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# TEMPORAL VARIABILITY IN THE COMMUNITY STRUCTURE OF FISH ON CORAL PATCH REEFS AND THE RELATION OF COMMUNITY STRUCTURE TO REEF STRUCTURE<sup>1</sup>

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**Abstract.** Fish assembled on 20 lagoonal patch reefs were censused eight times over 33 mo. Reefs, which ranged in size from 2.71 m<sup>2</sup> to 28.35 m<sup>2</sup> surface area, supported an average of 128 fish of 21 species at any one time. These were drawn from a total pool of 143 species, and, because of successive recruitments and losses of individual fish, each reef supported many more species during the study than were present at any one census.

Structure of the assemblages on each reef, in terms of species number, number of fish, and species composition, varied through time. Mean proportional similarity of assemblages on the same reef was 0.568,  $\approx$  15% greater than that between assemblages on different reefs (0.422). Structural attributes of reefs, other than size, were of little value in predicting the structure of the fish assemblages formed. The results are compatible with an essentially nonequilibrium view of reef fish communities. This view holds that species recruit to reef sites at varying rates, and independently of each other, while individuals are lost from sites (through death or emigration) also in a way unstructured with respect to the species composition of the resident fauna.

**Key words:** *community structure; coral reef fish; habitat; nonequilibrium community; recruitment variability; temporal variability.*

## INTRODUCTION

On coral reefs, groups of fish are established through the successive recruitments of individual juveniles from the plankton. In the majority of cases, individuals remain resident in the immediate vicinity throughout life (see references in Sale 1980a). The typically speciose assemblages at local sites are thus reasonably expected to be interactive communities of relatively permanent residents.

Recent studies of the structure of reef fish communities have tended to reach one of two diametrically opposed conclusions. On one hand, a number of studies have led to the perhaps more conventional view that these assemblages of fish exist at a more or less stable equilibrium maintained through biotic (chiefly competitive) interactions (Smith and Tyler 1972, 1975, Brock et al. 1979, Molles 1978, Gladfelter and Gladfelter 1978, Gladfelter et al. 1980, Anderson et al. 1981, Ogden and Ebersole 1981). Other studies have led to the conclusion that these are nonequilibrium assemblages of fish, strongly influenced by variations in recruitment from the plankton, and perhaps also by predation and other causes of mortality (Russell et al. 1974, Sale and Dybdahl 1975, 1978, Sale 1977, 1979, 1980b, Talbot et al. 1978, Bohnsack and Talbot 1980, Williams 1980).

These two groups of studies differ in two important respects. (1) There is a geographic separation, with all but one of the latter group (Bohnsack and Talbot 1980)

dealing exclusively with communities on the Great Barrier Reef. The first group chiefly concerns Caribbean studies, but includes some from Pacific sites (Hawaii, Gulf of California, Barrier Reef). (2) The "Australian" studies primarily concern assemblages of fish on small isolated coral heads, and small artificial reefs. The "Caribbean" group comprises a number of studies done at a larger spatial scale, although studies on small patch reefs (Smith and Tyler 1972, 1975) or small artificial reefs (Molles 1978) are included. It is possible that the difference in spatial scale of studies is alone responsible for the different conclusions drawn (Brock et al. 1979, Gladfelter et al. 1980, Ogden and Ebersole 1981). The larger scale "Caribbean" studies would be more relevant for the usual situations in which fish occur on reefs. Also, conclusions drawn from studies of artificial reefs (e.g., Talbot et al. 1978) may be of questionable applicability to real situations.

Few studies in either group have been of sufficient duration to provide direct evidence of the nature and extent of temporal variation in structure of fish assemblages. The present paper is the first of a series analyzing the structure of naturally occurring fish assemblages on each of 20 undisturbed small patch reefs, monitored over 33 mo. Community structure can be assessed in a number of ways, and we use the species richness, the number of individuals, and the species composition as measures of it. In the present paper we consider (1) temporal constancy in the assemblages present, and (2) the relationships between the fish fauna and various physical and biotic attributes of the patch reefs. The results are used to evaluate the conflicting

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views of the structure of reef fish communities in an attempt at resolution.

#### METHODS

This work was done in the main lagoon of One Tree Reef, Capricorn Group, Great Barrier Reef (23°30'S, 152°06'E), Australia. Data were obtained on the fish assembled at each of 20 patch reefs, 10 in the north-eastern quadrant and 10 in the southern (windward) quadrant of the lagoon. The reefs varied in size from 2.71 to 28.35 m<sup>2</sup> surface area (1.10 to 3.75 m diameter), and in the size and composition of their corresponding fish faunas. All reefs were in 3–5 m of water (low tide), and none was emergent. They were isolated from each other and from other patch reefs or nearby reticulated reef by open sand at least 2 m and usually well in excess of 5 m in extent.

The procedure used to census the fish at each reef has been described and evaluated by Sale and Douglas (1981). Briefly, a series of three or four separate visits by single divers is made to each reef over 3 or 4 d. On each visit a careful enumeration is made of all fish sighted. These enumerations are kept independent to the extent that no records from previous visits are carried by the diver while censusing each reef. The three or four enumerations are combined into a census which seeks to be the best estimate of the fauna actually present. For most species (residents) the maximum number recorded in any one enumeration is the number listed as present. For a small number of species which we know move about between patch reefs (wanderers), the number of individuals recorded as present is the largest number seen in two or more separate enumerations. Censuses built up this way are reasonably accurate records of that component of the fauna accessible to visual census, recording >85% of the species actually present, and 75% of the individuals. They are as accurate as complete rotenone collections, although each of these methods samples a different component of the total fauna (Sale and Douglas 1981). Eight censuses were made of each reef during a 33-mo period: August, December 1977; May, August, November 1978; May, August 1979; and April 1980.

Ten structural characteristics of each patch reef were measured in order to relate the nature of a reef to the fish fauna that lived there. These were (1) surface area, (2) volume, (3) maximum height, and (4) mean diameter of the reef, (5) its substratum diversity, and (6) topographic complexity, and the percentage cover of living (7) branched, and (8) massive stony corals, (9) sponges, and (10) bare or algae-covered rock surfaces.

A polyvinyl chloride tape measure was used to measure maximum width, length and height, and the circumference at the reef base. Reef surface area and volume were calculated using the maximum height and circumference, and considering the reef as a segment of a sphere. Mean diameter was the average of width and length.

