.05$ |
| B | $b = -0.04, P < 0.005$ | $F_{1, 8} = 0.50, n. s.$ | $F_{1, 9} = 0.05, n. s.$ |
| C | $b = -0.03, P < 0.005$ | $F_{3, 16} = 0.23, n. s.$ | $F_{3, 19} = 0.38, n. s.$ |

^a In test A all six classes of comparison were examined. Test B compared C-across-Unit and P-across-Unit comparisons. Test C compared B-across-Unit, B-C, B-P, and C-P comparisons

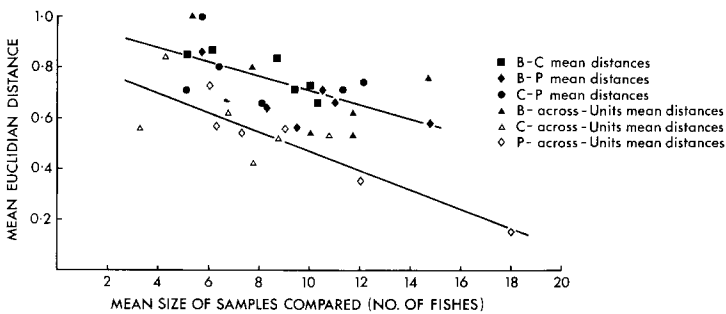


Fig. 3. Comparisons among samples from B-units, or between pairs of samples from units of differing type at the slope site (*upper line*) show less faunal similarity (i.e. greater Euclidean distance) than do comparisons among samples from P-units, or from C-units (*lower line*). In both instances the degree of faunal similarity increases significantly with the size of the samples being compared. Further details in text

Data from the slope site are substantially more complex. This is only partly due to the fact that instead of three, there are six types of comparison to examine. These are comparisons of pairs of samples taken from units of each of the three types, and three separate types of comparisons of samples taken from units of different type (i.e. B-P, B-C, and P-C comparisons).

A preliminary analysis of covariance incorporating all six classes of comparison (Table 3) indicated a slight overall negative regression of Euclidean distance on size of samples compared. A significant difference in elevation of this regression existed among the data from the different classes of comparison. A series of subsequent analyses established that the six classes of possible comparison yielded Euclidean distances that fall into two groups. On the one hand (Table 3, Fig. 3,) small Euclidean distances were obtained when comparing samples of given size from pairs of P-units, or from pairs of C-units. Significantly greater distances were obtained when comparing samples of this same size from pairs of B-units, or when comparing pairs of samples from dissimilar units.

Table 4. Covariance analysis of the mean Euclidean distance/mean sample size relationship for comparisons of pairs of single samples from each type of unit on the reef slope. For each unit type, the relationship obtained for comparisons 'across-units' is compared with that for comparisons 'across-times'

| Unit type | Pooled regression | Differences in | |
|-----------|---------------------------|-------------------------|-------------------------|
| | | Slope | Elevation |
| B-units | $b = -0.02$, n.s. | $F_{1,5} = 1.20$, n.s. | $F_{1,6} = 0.35$, n.s. |
| C-units | $b = -0.03$, n.s. | $F_{1,6} = 0.04$, n.s. | $F_{1,7} = 0.66$, n.s. |
| P-units | $b = -0.05$, $P < 0.001$ | $F_{1,5} = 1.97$, n.s. | $F_{1,6} = 5.74$, n.s. |

2. *Similarity of Samples from the Same or from Similar Units.* We next considered the question of whether successive samples from a single unit were more similar to one another than were samples taken from units of the same type at the same time. The picture obtained from the lagoon site is again the least complex. When Euclidean distances among pairs of samples from a single unit were compared with those obtained from samples taken from different units of the same type, a slight but significant negative regression on size of the compared samples existed ($b = -0.012$, $P < 0.05$). Nevertheless, analysis of covariance showed no significant differences in slope ($F_{3,14} = 0.69$, n.s.) or elevation ($F_{3,17} = 0.75$, n.s.) of this relationship. The Euclidean distance between samples from single D-units, from single L-units, from pairs of D-units or from pairs of L-units is a function of the size of the samples being compared, not of the source of the samples compared. The best estimate of the size of the Euclidean distance for all four types of comparison is given by:

$$y = 0.6941 - 0.012 x$$

where y = mean Euclidean distance and x = mean number of fish in the samples compared.

