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CORAL REEF FISH COMMUNITIES: UNSTABLE, HIGH-DIVERSITY SYSTEMS?[1]

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Abstract. We examined the pattern of development of assemblages of coral reef fishes on artificial reefs at One Tree Reef, Great Barrier Reef. Two sets of 8 reefs were built. To investigate the effects of habitat structure on species diversity, each set consisted of replicate pairs of 4 different reef types: plain (no holes), small-holed, medium-holed, and large-holed reefs. To examine seasonal differences in colonization, 1 set was established in summer (October 1971) and the other set in winter (July 1972). Visual censuses of the reefs' fish assemblages were made at monthly intervals over 32 mo (summer set) and 23 mo (winter set).

We recorded a total of 105 resident species from the artificial reefs. Although less diverse, the fish assemblages differed little in terms of species composition from those of small natural patch reefs. Artificial reefs showed a high between-reef variability in species composition that was largely unrelated to habitat structure. Competitive interactions between species appeared unimportant in explaining the distribution of species between reefs. Likewise, possible positive associations between species were indicated for only a few species.

Almost all settlement of the artificial reefs was by juvenile fishes. Recruitment was markedly seasonal and occurred mainly over summer (September–May). Juvenile recruitment patterns showed little year-to-year constancy. Most species tested showed nonrandom, clumped patterns of settlement on replicate reefs. More than half of species tested showed no significant differences in numbers of individuals which settled on different reefs, but the remainder showed significantly greater settlement on some reefs, suggesting habitat selection. For a few species, there was also greater recruitment to reefs already occupied by conspecifics, suggesting possible social facilitation of settlement. For most species, there were no significant interspecific interactions between adults and newly settling juveniles.

Between-census variability in species composition was high and species turnover ranged from ≈17% of species/mo in winter to ≈39% in summer. Maximum times of persistence for most species were <12 mo, and for many individuals survivorship was of the order of only a few months. Much of the high turnover appears due to losses through predation.

There was no evidence that a persistent species equilibrium was attained during colonization. Because of predation and the seasonally varying, uncertain nature of recruitment, we see the development of any long-term species equilibrium as unlikely. We suggest that nonequilibrium conditions are a characteristic of coral reef fish communities and that because of these conditions, high within-habitat diversities are maintained.

Key words: artificial reefs; Australia; colonization; coral reef fish communities; Great Barrier Reef; predation; seasonal; species equilibrium; turnover; within-habitat diversity.

INTRODUCTION

Coral reefs have enjoyed a long and comparatively stable paleoecological history, probably since the Tertiary (Newell 1971) and it is conjectured that at least 1 consequence of this is the great diversity of organisms that characterize present day reefs (Fischer 1960, Grassle 1974). For example, at One Tree Reef near the southern-most extremity of the Great Barrier Reef, we have recorded nearly 800 species of fish, and a single rotenone collection from <50 m^2 has yielded as many as 150 species (Goldman and Talbot 1976).

Understanding how so many species are able to coexist remains a major ecological problem. Fine partitioning of resources and increasing specialization have been suggested as ways by which such high diversities may be maintained (MacArthur and Levins 1967; Smith and Tyler 1972, 1973*a*, 1973*b*, 1975), and among coral reef fishes we can find numerous examples where this seems to be true, e.g., food and habitat specialization (Hiatt and Strasburg 1960, Randall 1967, Tyler 1971, Tyler and Bohlke 1972, Luckhurst and Luckhurst 1976), commensalism (Allen 1972), symbiosis (Feder 1966), and mimicry (Russell et al. 1976).

However, there are a great many fish species which are not particularly specialized (Hiatt and Strasburg

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FIG. 1. Oblique aerial photograph of One Tree Island and adjacent reef. The locations of the 2 sets of artificial reefs in the lagoon are marked by arrows (upper arrow: summer set; lower arrow: winter set).

1960; Randall 1967; Emery 1973; Barlow 1974; Choat and Robertson 1975; Sale 1974, 1975, 1977; Itzkowitz 1977). Many of these have similar ecological requirements and occur within the same habitats, and it is difficult to show any clear-cut partitioning of resources (Sale and Dybdahl 1975, Sale 1977, Clarke 1977). For these species, evidence suggests that factors other than differences in ecological requirements or competitive abilities determine the sorts of species which occur together.