Three line transects were placed across each reef, oriented at 60° to one another, using the tape measure stretched taut across the reef surface. Lengths of line segments overlying each of a number of categories of substrata were calculated (e.g., living branched *Acropora* spp., plate-like *Acropora* spp., *Pocillopora damicornis*, *Seriatopora hystrix*, *Porites andrewsi*, other *Porites* spp., other massive or encrusting corals, and plate-like *Montipora* spp.; dead branched coral; other dead coral or rock, usually covered by a fine sparse algal turf; sand; coral rubble; holes [deeper than the mouth diameter]; sponges and anemones). The lengths of line segment on the three transects were used to determine the proportion of the reef's surface composed of each type of substratum. These values were used to compute substratum diversity (using Levins' [1968] *B*). Subsequently, the various types of coral were combined into branched and massive categories, and the percentage cover of each substratum type determined. Only substrata which comprised at least 4% of reef surface on 10 or more reefs were used in subsequent analyses. On each transect, the tape was then positioned to follow the contours of the reef as closely as possible, yielding a "contour" length for the transect. The mean of the ratios of contour length/stretched length for the three transects was used as an index of topographic complexity of the reef (cf. Risk 1972, Luckhurst and Luckhurst 1978).

Multiple linear regression techniques were used to assess the degree to which these physical measurements could be used to predict the number of species or of fish, or the number of fish of particular species present on the reefs.

Temporal changes in the fauna of a reef and similarity of assemblages on different reefs were assessed by computing the similarity between censuses as:

$$C_{ij} = 1 - 0.5 \sum_{n=1}^s |p_{in} - p_{jn}|$$

where  $C_{ij}$  is the proportional similarity between censuses  $i$  and  $j$ , where there are  $s$  species, and where  $p_{in}$  and  $p_{jn}$  are the proportions of the total number of fish seen in the  $i^{\text{th}}$  and  $j^{\text{th}}$  censuses, respectively, that belong to the  $n^{\text{th}}$  species. The index ranges from 0.0 when two censuses have no species in common to 1.0 when the distribution of individuals among species is identical between censuses.

Numerical data were subjected to Bartlett's test before each parametric analysis was performed, and were transformed where necessary to stabilize variances. The analyses used (regression, analysis of variance and covariance) are, in any event, very robust, and tolerant of moderate departures from underlying assumptions of normality. Regression analysis was done on untransformed variables, and used a step-up procedure in which successive independent variables were added to the regression in that sequence which, at each step, maximized the variance accounted for. The procedure was

TABLE 1. Distribution of the 25 most common species among reefs and censuses. Shown are the number of reefs occupied at least once and the number of censuses at which the species was present on at least one reef. (*Pomacentrus* sp. = undescribed species illustrated in Allen [1975:216].)

Species	Family	Sightings	Reefs	Censuses
<i>Apogon doederleini</i>	Apogonidae	4891	18	8
<i>Asteropteryx semipunctatus</i>	Eleotridae	2622	20	8
<i>Acanthochromis polyacanthus</i>	Pomacentridae	1731	19	8
<i>Cheilodipterus quinquelineata</i>	Apogonidae	1143	20	8
<i>Amblygobius phalaena</i>	Gobiidae	948	20	8
<i>Apogon gracilis</i>	Apogonidae	839	6	5
<i>Chromis nitida</i>	Pomacentridae	724	16	8
<i>Pomacentrus</i> sp.	Pomacentridae	679	20	8
<i>Dascyllus aruanus</i>	Pomacentridae	524	11	8
<i>Pomacentrus popei</i>	Pomacentridae	503	9	8
<i>Ecsenius mandibularis</i>	Blenniidae	475	19	8
<i>Pomacentrus amboinensis</i>	Pomacentridae	465	18	8
<i>Thalassoma lunare</i>	Labridae	436	19	8
<i>Gobiodon okinawe</i>	Gobiidae	357	4	8
<i>Atrosalarius fuscus</i>	Blenniidae	327	12	8
<i>Coris variegata</i>	Labridae	246	20	8
<i>Apogon cyanosoma</i>	Apogonidae	238	14	8
<i>Cirrhilabrus temmincki</i>	Labridae	209	18	8
<i>Scarus sordidus</i>	Scaridae	201	16	8
<i>Dascyllus reticulatus</i>	Pomacentridae	186	6	8
<i>Labroides dimidiatus</i>	Labridae	178	19	8
<i>Petroscirtes fallax</i>	Blenniidae	155	15	8
<i>Pomacentrus pavo</i>	Pomacentridae	155	12	8
Eleotridae sp. 1	Eleotridae	149	9	8
<i>Gobiodon quinquestrigata</i>	Gobiidae	148	10	8

halted when no remaining variable significantly improved the regression equation (Snedecor and Cochran 1967). When sets of similarity values were to be compared, values used were randomly selected so that data from any census of a single reef were not used more than once.

## RESULTS

### *The fauna present*

The fauna sighted on the 20 reefs was made up of 143 species of fish. With the exception of 33 species classified as "wanderers," the fish seen on each patch reef were reliably present from day to day. Depending on habits and size, the individuals ranged widely over and around the reef, or were more sedentary, remaining over a small portion of it and consistently using certain specific shelter sites. The species differed greatly in abundance, with four common ones accounting for >50% of sightings of fish. Twenty-five species accounted for >90% of sightings. These 25 belonged to 7 families, of which the Apogonidae and Pomacentridae were numerically the most important. These 25 species are listed in Table 1, with the number of sightings made of each, the number of reefs they occupied, and the number of censuses in which they occurred. (The number of sightings of a species is not a measure of the size of its population, since many individuals would have been present in two or more censuses.) Fig. 1 shows the species abundance curve based on total sightings. Of the 143 species, 25 were sighted only once during the study.

On average, single patch reefs supported 128 fish of 21 species at any one census. These mean numbers varied among reefs from as many as 378 fish of 38 species (reef 19) to as few as 34 fish of 9 species (reef 5). Over the eight censuses, each reef supported substantially more species than at any one census (Table 2).

### *Differences in the fauna occupying reefs*

The relationship between number of species seen and total number of sightings of fish was used to assess the degree to which each reef was potentially able to support all 143 species. Theoretically, the relation between number of species and number of individuals should be a curve rising from the origin to an asymptote at the total species for the habitat. Quadratic regressions of number of species on number of fish were, therefore, fitted to data from each reef (over eight censuses) and from each census (of 20 reefs). In both cases, quadratic curves gave a significantly better fit to the data than did straight lines (improvement in variance due to regression: reefs  $F_{1,17} = 13.01$ ; censuses,  $F_{1,5} = 11.4$ ,  $P < .01$  for both), although in both cases the estimated intercept was significantly greater than zero. A quadratic analysis of covariance disclosed a significant overall regression of species number on sightings (accounting for 77% of the variance in numbers of species when all reefs were considered, and 83% of that when all censuses were considered), but a significant difference in intercept between the two sets of data (Fig. 2, Table 3). This shows that for a given number of sight-

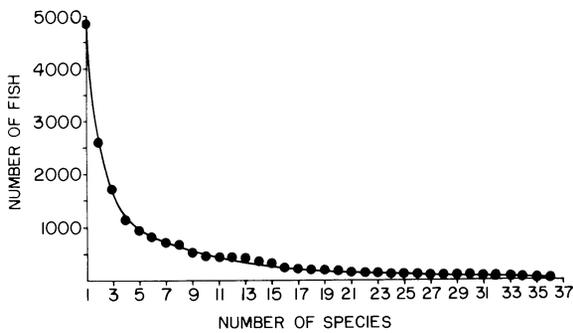


FIG. 1. Species abundance curve based on sightings of fish over the eight censuses. The fish are typically lognormally distributed among species.

ings, about seven more species occurred in a census of 20 reefs, than on a single reef over eight censuses, suggesting that spatial variability in the patch reef fish assemblages is only slightly greater than temporal variability.