A more complex situation exists at the slope site. A series of analyses of covariance (Table 4) indicated that when samples taken from units of only one type are considered, no significant difference exists between Euclidean distances calculated among pairs of samples from single units, and those calculated among samples from pairs of units. However, the Euclidean distance obtained for a comparison of samples of given size is dependent upon the class of unit from which those samples were obtained. Euclidean distances are smaller among samples from P-units, and significantly larger ($P < 0.05$) among samples from B-units. Distances computed among samples from C-units are intermediate in size to these.

The Euclidean distances are independent of sample size except in the samples from P-units (Table 4), however, the best estimates of Euclidean distances are as follows:

- a) between samples from B-units, $y = 0.899 - 0.02 x$,
- b) between samples from C-units, $y = 0.801 - 0.03 x$,
- c) between samples from P-units, $y = 0.958 - 0.04 x$.

In all cases, y = Euclidean distance and x = mean size of samples being compared.

Table 5. Analyses of variance comparing the similarity of the initial and the subsequent faunas in each unit at the lagoon site

A) Comparing 5 Euclidean distances of all subsequent to the original fauna in a unit, with 5 randomly chosen distances among pairs of the subsequent faunas in that unit

| Source | df | SS | MS | <i>F</i> | <i>P</i> |
|------------|----|--------|--------|----------|----------|
| Distance | 1 | 0.2142 | 0.2142 | 5.74 | 0.05 |
| Coral unit | 9 | 2.2293 | 0.2477 | 15.36 | 0.01 |
| D × U | 9 | 0.3358 | 0.0373 | 2.31 | 0.05 |
| Residual | 80 | 1.2902 | 0.0161 | | |
| Total | 99 | 4.0695 | | | |

B) Comparing the Euclidean distances of December, January and May faunas from September, 1972 (initial), and from September, 1974, faunas in each coral unit. Analysis performed on data transformed as Log_e Euclidean distance

| Source | df | SS | MS | <i>F</i> | <i>P</i> |
|------------|----|---------|--------|----------|----------|
| Distance | 1 | 0.3126 | 0.3126 | 2.54 | n.s. |
| Coral unit | 9 | 4.7388 | 0.5265 | 7.73 | 0.01 |
| D × U | 9 | 1.1087 | 0.1232 | 1.81 | n.s. |
| Residual | 60 | 4.0848 | 0.0681 | | |
| Total | 79 | 10.2450 | | | |

3. *Similarity of September 1972 and Subsequent Samples.* Because the corals used as experimental units were in situ, the collections made in September 1972 were collections of "mature" assemblages of fishes. We examined the degree to which these first collections differed from subsequent collections made from each coral unit, using two analyses of variance. In the first, the Euclidean distances between the initial and each of the five subsequent samples from a unit were compared with five distances randomly chosen from those among the subsequent samples. In the second, Euclidean distances from the initial (September, 1972) sample to December, January, and May samples from a unit were compared with those between the September, 1973 sample, and December, January, and May samples.

The results for the lagoon site are shown in Table 5. The first analysis yielded a significant treatment × unit interaction ($F_{9, 80} = 2.31$, $P < 0.05$). Inspection of means indicated that for five of the units September 1972 samples differed more from subsequent samples than the latter did amongst themselves, but that for three units significant differences did not exist, and for two units the September 1972 sample was more similar to subsequent samples than they were amongst themselves ($P < 0.05$, Student-Neuman-Keuls test in all cases). The second analysis, which directly compared the similarities of the two September samples to all other samples collected from each unit showed no significant differences in Euclidean distances obtained. That is, the original fauna from each unit did not differ any more from December, January, or May samples from that unit than did the other September sample.