TABLE 1. Characteristics of the 3 size classes of fishes that occurred on the artificial reefs

CLASS I	Small individuals with little or no pigmentation, considered to be recently metamorphosed, newly settled post-larvae or very young juveniles. Sometimes identified with certainty only after full development of adult pigmentation.
CLASS II	Older juveniles and subadults, smaller than known adults.
CLASS III	Adults. Larger fishes of a size known to be reproductively active or approaching known upper size limits for the species.

Recent work (Sale 1974, 1975, 1977; Sale and Dybdahl 1975) instead points to the role that environmental unpredictability, spatial patchiness and chance colonization play in the co-existence of similar species.

In this paper we present evidence which largely supports the idea that coral reef fish communities are not highly organized, stable systems and that chance factors are important in the maintenance of high within-habitat diversity. Our work is based on a detailed 3-yr study of the development and dynamics of the fish assemblages on small artificial reefs.

METHODS

The study was conducted in the lagoon at One Tree Island (Fig. 1), a small coral reef in the Capricorn Group at the southern end of the Great Barrier Reef of Australia (Lat.23°30′S, Long. 152°06′E). One Tree Reef is a raised platform reef that encloses a protected, shallow lagoon system (Davies et al. 1976). Extensive areas of reticulated reef are scattered throughout the lagoon with smaller submerged patch reefs of mixed living and dead coral separated by stretches of open sand. These patch reefs range up to 15 m^2 in size.

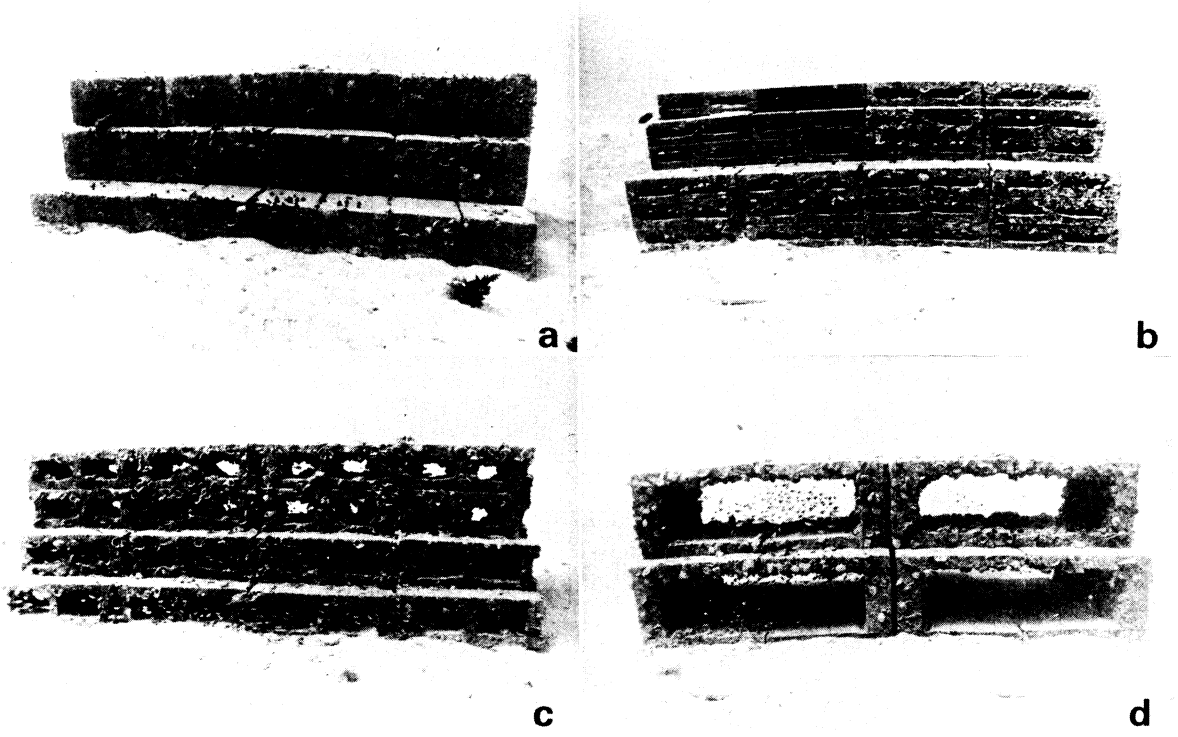

FIG. 2. The artificial reefs: (a) solid reef, plain with no holes; (b) small-holed reef; (c) medium-holed reef; (d) large-holed reef. All reefs are ≈12 mo old.