Despite the fact that the northeast and south sets of reefs were similar in structure (see below), were situated only 1500 m apart and in a similar depth of water, and supported similar numbers of fish (54% of sightings were on south reefs), some differences existed in the faunas they supported. Only 17 of the 25 species most abundant on the northeast reefs were also among the 25 most abundant on the south reefs. This locational difference in the numerically dominant fauna was sufficient that when the ranks of all species among the 25 commonest at either site were compared, no significant association existed (Spearman's  $r_s = -0.11$ , 31 df, NS). Although *Apogon doederleini* and *Asteropteryx semipunctatus* were respectively the first and second most common species at both sites, there were wide variations between sites in ranking of the other common species.

Differences in the fauna among individual reefs were assessed by calculating the similarity ( $C_{ij}$ ) between all pairs of assemblages at single censuses. The May 1978 census provides typical data. Substantial differences in composition exist between assemblages on different reefs; mean similarity in May 1978 was  $0.422 \pm 0.005$  (SE). Despite the overall faunal differences between the northeast and south sets of reefs, neighboring individual reefs were not significantly more similar to one another than to reefs in the other set (Table 4), although the mean similarities within and between sets do show that trend.

#### Relation of fish fauna to reef structure.

Reefs were chosen at each site to represent a range of sizes and structure. Nevertheless, an attempt was made to ensure that the two sets of reefs were closely comparable. We were reasonably successful in achieving this (Table 5). Only in percent live coral cover were

differences between sites pronounced (south reefs averaged twice the live coral cover of northeast reefs). Even here, differences among reefs at the same site were great enough that the difference between sites was non-significant (Table 5).

The relationships between the faunas seen on reefs, and the 10 measured attributes of reefs, were examined by step-up multiple linear regression. Among the 10 independent variables, there were 11 cases of significant intercorrelation ( $r > +0.44$ ). Those among reef volume, surface area, height, and diameter were expected, and accounted for 5 of the 11 cases. Intercorrelations were borne in mind when results of regression analyses were examined. None occurred between apparently important variables.

The total number of species seen on a reef over all censuses regressed significantly on 6 of the independent variables when they were separately tested. These were, in descending order of importance, surface area ( $r^2 = 0.677$ ), volume ( $r^2 = 0.593$ ), mean diameter ( $r^2 = 0.453$ ), percent cover of bare and algae-covered rock ( $r^2 = 0.444$ ), topographic complexity ( $r^2 = 0.308$ ), and percent cover of branched coral ( $r^2 = 0.213$ ). The relationship with surface area was significantly improved by including percent cover of bare and algae-covered rock ( $r^2 = 0.807$ ), or (to a much smaller degree,  $r^2 = 0.765$ ) percent cover of living branched coral. Further addition of variables gave no significant improvement. The predictive equation for total number of species is thus:

$$Y = 47.63 + 1.53X_1 - 0.27X_2$$

where  $Y$  = total number of species occurring on a reef,

TABLE 2. Numbers of fish and species present on each patch reef: mean number per census and total over the study.

Reef number	Number of species		Number of fish	
	Total	Per census	Total sightings	Per census
1	65	29.75	1927	240.88
2	45	17.38	1627	203.38
3	38	19.63	1003	125.38
4	27	14.38	1145	143.13
5	24	8.50	268	33.50
6	36	18.00	469	57.88
7	38	18.25	789	98.63
8	36	17.75	390	48.75
9	37	14.25	1072	133.88
10	43	18.63	709	88.63
11	48	19.38	582	72.75
12	52	25.00	821	102.63
13	48	19.50	498	61.25
14	42	21.25	656	82.00
15	50	17.63	744	93.00
16	50	23.88	669	83.63
17	41	15.88	408	51.00
18	72	34.38	2165	270.63
19	76	38.38	3033	376.63
20	63	29.25	1487	185.75

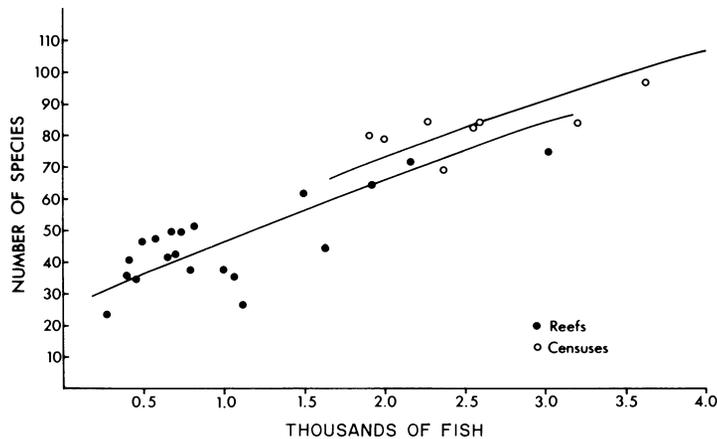


FIG. 2. The quadratic relationship between number of species and number of fish obtained from (a) single censuses of all 20 reefs, and (b) eight censuses of single reefs. A significant difference in elevation of the curves exists (Table 3), indicating that, for a given number of fish, a census of several reefs yields about seven more species than repeated sampling of a single reef.

$X_1$  is the surface area of that reef, and  $X_2$  the percent bare and algae-covered rock on it. This relationship accounts for 80.7% of the variance in number of species.

The mean number of fish present on a reef at a census was related to surface area ( $r^2 = 0.77$ ), to reef volume ( $r^2 = 0.72$ ), and to reef diameter ( $r^2 = 0.67$ ), but to no other measured variable. Inclusion of a second independent variable with surface area did not improve the relationship significantly.

Thus the size of a reef, particularly when expressed as surface area, is the single most important measured attribute in predicting the richness or abundance of the fish fauna assembled on it. An improvement in prediction of the number of species is afforded by including information on the proportion of bare or algae-covered rock on the reef, but other measured attributes were not useful.

Similar regression analyses were performed on the numbers of each of the 10 species most abundant over the censuses, to examine possible preferences of these species for particular features of the reefs. Where a significant difference between sites occurred in the mean abundance of a species (assessed by Mann Whitney  $U$  test with  $P < .05$ ), data from the northeast and the south reefs were considered separately.