Table 6. Analyses of variance comparing the similarity of the initial and the subsequent faunas found in each unit on the slope site

A) Comparing 5 Euclidean distances of all subsequent faunas to the original fauna in a unit, with 5 randomly chosen distances among pairs of the subsequent faunas in that unit

| Source | df | SS | MS | <i>F</i> | <i>P</i> |
|------------|----|--------|--------|----------|----------|
| Distance | 1 | 0.2089 | 0.2089 | 3.65 | n.s. |
| Coral unit | 9 | 1.5859 | 0.1762 | 3.49 | 0.01 |
| D × U | 9 | 0.5148 | 0.0572 | 1.13 | n.s. |
| Residual | 80 | 4.0368 | 0.0505 | | |
| Total | 99 | 6.3464 | | | |

B) Comparing the Euclidean distances of December, January, and May faunas from September, 1972 (initial), and from September, 1973 faunas in each coral unit. Analysis performed on data transformed as Log_e Euclidean distance

| Source | df | SS | MS | <i>F</i> | <i>P</i> |
|------------|----|--------|--------|----------|----------|
| Distance | 1 | 0.0150 | 0.0150 | 0.14 | n.s. |
| Coral unit | 9 | 3.8218 | 0.4246 | 7.58 | 0.01 |
| D × U | 9 | 0.9461 | 0.1051 | 1.88 | n.s. |
| Residual | 60 | 3.3606 | 0.0560 | | |
| Total | 79 | 8.1436 | | | |

Table 7. Summary of results of contingency analyses for simultaneous occurrences of pairs of species among single units of the same type

| Unit | Number of species tested ^a | Number significant associations | |
|---------|---------------------------------------|---------------------------------|----------|
| | | Positive | Negative |
| Lagoon | | | |
| L-units | 12 | 3 | 0 |
| D-units | 12 | 4 | 0 |
| Slope | | | |
| B-units | 10 | 0 | 0 |
| C-units | 9 | 1 | 0 |
| P-units | 10 | 0 | 0 |

^a The 12 commonest species in each site were tested, but not all 12 occurred in all types of unit at the slope site

For once the results from the slope site were the more straight-forward. Table 6 shows that Euclidean distances between the September 1972 sample and all subsequent samples from a unit did not differ significantly from those among subsequent samples. Also, the September 1972 sample was no less similar to December, January or May samples from the same unit than was the Sep-

tember 1973 sample. Both analyses lead to the conclusion that the original fauna of each unit is comparable faunistically to the ones subsequently formed there during the course of the experiment.

Independence of Occurrences of Species among Units

We tested all pairs among the 12 commonest species at each site to establish whether distributions of individuals of a species among units of any type were independent of those of other species. The results of contingency tests seeking positive or negative associations of species are listed in Table 7. In no instance did we detect a negative association between species in their distributions. In more than 95% of cases, pairs of species were independent in their distribution among units of a given type.

Discussion

Rationale

Coral reef fishes partition habitat space on a broad scale (Hiatt and Strasburg, 1960; Jones, 1968; Sale, 1977). Recently (Goldman and Talbot, 1976; Talbot and Goldman, 1972) this fact has been quantitatively demonstrated for a reef 20 km from our study site. The species of fish found on a reef slope differ from those on a reef flat and this again differs from those found in a lagoon. Additional habitat subdivisions are possible.

Coral reefs support sufficient species of fish that despite this broadscale partitioning of space, large numbers of species still occur together in small areas. Goldman and Talbot (1976) cited collections of 150 (One Tree Reef) and 200 (Palau) species of fish in a single rotenone station. Smith and Tyler (1972) recorded the presence of 75 species on a single patch reef about 3 m diameter and 1.6 m high in the Bahamas. We have observed up to 35 species on patch reefs about $1/2$ this size in the One Tree Reef lagoon (unpublished data).