We chose to examine the fish assemblages of structurally simple artificial reefs largely because of the sheer diversity of structure and sizes of natural patch reefs and the difficulties of quantifying differences. The artificial reefs were designed to simulate small natural reefs, and were built using standard cement building blocks laid on fibro-cement bases to prevent them from settling in the sand. To investigate the effect of structural complexity on species diversity, we built 3 different types of reef of varying hole size and a control with no holes (Fig. 2). Each reef measured 160 × 60 × 60 cm and was similar in overall size, shape and volume. Two sets of 8 reefs were built, each set comprising replicates of the 4 reef types. To assess seasonal differences in colonization, 1 set was established at the beginning of summer, in October 1971, and the other set the following winter, in July 1972. Both sets of reefs were built from blocks dumped in the lagoon in September 1971. Thus, all the blocks were of the same 'age'; all had similar encrusting biotas.

The 2 sets of reefs were located in 3–5-m depth in 2 areas of open sandy bottom in the eastern part of the lagoon 500 m apart (Fig. 1). To minimize interference, we sited individual reefs at least 15 m apart and none were closer than 10 m from the nearest patch reef.

Visual census of the fish populations were made using SCUBA usually at monthly intervals, giving observations over 32 mo for the summer set and 23 mo for the winter set. Fishes were identified and numbers of individuals counted. Individuals were assigned to 1 of 3 classes based on their sizes: juveniles, subadults and adults (Table 1). Small schooling fishes (e.g., apogonids) were difficult to count accurately and numbers of these fishes represent estimates. Some of the more cryptic species (e.g., *Eviota* spp.) also were difficult to census visually and their numbers were ignored. Species were assessed as either resident or transient. Residents included all fishes seen on 1 or more consecutive censuses, or fishes seen only once but known to be resident on patch reefs of similar size. Transients were fishes observed near reefs but which moved away during censusing. There were invariably adult fishes of larger roving lagoon species such as *Plectorhynchus pictus* and *Lethrinus nebulosus*, and their numbers were not included in the censuses. Where a species was a resident as a juvenile and transient as an adult, we included it as a resident.

RESULTS

Colonizing species.—Table 2 lists the resident species observed on the reefs, and the total numbers of each that were recorded as new arrivals. A total of 105 species colonized the 2 sets. Most of these were small fishes (<10 cm total length) with home ranges

TABLE 2. List of the resident species of fishes of the artificial reefs, their occurrence as adults (a) or juveniles (j), and the total numbers of individuals of each species that settled on the 2 sets of reefs during the study period