Distribution of 2 of the 10 species (*Dascyllus aruanus* and *Apogon gracilis*) was not related to any of the measured attributes (Table 6). Of the remaining 8 species, distributions of 4 were most significantly related to size of reef, either as surface area or volume, with no other attribute significantly improving the relationship. These were *Apogon doederleini*, *Acanthochromis polyacanthus*, *Cheilodipterus quinquelineata*, and *Chromis nitida* (the latter only on the northeast reefs). *Pomacentrus popei* had a distribution on the northeast reefs related to reef volume, but on the south reefs, its distribution was best predicted jointly by percent cover

of bare and algae-covered rock, reef surface area, and volume (in order of importance). The three remaining associations were with substratum diversity (*Asteropteryx semipunctatus*), percent cover of bare and algae-covered rock (*Pomacentrus* sp.), and percent cover of massive corals (*Amblygobius phalaena* on south reefs only). Worth noting in Table 6 are the facts that in only 1 of 14 associations examined was the regression improved by including more than one type of independent variable (*P. popei* on south reefs), that attributes related to reef size were included in 6 of the 14 relationships, and that in 5 of the 14 cases, no significant associations existed with any of the reef attributes included.

To assess the temporal constancy of the relationships between faunal structure and reef character, regressions were made of numbers of species and fish present at each census against reef attributes. Only reef attributes identified as important in analyses of the total data were used (surface area and percent rock cover for number of species, surface area alone for number of fish). Table 7 shows that for number of species and particularly for number of fish there is marked variation in the form of resulting regressions, and in the degree to which they account for variance in the dependent variable. All regressions were significant ( $P < .05$ ) except for that between number of fish and reef surface area in November 1978. This variability in relationships is illustrated in Fig. 3, which plots the proportion of variance accounted for by regression on the chosen variable(s) at each census.

Inspection of raw data suggested that part of the temporal variability in Table 7 and Fig. 3 might be because certain species recruited to some reefs in large numbers, and showed correspondingly large fluctuations in numbers present between censuses. The regression analyses were repeated after two apogonids (*Apo-*

TABLE 3. Covariance analysis of the relationship between number of species and number of fish present in (a) each of 20 patch reefs over eight censuses, and (b) each of eight censuses of 20 reefs. For a given number of fish, a census contains approximately seven more species than a series of samplings of one reef (see FIG. 2).

Source of variation	Deviations from regression				
	df	SS	MS	F	P
Reefs alone	18	1459.38	81.08		
Censuses alone	6	249.98	41.66		
Summed	24	1709.36	71.22		
Pooled	25	1782.33	71.29		
Differences between slopes	1	72.97	72.97	1.02	NS
Total	26	2412.75	92.80		
Differences between intercepts	1	630.41	630.41	8.84	<.01

*gon doederleini* and *A. gracilis*) and one pomacentrid (*Acanthochromis polyacanthus*) had been excluded from the data. This had little effect on regression of species number, but halved the variability in the amount of variance explained by regression of number of fish (Fig. 3). Regression coefficients and intercepts still varied about two-fold among censuses. Overall, the variability seen in these relationships of assemblages to reef structure makes them of little general predictive value.

#### Temporal variability in the assembled fauna

All but 1 of the 25 most common species occurred at all eight censuses, although numbers of each present varied. Since recruitment from the plankton shows a marked summer peak at One Tree Reef (Russell et al. 1977, Talbot et al. 1978), variation in number of fish present was not unexpected. A two-factor analysis of variance was applied to the census data on numbers of fish and of species. Reefs and seasons were the two factors, and the first six censuses provided two replicates of August, November–December, and May seasons. The final two censuses were not used. Both number of species and of individuals showed significant heterogeneity among reefs and among seasons. The interaction term was not significant (Table 8).

Student-Newman-Keuls analysis of the season effect showed that significantly more fish and species occurred on reefs during May than in the other two seasons ( $P < .05$  in both cases). No other significant differences existed in the numbers of species present, but there were more individuals present on the reefs in November–December than in August ( $P < .05$ ). Despite these significant seasonal differences, the seasonal effect accounted for only 3.6 and 1.5% of variance in number of fish and species, respectively. Variation among all reefs accounted for 68.0 and 84.0%, respectively, leaving 28.4% of variance in number of fish and 14.5% of variance in number of species due to other factors.

For each reef, we determined the proportional similarity of the fauna recorded at each census to that at each of the other censuses. Fig. 4 plots the means of these similarity values for each census of each reef. Three points emerge from Fig. 4:

1) The fauna present at a reef at one census is seldom very similar in species composition to that present at the same reef at the other seven census times. The mean degree of similarity over the 20 reefs was  $0.568 \pm 0.009$  (SE).

2) Reefs vary in the average level of similarity among censuses, and also in the degree to which censuses differ in their levels of mean similarity.

3) Where successive censuses show marked changes in degree of similarity to others, the pattern of changes does not readily appear common to a majority of reefs.

We searched for patterns in these similarity data in two ways. To determine the extent to which mean intercensus similarity was influenced by reef size (surface area), or by size of the fish assemblage, we ran a multiple linear regression of mean similarity over all censuses against these two factors. Mean intercensus similarity was positively related to both factors when tested separately. Of the two factors, surface area accounted for the greater proportion of variance in similarity ( $r^2 = 0.318$  and  $0.255$  for surface area and number of fish, respectively). Inclusion of both in a regression did not significantly improve its predictive power, and a substantial amount of variance remained unaccounted for.

Our second approach used a two-factor analysis of variance to examine the effects of censuses and reefs on intercensus similarity. To avoid repeated use of similarity values, this analysis was run on a subset of the data matrix. For each census of a reef, similarity to three other randomly chosen censuses of that reef provided three replicates for the analysis. Randomization was controlled so that these three were not also used as values for their other censuses. The analysis

TABLE 4. Analysis of variance comparing the similarities of assemblages among northeast reefs, among south reefs, and between northeast and south reefs. To ensure independence of the data, similarity values were selected at random from all pairwise comparisons of northeast reefs, south reefs, and northeast/south reef combinations with each reef used only once.

Comparison		n	$\bar{x}$	SE
Between northeast and south reefs		10	.360	.048
Among northeast reefs		5	.477	.071
Among south reefs		5	.429	.050
Source	df	MS	F	P
Between	2	.0244	1.16	>.05
Within	17	.0210		
Total	19			
Cochran's C = .410 NS				

disclosed highly significant census and reef effects, but no interaction between them (Table 8).

The lack of significant interaction confirms that the variation among reefs is independent of that through time. Although we ran Student-Newman-Keuls comparisons of both census means and reef means, the results did not usefully discriminate groups of reefs or censuses. Both sets of mean similarities were broadly overlapping (census means ranged from 0.49 to 0.62, reef means from 0.46 to 0.71). We could detect no obvious temporal patterns among the census means, nor ones related to reef attributes among the reef means. For example, the two reefs on which assemblages showed the greatest and the least intercensus similarity (reefs 18 and 16, respectively) differed in size (reef 18, third largest, was twice the size of reef 16), but were nearly identical in all other attributes. Furthermore, while the five reefs with assemblages showing the greatest intercensus similarity included the three largest, the second smallest was also among them.