We have been concerned with understanding the factors affecting distribution of species of fishes on this local scale. That fish partition space on a broader scale is evidenced by the difference in the fauna we collected from our three sites. The sites were separated by less than 2 km of reef, and the faunas contain many species in common. However, different species dominate each and the diversities of the three faunas differ also. The faunas are comparable, because in all three sites we have collected those species of small fishes which are resident in isolated colonies of coral of various types. The species collected are ones which, in most cases, would have spent their lives in the immediate vicinity of the colony of coral from which they were removed. Many of the recruits to our colonies were young adults and juveniles, but many were newly settling larvae from the plankton. In general the more isolated units obtained a greater proportion of recruits from the plankton, although in no case was

all recruitment by this route. We believed (Sale and Dybdahl, 1975) that the results obtained from analysis of the data from our reef flat grid would have wider generality for reef fish communities. The studies reported in the present paper substantially support those results, and are important because although we again examine fishes resident in small isolated corals, the corals used had not been moved prior to the experiment and were located in parts of the reef that are physically less disturbed than is the reef flat. In that way the lagoon and slope sites are perhaps more typical reef habitats than was the reef flat site.

Adequacy of Time for Recruitment

The broad significance of our results depends heavily on the assumption that the length of time left between successive removals of fishes was sufficient for recruitment of fishes to have been completed. The present studies, because of the slightly different procedure used, provide additional evidence supporting this assumption.

In the reef flat study we used data obtained from visual censuses of control corals and published data on recruitment to artificial reefs 20 km from our site (Russell et al., 1974) to argue that the length of time provided for recruitment between successive collections was sufficient to ensure that numbers of fishes and species reached that normal for isolated colonies of the types used. We also argued that the species present in our reef flat units were comparable to those found on naturally occurring isolated colonies of similar size and form on the reef flat.

At the lagoon and reef slope sites we selected corals but left them in situ. Because of this we have been able to test whether recruitment following denudation was complete in terms of species composition as well as species number and number of fishes. Despite a weak seasonal cycle in numbers of fish and species recruiting to the coral units, mean numbers of fish and of species present in single units of each type did not differ significantly among collections. As on the reef flat grid, the time allowed between collections was sufficient for numbers of individuals and species to be restored. Our analysis of faunal similarities in Tables 5 and 6 indicates that both in the lagoon and reef slope sites recruitment following denudation results in a species composition faunistically indistinguishable from that which existed in each coral unit at the start of the experiment. The possibility that successional processes taking longer than about four months might be important in determining the species composition of assemblages in isolated corals of the types examined can be dismissed. The time allowed between denudations was sufficient for recruitment to have been completed.

Principal Results

The principal results reached from the reef flat study (Sale and Dybdahl, 1975) are fully borne out in the present data. These are that the fish distribute themselves among the coral units with an apparent absence of temporal partitioning

of habitat, and of fine scale habitat discrimination, only slight discrimination among the types of habitat offered, and apparently no mutual avoidance or antagonism. In short, chance of colonisation overwhelmingly determines the species composition of the group of species present in a habitat unit.

1. Lack of Temporal Habitat Partitioning. Evidence is available for very few species indicating that those species were not potentially able to recruit at all seasons. There is no evidence to suppose that the species of fish which use isolated corals are segregating by season of recruitment such that corals with space available at one season are occupied by one group of species while those with space open at another season are occupied by a predominantly different group of species.

Our data indicate that 8 common species might not recruit to particular sites at all three seasons. For three of them, recruits arrived in all three seasons if data from all sites are combined. The impression we have gained from our data has not been that recruitment of many species is seasonal, but rather that recruitment of most species is decidedly patchy. A given species may be common at a given season one year, but not at the same season in the subsequent year. Or it may be common as a recruit at one site while absent at other sites, only to become common at these sites at another time. Data from other authors have indicated the same phenomenon (Luckhurst and Luckhurst, 1977; Russell et al. 1977).