Species	STAGE	*N*
Family Muraenidae		
Gymnothorax favigineus	(a)	18
G. flavimarginatus	(a)	3
Family Synodontidae		
Synodus englemani	(a)	2
Family Batrachoididae		
Halophryne diamensis	(a)	2
Family Atherinidae		
Pranesus capricornensis	(j)	30
Family Syngnathidae		
Corythoichthys intestinalis	(j, a)	5
Corythoichthys sp.	(j, a)	78
Micrognathus brevirostris	(j)	1
Family Scorpaenidae		
Dendochirus zebra	(j)	1
Dendroscorpaena sp.	(j)	1
Pterois volitans	(j, a)	5
Scorpaenodes guamensis	(j)	1
Family Serranidae		
Cephalopholis pachycentron	(a)	1
Epinephelus merra	(a)	4
Family Pseudochromidae		
Pseudochromis novaehollandiae	(j, a)	12
Family Apogonidae		
Apogon augustata	(j, a)	4254
A. cooki	(j)	1
A. cyanosoma	(j, a)	46
A. frenatus	(j)	1
Apogon sp. 1	(j, a)	234
Apogon sp. 2	(j, a)	2747
Apogon sp. 3	(j, a)	5431
Apogon sp. 4	(j)	2
Cheilodipterus quinquilineata	(j, a)	268
Family Lutjanidae		
Lutjanus carponotatus	(j)	1
Caesio caerulaureus	(j)	9
Family Nemipteridae		
Scolopsis dubiosus	(j)	1
S. personatus	(j)	85
S. trilineatus	(j)	1
S. bilineatus	(j)	1
Family Gerreidae		
Gerres oyeana	(j)	45
Family Pomadasyidae		
Plectorhynchus pictus	(j)	1
Family Lethrinidae		
Lethrinus nebulosus	(j)	36
Lethrinus sp.	(j)	4
Family Mullidae		
Mulloidichthys samoensis	(j)	4
Parupeneus barberinus	(j)	1
Family Pempheridae		
Pempheris sp.	(j)	1
Family Chaetodontidae		
Chaetodon auriga	(j)	15
C. flavirostris	(j)	2
Chaetodontoplus personifer	(j)	1
Chelmon rostratus	(j, a)	46
Family Pomancentridae		
Acanthochromis polyacanthus	(j, a)	354
Chromis nitida	(j, a)	703
Dascyllus trimaculatus	(j, a)	11
Glyphidodontops rollandi	(j, a)	1
Neopomacentrus cyanomos	(j, a)	2
Pomacentrus amboinensis	(j, a)	11
P. australis	(j)	4
P. rhodonotus	(j)	1
P. melanochir	(j, a)	137
P. pavo	(j, a)	54
P. wardi	(j)	7
Family Cirrhitidae		
Cirrhites aprinus	(j, a)	7
Family Sphyraenidae		
Sphyraenella chrysotaenia	(j)	1
Family Labridae		
Cheilinus fasciatus	(j)	3
Cirrhilabrus temmincki	(j)	17
Coris variegata	(j, a)	54
Coris sp.	(j)	2
Halichoeres biocellatus	(j)	1
H. hartzfeldi	(j)	1
H. trimaculatus	(j, a)	128
Labroides dimidiatus	(j, a)	40
Pseudolabrus guntheri	(j, a)	62
Thalassoma lunare	(j, a)	108
Family Scaridae		
Scarus ghobban	(j)	10
Scarus niger	(j)	1
Scarus sp.	(j)	84
Family Mugiloididae		
Parapercis cylindricus	(j, a)	29
P. polyopthalma	(a)	13
Family Blenniidae		
Ecsenius bicolor	(j)	1
E. mandibularis	(j, a)	48
Enchelyurus kraussi	(j)	3
Meiacanthus lineatus	(j)	5
Petroscirtes fallax	(j, a)	119
P. mitratus	(j, a)	73
P. variabilis	(j, a)	40
Pictiblennius intermedius	(j)	2
Salarius fasciatus	(j, a)	15
S. irroratus	(j)	1
Family Congrogadidae		
Congrogadus subducens	(a)	1
Family Gobidae		
Acentrogobius ornatus	(a)	228
Acentrogobius sp.	(a)	401
Amblygobius albimaculatus	(j, a)	646
Asteropteryx semipunctatus	(j, a)	882
Ctenogobiops maculosus	(a)	7
Fusiogobius sp.	(a)	351
Ptereleotris microlepis	(j, a)	79
Valencienna longipinnis	(a)	212
V. sexguttatus	(a)	12
Valencienna sp.	(a)	7
Yongeichthys criniger	(a)	153
Goby—unidentified	(j)	25
Family Acanthuridae		
Acanthurus mata	(j)	22
Naso annulatus	(j)	10
N. tuberosus	(j)	2
Family Siganidae		
Siganus chrysospilos	(j)	2
S. oramin	(j)	1
Family Balistidae		
Aleutera sp.	(j)	5
Pseudobalistes fuscus	(a)	1
Rhinecanthus aculeatus	(j, a)	8
Family Ostraciontidae		
Ostracion cubicus	(j, a)	16
Family Tetraodontidae		
Arothron hispidus	(a)	2
A. nigropunctatus	(a)	4
Canthigaster bennetti	(j)	7
C. valentini	(j, a)	39