#### DISCUSSION

##### *A representative reef fish assemblage*

This study has shown that assemblages of fish resident on small, natural, undisturbed, patch reefs at One Tree Reef possess a structure which (a) is related only weakly to attributes of the reefs, other than their size, and (b) varies substantially through time.

In our view, the variability observed, both among reefs and among censuses, is substantial. While we acknowledge the subjective judgment this term implies, we point to the data of Fig. 3 and Table 7 which show wide variation in form and in success of equations predicting numbers of species and fish on patch reefs, and to the data in Fig. 4 showing that mean similarity among censuses of single patch reefs is only 0.568 (i.e., successive censuses of an assemblage differ on average by 43%). We do not believe such results are readily reconciled with an equilibrium view of reef fish assemblages. How typical, therefore, are the assemblages we studied?

The fauna sampled is a taxonomically and trophically diverse one showing a typical lognormal distribution of relative abundances. It occurred on 20 patch reefs typical in size and appearance of the large number of such reefs which occur scattered through the One Tree lagoon. In addition to these nonemergent reefs, the lagoon contains large emergent patch reefs as much as 200 m in diameter, and extensive, anastomosing reef walls, also usually emergent (Davies et al. 1976). All of these structures support resident fish, many of which are of species found on patch reefs in this study.

##### *Habitat segregation*

Species of fish are not distributed randomly over the habitats of a coral reef. On a broad spatial scale there is clear habitat segregation, with substantially different

TABLE 5. Structural attributes of 10 northeast reefs and 10 south reefs (mean and SE). Test of difference in surface area of reefs was done on data transformed as  $\log_e$  due to heterogeneity of variances. All other tests on untransformed data (variances homogeneous, Cochran's test,  $P = .05$ ).

Attribute	Northeast reefs		South reefs		$t_{18}$	$P$
	$\bar{x}$	SE	$\bar{x}$	SE		
Diameter	1.84	.05	1.95	.17	.42	>.5
Surface area	6.63	1.15	9.87	2.32	1.27	>.2
Volume	2.29	.68	3.60	1.18	.96	>.4
Topographic complexity	1.64	.10	1.64	.06	.05	>.5
Substratum diversity	3.22	.29	2.94	.25	.73	>.4
Percent dead coral rock	43.14	5.26	44.02	5.49	.11	>.5
Percent live coral	16.06	4.85	33.78	7.35	2.01	>.05

groups of species found on seaward slopes, reef flats, and lagoons (Hiatt and Strasburg 1960, Chave and Eckert 1974, Clarke 1977, Sale 1977, 1980a). In lagoon sites at One Tree Reef, Goldman and Talbot (1976) recorded 100 species, of which 20% were endemic to lagoons.

On smaller spatial scales habitat segregation continues but is less pronounced, being reflected in different relative abundances rather than in presence and absence of species among habitats. With a few exceptions, the 143 species we observed are all typical lagoonal forms, and can be found on small patch reefs throughout life. However, many of them occur in other lagoonal habitats as well (such as large emergent patch reefs), and some, like *Pomacentrus coelestis*, recorded once in our study, are more common in nonlagoon sites.

Although large in number of species, this patch reef fauna is a distinct subset of the total lagoon fauna. A number of common species occupy open sandy regions of the lagoon and did not appear in the censuses. Others, such as *Pomacentrus flavicauda* or *Hemigymnus melapterus* were present on the patch reefs, but are much more common on larger emergent reefs (P. J. Doherty, *personal communication*). Still others, such as *Siganus chrysospilus*, were present only as juveniles, moving to other lagoon habitats at maturity. Also, the difference in relative abundances of species which we detected between the northeast and the south reefs indicates that there is further subtle habitat segregation (perhaps in response to aspects of water quality at these windward and leeward locations) within the set of species occupying lagoonal patch reefs.

The existence of (increasingly subtle) habitat segregation at these smaller spatial scales indicates that few if any species are totally passive in their selection of habitats at the time of settlement. The possibility exists, therefore, that knowledge of habitat characteristics

TABLE 6. Results of multiple regression analyses relating abundance on reefs of each of the 10 most common species to 10 structural attributes of reefs. Further details in text.

Species	Reef attribute	$r^2$
<i>Apogon doederleini</i>	volume	.768
<i>Asteropteryx semipunctatus</i>	substratum diversity	.230
<i>Acanthochromis polyacanthus</i>	volume	.806
<i>Cheilodipterus quinquelineata</i>	surface area + volume	.828
<i>Amblygobius phalaena</i> (northeast)	no predictors	...
(south)	percent live massive coral	.494
<i>Apogon gracilis</i>	no predictors	...
<i>Chromis nitida</i> (northeast)	surface area	.730
(south)	no predictors	...
<i>Pomacentrus</i> sp.	percent dead massive coralline rock	.401
<i>Dascyllus aruanus</i> (northeast)	no predictors	...
(south)	no predictors	...
<i>Pomacentrus popei</i> (northeast)	volume	.809
(south)	percent dead massive coralline rock + surface area + volume	.939

can be used to predict the structure of the fish assemblage on individual patch reefs.

#### Relation of faunal structure to reef structure

Species varied in their abundance from reef to reef, and adjacent reefs supported different groups of species. Difference among reefs was the most important component of variability in numbers of fish and species during the first six censuses (68 and 84% of variance respectively, Table 8). Despite this, we were unable to find relationships between the structure of assemblages and attributes of the reefs which reliably accounted for much of this variability. Simple size of reef, crudely measured as surface area, was the best predictor of the number of fish supported, and, with the addition of percent cover of bare and algae-covered rock, of the

number of species. Analyses run for each census in turn, however, showed both of these relationships to be very variable, both in the magnitudes of coefficients derived, and in the proportion of variance in number of fish or species accounted for (Table 7, Fig. 3). One reason is that certain species recruit seasonally in large numbers to some reefs, but this by no means explains fully the observed variability.

The distribution when all reefs are considered of the 10 most common species was also poorly accounted for by information on reef structure (Table 6). Again, reef size was the attribute most likely to be of value.

The failure of attributes such as percent cover of live branched or massive coral, substratum diversity, and topographic complexity to be more important as predictors of assemblage structure requires comment. To-

TABLE 7. Variation among censuses in (A) the relationship of number of species to reef surface area ( $X_1$ ) and percent bare coralline rock ( $X_2$ ), and (B) the number of fish to reef surface area ( $X_1$ ). Also shown are similar relationships but with two species of apogonid (*Apogon doederleini* and *A. gracilis*) and one pomacentrid (*Acanthochromis polyacanthus*) omitted from the data.