2. Some Discrimination among Types of Habitat Unit. Fish do discriminate among the classes of habitat unit used, but generally to a lesser extent than we would have predicted considering the difference in structure of the units supplied. This discrimination among types of unit differed among sites. It was most pronounced at the slope site, principally because of the degree to which species of fish discriminated the P-units from the others. The P-units maintained a distinct fauna comprising only 21 of the 66 species collected at this site. Overall, only 8 common species occurred in all three habitat types at the slope site, and 7 common species were missing from at least one type of unit.

By contrast, in the lagoon site, discrimination among the two types of habitat unit offered was less than that previously found for the reef flat site, and clearly less than that found on the reef slope. Single samples from D-units were faunistically no more similar to one another than to samples from L-units, and vice versa. Only one species absent from units of one type was common enough for its absence to be unlikely to have been a chance event. (Yet although 8 individuals of that species were collected, they were taken as a single group of juveniles occupying a single L-unit in September 1973. Any conclusion on unit preference of this species must remain tentative.) Five of the 7 commonest species in D-units were also among the 7 commonest species in L-units.

3. No Fine-Scale Habitat Discrimination. There is no evidence in any site that the species present have precise microhabitat requirements leading them to discriminate among units of the same class. This was shown by an analysis of the relationship between the number of species present and the number

of individuals present in samples pooled over several units of the same type, or over several collections from a particular unit.

It is clear that units of one type differ among themselves in structure and might be discriminated by species which chose to live in some but not in other units of the same type. If this occurred, then by pooling successive samples from a single unit, we'd expect to obtain, for a given number of fishes, a smaller number of species than if we were to pool samples collected from several units of that type. That our regression of number of species on size of sample was shown to be independent of whether the samples were pooled over units or over successive samples within units, and that this result applied to all types of unit used (Figs. 1 and 2), is convincing evidence that species of fish do not partition units in this way.

In the lagoon, the regression of number of species on size of pooled sample was the same for samples from D- and those from L-units. That is, the number of species in a pooled sample is dependent upon how big the sample is, not on whether it was formed by pooling successive collections from one unit, or by pooling collections from several units of the same type, nor on whether the collections came from L- or from D-units. This result had been obtained previously for the reef flat site (Sale and Dybdahl, 1975).

On the slope this is not true. The number of species yielded by a pooled sample of given size is greatest if the samples pooled had come from B- and C-units, and significantly smaller if the samples pooled had been collected from P-units. Nevertheless, despite this further evidence of the differences in the faunas attracted to the three types of unit, there is again, no evidence that the fishes discriminated among units of a single type.

Our results from the lagoon and reef slope sites in no way imply that the species of fish studied do not have microhabitat preferences such that different species use the coral units differently. It is obvious from the briefest observation that a planktivorous fish like *Pomacentrus popei* uses coral very differently to a fish like *Gobiodon quinquestrigata*. But our results do confirm the conclusion reached from the reef flat data. This is that microhabitat preferences do not function in such a way that species of fish discriminate among single units of the same type as suitable or as unsuitable living sites. In other words, if C-units on the slope, or L-units in the lagoon are suitable habitats for a particular species, all such units will be so. Microhabitat requirements must generally be broad enough that any unit of given type can provide suitable space for a species using that type of unit. Microhabitat preferences, particularly on the reef slope, must have played a major role in determining the distribution of species among the different types of unit.

4. No Mutual Avoidance. In none of the three sites have we been able to locate pairs of species, members of which appear to avoid one another in occupying coral units. In our reef flat study (Sale and Dybdahl, 1975) we used a regression analysis of the numbers present of each of a pair of species in each unit. Although we located several pairs of species whose distributions over units were positively correlated—members of the pair were common in the same units, and rare in others—we located no pairs that were negatively correlated in occurrence.