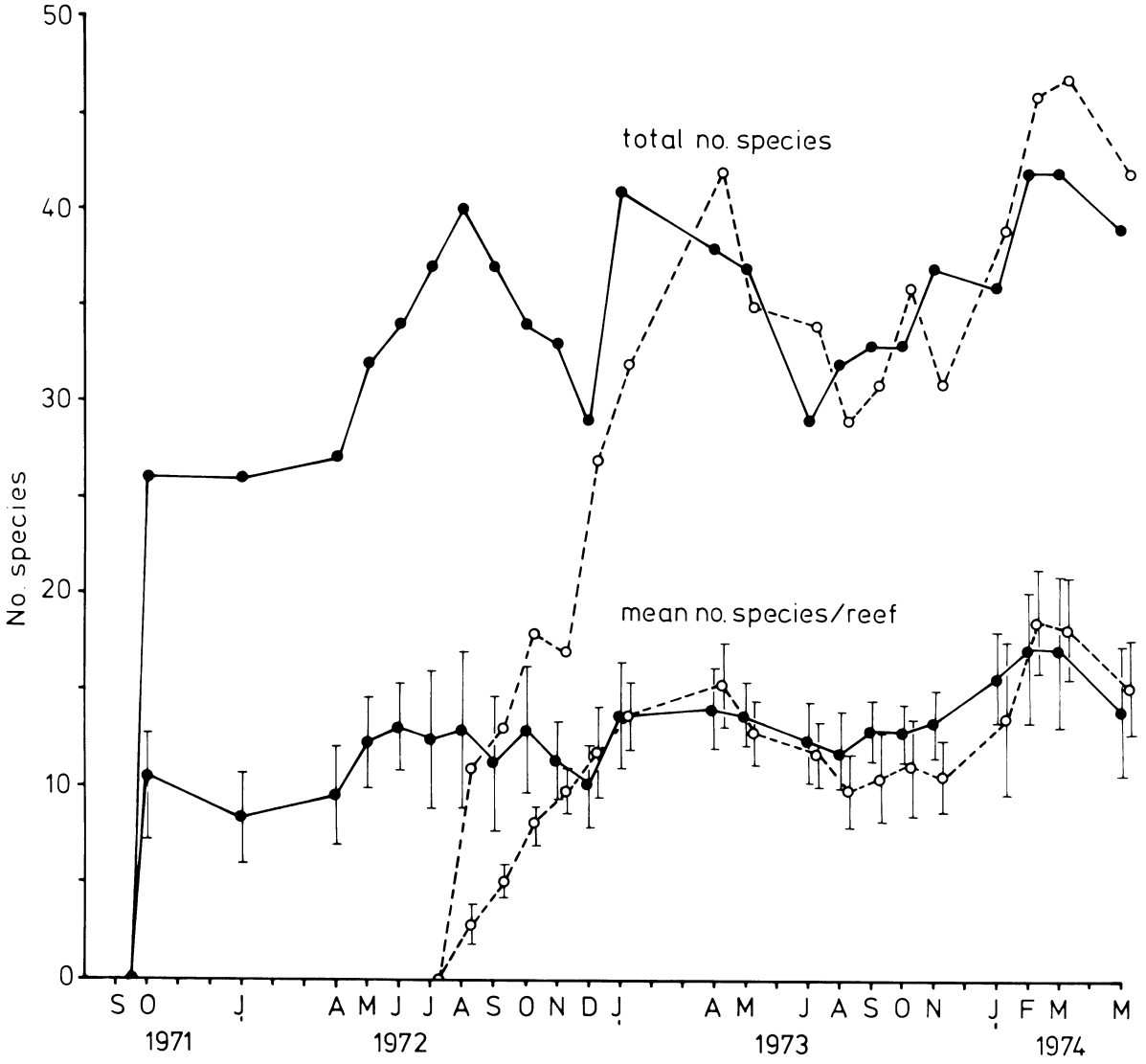

FIG. 3. Colonization curves for the summer (solid line) and winter-laid reefs (dotted line) showing the mean number of species and total number of species present on each census. Vertical bars indicate 95% confidence limits.

generally <1 m^2. Except for a few species which occurred only as juveniles, and adults of which are known to have different habitat requirements or much larger home ranges, there appeared to be little emigration of initial colonizers. Some species, such as apogonids, disperse at night to feed, but these fishes return to the same shelter site each morning (Collette and Talbot 1972). Most species thus have at least the expectation of spending their entire lives on the same small area of reef.