Census	Total data				Three species omitted			
	$a$	$b_1$	$b_2$	$r^2$	$a$	$b_1$	$b_2$	$r^2$
A. Number of species ( $y = a + b_1X_1 + b_2X_2$ )								
Aug 1977	20.25	.64	-.10	.554	18.86	.60	-.09	.546
Dec 1977	19.29	.67	-.11	.657	17.75	.64	-.10	.654
May 1978	22.31	1.10	-.14	.865	20.93	1.04	-.12	.802
Aug 1978	19.64	.94	-.13	.868	17.71	.92	-.12	.870
Nov 1978	20.33	.97	-.13	.865	19.61	.90	-.14	.865
May 1979	16.75	1.09	-.09	.810	14.59	1.09	-.08	.818
Aug 1979	14.80	1.12	-.09	.790	13.29	1.09	-.08	.788
Apr 1980	20.08	.87	-.09	.662	18.84	.82	-.09	.636
B. Number of fish ( $y = a + b_1X_1$ )								
Aug 1977	-14.01	13.23		.837	25.32	5.25		.468
Dec 1977	33.11	10.38		.488	23.11	5.24		.540
May 1978	-67.54	29.95		.886	55.28	6.83		.551
Aug 1978	6.89	12.83		.822	35.62	6.00		.560
Nov 1978	87.01	8.87		.122	26.12	7.22		.515
May 1979	52.64	9.25		.254	26.06	6.80		.858
Aug 1979	36.25	7.61		.425	30.53	4.75		.651
Apr 1980	22.55	12.65		.648	24.95	6.72		.760

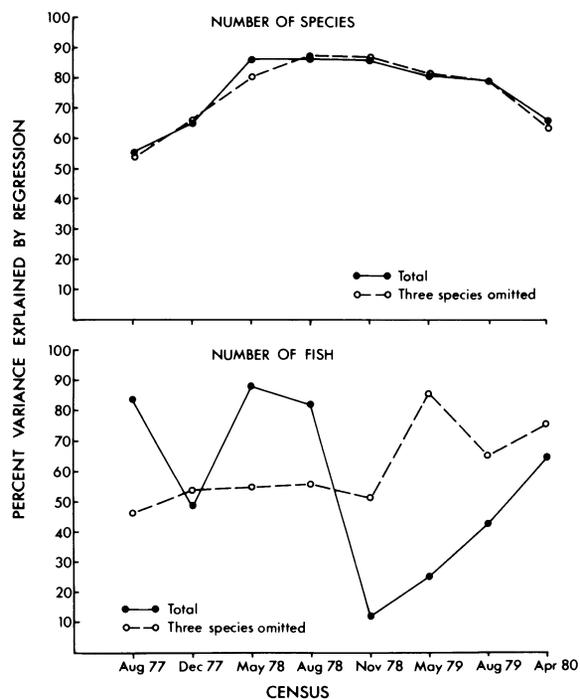


FIG. 3. Graphs showing marked and irregular variability among censuses in the extent to which numbers of species and fish on reefs can be predicted by regression on chosen reef attributes. Part of this variability is eliminated by deleting from consideration three species which recruit in large numbers to some reefs. Further details in text.

pographic complexity has several times been identified as an important predictor of the diversity of reef fish assemblages (Talbot 1965, Risk 1972, Talbot and Goldman 1972, Luckhurst and Luckhurst 1978), yet here, it has failed to survive as a significant independent variable in any of the regressions. On its own, this attribute predicted total species richness poorly (30.8% of variance accounted for), and did not significantly enhance the predictive power of other attributes when added to them. It was also a predictor, on its own, for abundances of two single species on the northeast reefs (*Chromis nitida*, 58% of variance, *Pomacentrus popei*, 54% of variance). For both species, other reef attributes were much more effective (Table 6).

The discrepancy with earlier studies is surprising, but may be due to two factors. Risk (1972) and Luckhurst and Luckhurst (1978) rigorously excluded from consideration all species not very strongly associated with the substratum, whereas we included all species present on our reefs that we could census visually. Other authors reached their conclusions on the importance of topography on the basis of suggestive but statistically inadequate data relating diversity to topography (see discussion in Sale 1980a). Perhaps they were influenced by the attractiveness of the parallel to the importance of structural complexity in predicting diver-

sity in bird (Mac Arthur and Mac Arthur 1961), and lizard (Pianka 1966) communities. Whatever its cause, the discrepancy is real. Topographic complexity was not significantly correlated with other independent variables, and could not have been omitted by our regression procedure if it had had a significant effect.

The present data indicate that topographic complexity is not a useful predictor of the species richness of reef fish assemblages on patch reefs at One Tree Reef. Substratum diversity appears a similarly weak predictor. Percent bare or algae-covered rock, however, does significantly assist in predicting total species richness. This attribute also was the most useful predictor of numbers for 2 of the 10 most common species. While it is true that by choosing a wide range of sizes of reef we expect attributes related to size to be important in predicting the structure of assemblages, other descriptors of the reefs, if reliably related to aspects of the fish assemblage, would still contribute significantly in a multiple regression. That, in general, they did not, suggests that the measured attributes are not closely related to those characteristics of a reef which make it attractive and suitable to fish, or that fish show broad tolerances when responding to habitat features.

It remains possible that other attributes of reefs will be found which are good predictors of the fish assemblages present on them, although the variation among censuses in the relationships with reef size (Fig. 3) makes this possibility seem remote.

A useful approach may be to examine the microhabitat requirements of newly recruiting juveniles and relate the presence of these features on patch reefs to the species of fish resident there. Certainly, species of *Dascyllus* and *Gobiodon* are strongly tied to specific microhabitats (Tyler 1971), and measures assessing availability of these may usefully predict numbers of these species. Data on microhabitat choices by recruits to these reefs are now being collected.

TABLE 8. Analyses of variance of number of species (A) and fish (B) present on 20 reefs at two censuses in each of three seasons (data transformed as  $\log_{10}x$  prior to analysis). Further details in text.

Factor	df	SS	MS	F	P
<b>A. Species</b>					
Season	2	.230	.115	4.58	<.05
Reef	19	12.974	.683	27.18	<.001
S × R	38	.734	.019	.77	NS
Residual	60	1.508	.025		
Total	119	15.446			
<b>B. Fish</b>					
Season	2	2.336	1.168	7.08	<.01
Reef	19	43.756	2.303	13.96	<.001
S × R	38	8.399	.221	1.34	NS
Residual	60	9.900	.165		
Total	119	64.391			

TABLE 9. Analysis of variance of similarities of assemblages on reefs at each census to other randomly selected assemblages on the same reef. The lack of significant interaction confirms that the variability across reefs apparent in Fig. 4 is independent of variation across censuses.

Source of variation	df	SS	MS	F	P
Censuses	7	1.088	.1555	8.37	<0.001
Reefs	19	2.838	.1494	8.04	<0.001
C × R	133	2.574	.0194	1.04	NS
Residual	320	5.945	.0186		
Total	479	12.445			

### Temporal variability

Pronounced change through time in the relationship between numbers of fish or species and reef size (Table 7) is but one indication of temporal variability in the structure of the assemblages studied. While significant seasonal variation occurred in numbers of fish and species over the first six censuses, this accounted for only a very small component of the total variability present in the data (3.6 and 1.5% of variance in number of fish and species, respectively, Table 8). Residual variation, due neither to overall seasonal nor reef effects accounts for 28.4 and 14.5% of variance in number of fish and species. Aseasonal temporal change and changes unique to particular reefs must be pronounced.