Correlation analysis may not have been the most appropriate. Firstly because of the rarity of even the commonest species many double zero values would be entered into each correlation analysis. Secondly, the small numbers of fish in all units made significant correlations of either sign unlikely. In analysing the lagoon and reef slope data we used an alternative procedure—contingency analysis of presence/absence data for each pair of species over all units of one type. Once again we reached the same conclusion. No pair of species in any type of unit appeared to avoid one another.

Degree of Order

Because of the variation among sites in the degree to which species of fish have discriminated among the types of unit offered, we tentatively suggest the slope site fauna shows the greatest degree of orderliness in distribution of species among units, while the lagoon site shows the least. At the lagoon site, fish did not discriminate between L- and D-units, even to the extent they did on the reef flat.

It is possible that this conclusion is an artifact arising from our use of units of different kinds in the three sites. Plate-like *Acropora* spp (our P-units) are very distinctive in form, and may strongly constrain the morphologies and locomotory patterns of species which can live among their branches. It would be interesting to determine if the fishes present at the slope site would show greater discrimination than those at the lagoon or reef flat sites if they had been offered a choice between comparable L- and D-units.

Conclusions

We believed (Sale and Dybdahl, 1975) that the results of our reef flat study held broad implications for understanding of the ecology of reef fish communities. However, the reef flat is a physically disturbed site, so it was possible that chance might play a large role in determining the distribution and abundance of reef fishes on the reef flat, but not in other, more predictable reef environments. In the latter, interactions among the species present at a site might lead to development of an ordered community that would not have time to develop on the reef flat where physical disturbances interrupted any successional processes.

Of the three sites we have studied the slope site is physically the most predictable. On the southern slope of Heron reef, it is the side least disturbed by major storms over the last 10 years (J. H. Connell, pers. comm.), and in 8 to 10 m water, temperature and salinity fluctuations can be expected to be less intense. The lagoon site is intermediate in conditions to the others. Our results indicate, however, that chance of colonisation is of primary importance in both these less disturbed reef sites as well as on the reef flat.

This conclusion leads us to doubt that the concept of an equilibrium community, organised through competitive processes among the species present is ever

important when considering communities of small reef fishes. In making this statement, we do not imply that species of reef fish do not differ in their requirements, or their competitive abilities. The many species present at any of our three sites certainly differ in the things they need and in their abilities to obtain them. Such differences may, and probably do, convey competitive advantages to particular species in particular habitats. These competitive advantages would have important evolutionary consequences, although demonstrating such competitive advantages experimentally would be very difficult.

However, on the basis of our results, at least for fish resident in isolated coral patches, such differences in requirements or competitive abilities as may occur do not play a major role in determining the small-scale distribution of species among sites that one sees on the reef. This local distribution is achieved almost entirely through chance recruitment and loss of individual fishes from the species pool available.

This interpretation leads logically to the statement that the small-scale distribution of species that one observes in a site at a particular time is not a constant phenomenon. It can be expected to change through time as new recruits arrive and residents are lost. The fish present at a given time are but a sub-set of the total pool of species which may use that site through time.

On the local scale at which we have worked, the diversity of species maintained is a function of a) the number of individual fishes present, and b) the number of species in the pool of potential recruits to that site. Factor a) is itself usually a function of the amount of living space—perhaps simply of the number of shelter spaces provided at the site—, although overlying this may be a seasonal fluctuation in the rate of recruitment so that during the winter months some available space is not filled by fishes. Indeed, in some habitats low recruitment may keep numbers always below any limit set by space (D. Williams, pers. com.).

Factor b) is a function of other factors outside the site including the fecundity, the potential larval longevity, and the extent of dispersal of larval fishes which might occupy that site. They will also include evolutionary and biogeographic aspects of reef fish communities.

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