Of the total species, 88 occurred on the summer set (32 mo) and 77 on the winter set (23 mo). Sixty-one species were common to both sets of reefs, these representing 69.3% and 79.2% respectively of the total species in each set. A comparison of ranked abundances of all shared species showed no significant differences between the 2 sets (Spearman Rank Correlation Coefficient, $r = .833$, $P < .001$) (Siegal 1956). Rare species were a major component of the communities of both sets of reefs. Of the combined samples (all reefs over all censuses), only 13 species (12.4%) were represented by more than the mean of 184.9 individuals, and 26 species (24.8% were represented by only single individuals).

Total numbers of species and mean numbers of species/reef were significantly lower on artificial reefs compared with natural reefs of similar size (Table 3, t-test, $P < .05$). The mean number of individuals/reef also was lower for the artificial reefs, although sample variance was high and differences were nonsignificant (t-test, $P > .05$). Much of the variation between natural and artificial reefs probably largely reflects the

TABLE 3. Comparison of the fish assemblages of the 2 sets of artificial reefs with those of natural isolates of about the same overall volume ($\approx 0.6^3$). All reefs were from the same part of the lagoon and all were censused at the same time (March 1974)

		Artificial reefs	
	Coral isolates $n = 9$	Summer set $n = 8$	Winter set $n = 8$
Total species	74	42	47
Number of species shared with coral isolates (%)	...	34(81%)	44(93.6%)
Mean number of species/reef (±95% confidence limits)	27.6 (±4.2)	17.1 (±3.7)	18.3 (±2.6)
Mean number of individuals/reef (±95% confidence limits)	260.4 (±260.1)	143.1 (±72.2)	129.9 (±49.6)
Mean between-reefs similarity[a] (±95% confidence limits)	0.374 (±0.027)	0.322 (±0.035)	0.318 (±0.032)

[a] Jaccard's Coefficient of Community (Goodall 1973), $CC = n_c/n_j + n_k - n_c$ is the number of species in common, and n_j and n_k are the number of species in samples j and k.

much simpler habitat structure and possibly lower carrying capacity of the artificial reefs. In terms of overall species composition, there was a high faunistic resemblance, and 81% of species on summer-laid reefs and 93.6% of species on winter-laid reefs occurred also on natural coral isolates (Table 3). Both artificial and natural reefs were characterized by a similar high between-reef variability in species composition and there was no significant difference in the mean between-reef similarity values for natural isolates and either set of artificial reefs (Table 3, t-test, $P > .05$). Thus, we can regard the fish assemblages of artificial reefs essentially as smaller subsets of the same lagoon fish community that includes natural coral isolates and patch reefs.

Patterns of colonization.—The average numbers of species per reef and total numbers of species for each set of reefs are plotted as colonization curves in Fig. 3. Initial differences in colonization rates between the summer- and winter-laid reefs are striking, the former set showing a much more rapid increase in species numbers with a total of 27 species present on the 8 reefs after only 2 weeks. By comparison, the winter set took >4 mo to attain the same number of species. Mean numbers of species on both sets thereafter fluctuated between ≈10–18 species per reef. Testing for differences among mean numbers of species after 4 mo showed no significant differences between months for either set (Student-Newman-Keuls [S-N-K] test, $P > .05$) (Sokal and Rohlf 1969). Examining the total numbers of species for each set (Fig. 3), however, shows a much more marked seasonal fluctuation. Total numbers of species for the summer set showed a pronounced initial peak in winter, in August 1972, with subsequent peaks occurring in summer in January 1973 and February–March 1974. For the winter set, corresponding peaks occurred in April 1973 and March 1974. Reasons for the increase in overall species numbers on the summer set during the first winter are not readily apparent, and owing to gaps in our census data it is not possible to show whether an earlier summer peak occurred, similar to that seen in subsequent years. A single census in January 1972, though, suggests that there was no increase in the total number of species. Whatever the reason for this, the apparent low diversity of fishes during the first summer may account for the continued increase in total species numbers which occurred during winter. The winter peak thus appears to be a somewhat anomalous feature that was not a regular seasonal event.