The faunal similarity of assemblages present on particular reefs at successive censuses averaged 0.568 for all reefs and censuses. At successive censuses, rarer species appeared and disappeared, while numbers of commoner species fluctuated and their abundances relative to one another changed. Over the eight censuses, each reef supported substantially more species than were present at any one time.

Reefs differed in the degree to which their assemblages present at successive censuses resembled one another, and also in the extent to which censuses deviated from this average degree of similarity for a particular reef (Fig. 4). We found little pattern in this variation. When all reefs were considered, some censuses were significantly more similar (e.g., May, August 1978), and some were significantly less similar (e.g., August, December 1977) than others to average conditions, but there was no apparent seasonal component to this. Regression analyses showed that successive censuses on large reefs showed a significantly greater degree of similarity to one another than those on small ones, but the difference was slight ( $b = 0.0075$ ). Reef size accounted for 31.4% of variance in similarities of censuses. Inspection of raw data showed that recruitment of large numbers (20–200) of juveniles of three species (*Apogon doederleini*, *A. gracilis*, and *Acanthochromis polyacanthus*) to certain reefs, coincided with strong decreases in similarity of censuses on these reefs (e.g., reef 2, November 1978, reef 4, May 1979, reef 15, December 1977). However, these species did

not recruit to all reefs in such numbers, and some other cases of sharply reduced similarity (e.g., reef 8, November 1978, reef 12, August 1978) were not associated with large changes in numbers of these or other species.

The degree of faunal change found is very similar to that reported for an earlier study of denuded and undisturbed patch reefs in the One Tree lagoon (Sale 1980b) where the mean between-census similarity of faunas on single reefs was 0.51. Talbot et al. (1978) used Jaccard's Coefficient of Community, an index based on species presence and absence only. Although their data cannot be compared directly with ours, they also found (1) a high degree of change in assemblages between successive censuses (mean CC = 0.263 calculated from their Table 8), and (2) a similarly high degree of difference between reefs (mean CC = 0.342). As we show later, our similarity measurements are also comparable to those from at least one larger site.

### A model of assemblage formation

Despite evidence of fine-scale habitat segregation, and the precise microhabitat requirements of some species, our results indicate that assemblages of fish on small lagoonal patch reefs possess a structure largely independent of measured aspects of reef structure (except for reef size), and one which changes through time. Fig. 2 illustrates the degree of this independence from reef structure. By successively gaining and losing fish, an average reef can accumulate within seven species of the number that would be obtained by sampling an equivalent number of fish in a census of several different reefs. If reefs gained species in a way strongly influenced by the structure of the reef, a group of reefs possessing the range of physical characteristics of ours (Table 5) would support many more species of fish than would ever occur on a single reef. (Fig. 2 can be overinterpreted. Some individual reefs fall well below the regression line, indicating that they would be unlikely to accumulate all species even if sampled for substantial periods.)

On this basis we suggest the following initial model of assemblage formation. There exists a pool of 143 or so species of fish able to occupy small patch reefs of the type we studied. Recruits of each species will colonize patch reefs from time to time, and whether or not a particular species colonizes a particular reef will depend to a large extent upon whether a larva ready to recruit passes near that reef. It will depend to only a small extent, if at all, on the nature of that reef (at least, such aspects of reef structure as we measured). Larger reefs will be more frequently found by recruiting larvae, and perhaps for this reason alone will usually support more fish and more species than smaller reefs. By being larger they may also offer more microhabitats and thus be suitable for more species than smaller reefs.

Fish present on reefs will be removed by various causes of mortality, and in some species by movement

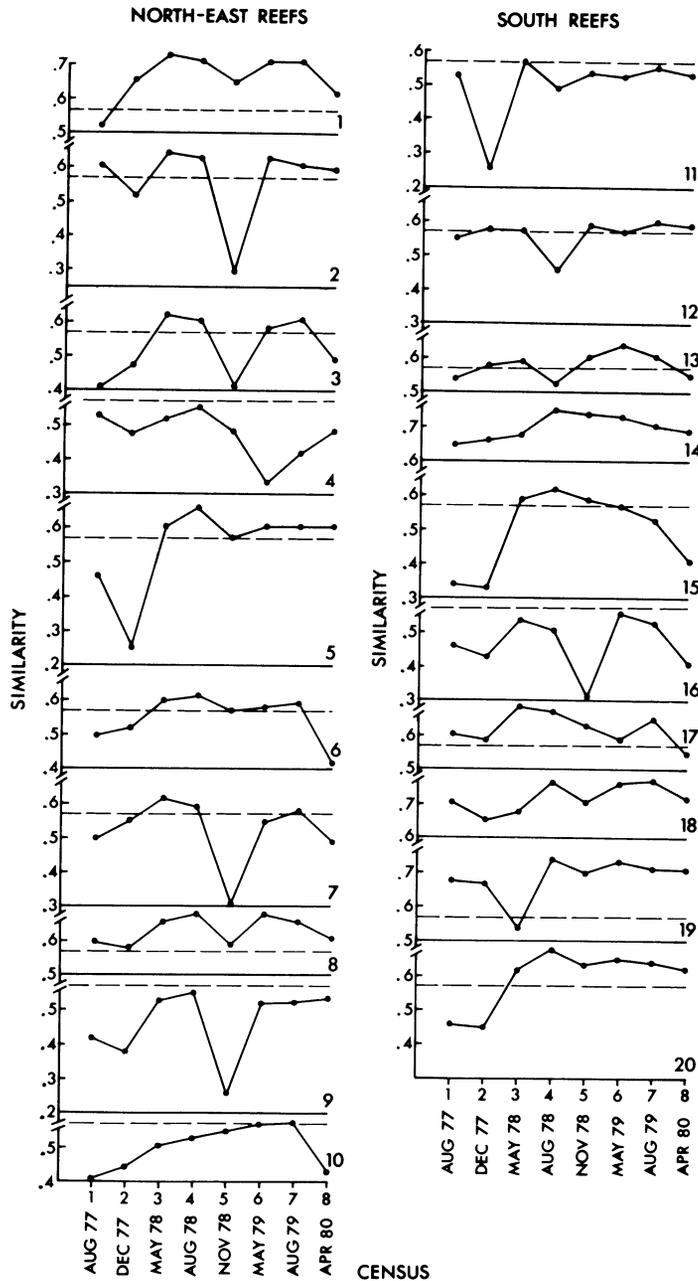


FIG. 4. The mean degree of similarity of the assemblage present at each census, to those at all other censuses of the same reef, for 20 patch reefs. Reefs vary, both in the average level of similarity of assemblages, and in the degree of variation around this average. The horizontal dashed line on each graph is the overall mean similarity (0.568) across reefs and censuses. Numbers on graphs identify individual reefs. Further details in text.

to other habitats following juvenile life. The particular number of fish present on a reef will result from the balance between the rates of recruitment and loss. The large seasonal component in variability of recruitment is responsible for the seasonal variation in sizes of assemblages. The strong aseasonal variation present in numbers of fish and species must arise because of aseasonal variation in rates of recruitment and/or loss of

fish. There are no data available on mortality rates, and variation in these, for fish in this habitat. Data currently being collected on the dynamics of patch reef assemblages will permit precise formulation and testing of this model. As presently conceived, the model does not require that fish respond positively or negatively to each other's presence on reefs, either when recruiting or subsequently. The degree to which dis-

tributions of fish species on these patch reefs are predictably influenced by those of other species will form the subject of a subsequent paper. However, previous attempts to detect such interspecies effects have been largely unsuccessful (Sale and Dybdahl 1975, 1978, Talbot et al. 1978).