TABLE 4. Comparison of the mean numbers of species for the 4 reef types. Data have been pooled from both sets over all censuses (n = 160 samples)

Reef type	Mean number of species (±95% confidence limits)
Plain	10.76 (±0.87)
Small-holed	12.05 (±0.77)
Medium-holed	12.15 (±0.87)
Large-holed	14.44 (±0.93)

Further evidence of the seasonal pattern of colonization can be seen in changes in the numbers of individuals per reef (Fig. 4). Although differences between months were nonsignificant (S-N-K test, $P > .05$) due to the high sample variance, a general seasonal pattern of change in mean numbers of individuals is nonetheless evident. For both sets of reefs, there was a general increase in numbers of individuals during summer (October–May) and a decline in winter (June–September). On some reefs, we observed up to 80× the number of individuals in summer compared with winter. Much of the increase in numbers of individuals was due to the heavy influx of juveniles of most species which occurred during summer. This was particularly marked in the apogonids where there were up to 3 orders of magnitude difference in numbers between summer and winter. Only 2 species, *Chromis nitida* and *Pseudolabrus guntheri*, appear to breed during winter and their numbers were primarily responsible for small increases in numbers of individuals on some reefs in winter.

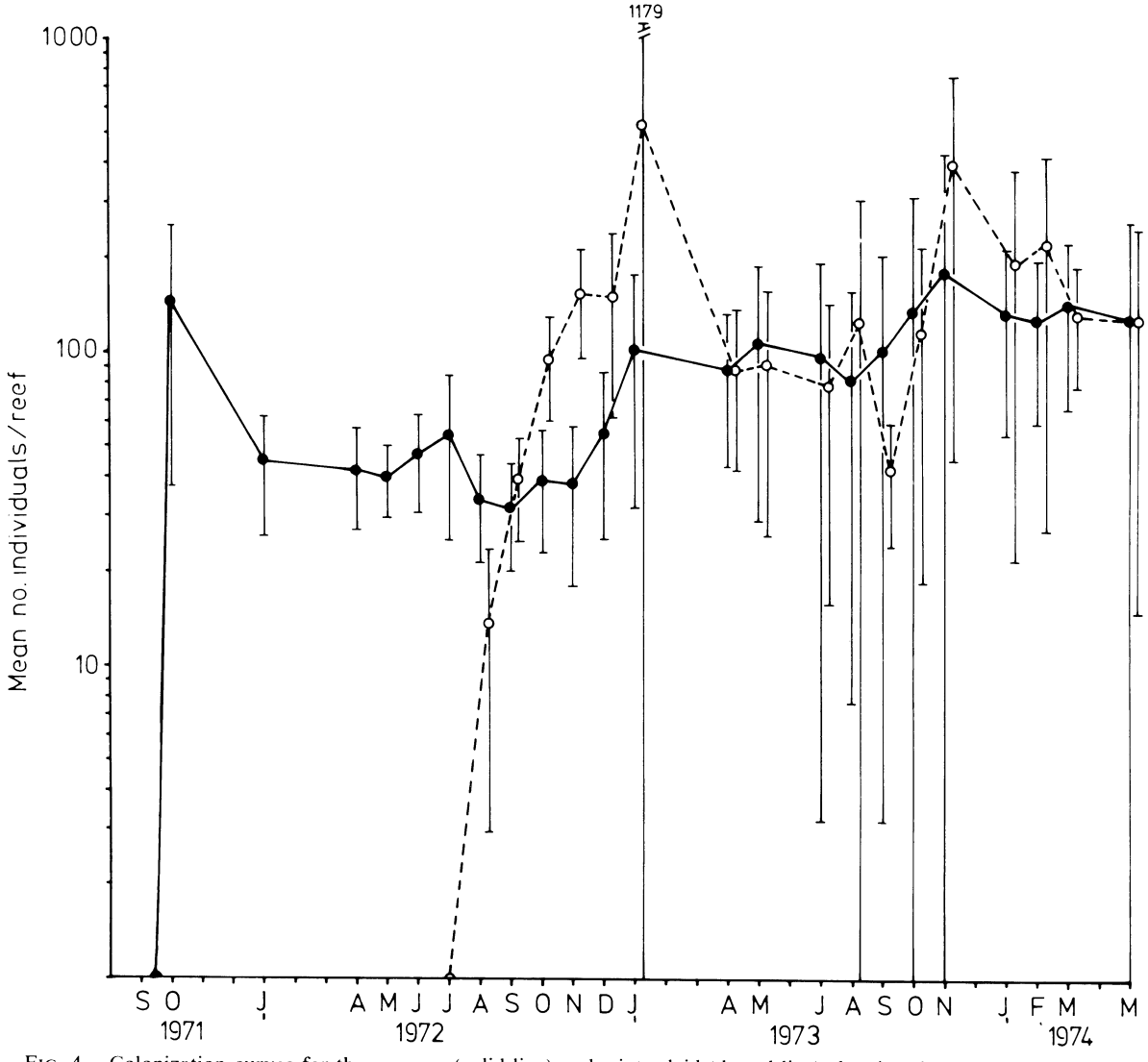

FIG. 4. Colonization curves for the summer (solid line) and winter-laid (dotted line) showing the mean number of individuals present on each census. Note the ordinate scale is logarithmic (log [n + 1]). Vertical bars indicate 95% confidence limits.