Nor does the model require that fish respond to any attribute of a reef other than its size. The response to size is passive: larger reefs are bigger traps for larvae.

The model is clearly too simple to account for all the details of distribution of some species. Some species, such as *Dascyllus aruanus*, will not occupy reefs lacking particular microhabitats. Others (such as *Amblygobius phalena* and *Chromis nitida*) apparently discriminated between the northeast and south reefs. However, it remains to determine whether the model is also inadequate to account for the other properties of assemblages we have considered: number of species, number of fish, and degree of change in these and in species composition through time. The model will be developed further in subsequent papers.

*Predictability of fish assemblages in larger sites.*

Under the crude model proposed above, we can predict the behavior of assemblages of fish on larger patch reefs in the One Tree lagoon. Assuming the pool of species is finite and reasonably estimated by our set of 143 species, it is clear that these larger assemblages will each be a larger sample from this pool.

Since, under this model, the samples are essentially random, each will contain a larger number of the available species than would samples from small patch reefs. Some species in the pool are so rare that they will only be present in low numbers even on these larger reefs. Through time, processes of addition and loss will cause them to enter and leave assemblages. More common species will fluctuate in numbers because of these same processes of recruitment and loss of individuals. Further, since at least part of the variation in numbers of individual species which occurs on small patch reefs is aseasonal, and different from reef to reef (see also Williams 1980), a large site, acting as the sum of a set of small sites, will show less of this variation. Additions to one part of it may replace losses at another. Overall, we expect: (1) that structure of the assemblage on a large reef will vary less through time than is so for those on small reefs, and (2) that neighboring large reefs will support more similar assemblages than will neighboring small reefs.

Results relating to both these expectations have been presented by others as evidence that reef fish assemblages are not structured in such a simple noninteractive, nonequilibrium way. Brock et al. (1979) compared results of two poisonings 11 yr apart (1966 and 1977) of a single large (1500 m<sup>2</sup> surface area) patch reef, and the composition of recruits to it during the year following the 1977 defaunation.

They reported that while only 40% of species were

common to the two poison samples, these comprised 95% of wet mass of fish collected in 1966, and 86% of this in 1977. This, plus an apparent consistency of trophic structure, were used to argue for temporal stability of the assemblage. Although they did not compute any similarity indices, their published data allow this. Using our index, the similarity of the two collections is 0.682. This is considerably greater than that among our much smaller (8.25 m<sup>2</sup>) reefs, but still represents more than a 30% difference in the structure of the assemblages present in 1966 and 1977.

Ogden and Ebersole (1981) compared five visual censuses made over 17 yr (four censuses in the last 5 yr) of a single large artificial reef (125 m<sup>2</sup> surface area). Forty-nine species were present in one or more of their four censuses done between 1975 and 1979. Of these 49 species, 29 were absent from at least one census. In 19 of the remaining 20 species, there existed at least a twofold difference in numbers present among the four censuses (in 8 of these there is more than fourfold variation).

Ogden and Ebersole (1981) measured similarity of censuses using Spearman's  $r_s$  and Jaccard's Coefficient of Community. Their values for Jaccard's Coefficient were substantially larger (0.60 vs. 0.32) than those obtained by Talbot et al. (1978) for small artificial reefs, and they also reported significant correlations of species' ranks among the censuses. On these results, they argued that the assemblage present was both stable and predictable. Their published data also allow computation of the percent similarity coefficients for direct comparison with our data. Their most similar pair of censuses (1977 and 1978) gives a value of 0.530, compared to the mean of 0.568 among censuses on our smaller reefs.

Gladfelter et al. (1980) sampled neighboring large patch reefs of several physical types. They emphasized the greater similarity of assemblages on structurally similar than on dissimilar reefs. Average similarities among their reefs, however, were 0.61 (Enewetak) and 0.62 (St. Croix) using a slightly modified formula closely related to ours, but using census data in which abundances were ranked on a 6-point scale. Use of ranking methods rather than actual counts of fish necessarily leads to greater similarity among censuses than our procedures would do.

Similarity among assemblages on our 20 reefs at the May 1978 census, when calculated using their scaling procedure and similarity index, is  $0.48 \pm 0.007$  (SE) (vs. 0.42 using our method), and the effect of scaling will be more pronounced on larger reefs where many species can be expected to occur in numbers greater than three or four individuals. Their mean similarities of 0.61 and 0.62 in two sites probably represent at least a 45% difference in composition of the assemblages compared. Their results do not appear inconsistent with ours, but the differing methods prevent closer comparison.

Anderson et al. (1981) dealt only with chaetodontid

fishes, and were primarily concerned with patterns of presumed niche replacement (Sale and Williams 1982). Pertinent here, however, is their Table 5, showing censuses of chaetodonts on 10 nearby patch reefs. We computed percent similarity of chaetodonts among 5 of these (the set behind Day Reef), and obtained a mean value of  $0.66 \pm 0.043$  (SE). This represents over 30% difference in composition of the assemblages compared despite the fauna comprising only seven species and being strongly dominated by one.

Elsewhere (Sale 1980a) comments have been made on the ways in which differing censusing techniques, intercensus intervals, and numerical methods used may have influenced results, and thereby contributed to the controversy over the structure of fish communities. As shown here, where data on similarity of assemblages on larger reefs can be compared, there is still abundant evidence of significant change through time, or differences between replicate reefs. While the approach in studies of these larger reefs has been to emphasize the degree of temporal persistence and spatial consistency of structure, in no case do the data collected contradict our expectations based on our smaller scale studies. Indeed, in one case (Ogden and Ebersole 1981) the larger assemblage is not any more persistent than are those on our smaller reefs.

We are unable to accept the usual conclusion from these large scale studies, that there is evidence that "a system of considerable predictability and stability is revealed, suggesting an orderly community structure" (Ogden and Ebersole 1981). The considerable variation in time and space in the composition of assemblages on both large and small patch reefs is most parsimoniously explained as a consequence of a continuing series of largely random recruitments and losses of individuals drawn from a pool of species capable of using that type of habitat.

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