Distribution of species

Spatial distribution.—Comparing the mean number of species for each reef type (Table 4, pooled data from both reef sets over all censuses), suggests some differences between reef types in numbers of species, with means ranging from 10.7 on the plain reefs to 14.4 on those with large holes. Testing differences between the means, however, revealed a significant difference only in the case of the large-holed reefs (S-N-K test, $P < .05$). Mean numbers of species on the other reefs were not significantly different ($P > .05$). These results suggest the relationship between numbers of species and habitat complexity, at least of the sort tested (hole size), is a weak one.

In terms of species composition, there were much greater differences between reefs. Using Jaccard's Coefficient of Community (Goodall 1973) to compare faunal similarity between reef pairs (all reefs in both sets over all censuses) yielded a mean between-reef similarity of only 0.342 (±0.004, 95% confidence limits), indicating a high degree of variability in species composition between reefs. Questions remain as to how much of this variability can be explained in terms of differences in habitat structure. If habitat differences are an important determinant of community structure, we might expect the fish assemblages from replicate reef pairs to resemble one another more than those of dissimilar reefs. To test this hypothesis, we computed similarity values for all possible reef pairs in both sets. Similarity values for both sets were combined and the mean between-reef similarity for the replicate reef types were compared with the mean be-

TABLE 5. Mean between-replicate similarity values (Coefficient of Community), date from both sets of reefs combined. Mean between-reef similarity for all nonreplicates = .338 (±0.008, 95% confidence limits). Difference between values for replicates and nonreplicate reefs tested using Student's t-test (ns = nonsignificant, $P > .05$; * = $P < .05$)

Reef type	Mean between-reef similarity (±95% confidence limits)
Plain	.407 (±.039)*
Small-holed	.338 (±.035)ns
Medium-holed	.326 (±.049)ns
Large-holed	.397 (±.029)*

tween-reef similarity for all nonreplicate reefs using Student's t-test (Table 5).

Mean between-reef similarity values were significantly higher for the large-holed and plain reefs (t-test, $P < .05$), suggesting that the fish assemblages on these reefs tend to be more distinct than those of other reefs. However, the overall low between-replicate similarity values suggest similarities in species composition are not especially marked.

Possibly factors other than habitat differences (e.g., current patterns, surrounding bottom sediments, proximity to nearby feeding grounds) may be more important in determining the sorts of fishes which occurred. If so, we might expect that those reefs closest together would show greatest similarity in species composition. However, comparing ranked mean between-reef similarities for each set with rankings of inter-reef distance for all the reef pairs indicates this is unlikely. (Spearman Rank Correlation Coefficients for both sets nonsignificant, $P > .05$).

Species associations.—Associations between species were tested using χ^2 test for associations based on the pooled data for all reefs over all censuses. This gave a maximum of 640 samples (16 reefs × 40 different censuses) and a total possible combination of 5050 species pairs to test. Numbers were sufficient, however, to test only 537 species pairs. Of these, ≈25% showed significant association: 92 pairs (17.1%) showed a significant positive association, and 42 pairs (7.8%) were significantly negatively associated.

There are several possible explanations for these associations. Positive association may reflect similar habitat preferences or some positive interaction between species (e.g., symbiosis, commensalism), while negative association between species may reflect either dissimilar habitat preferences or strong interspecific interaction (e.g., competition, predation) such that 1 species actively excludes the other. To distinguish between these various possible alternatives, we compared the degree to which all significantly associated pairs of species were associated also by habitat. As a measure of correlation on the latter, Contingency Coefficients based on the habitat association data were calculated for each pair and these were tested using χ^2 (Siegal 1956). To indicate the direction of the correlation, we also calculated the Spearman Rank Correlation Coefficient for each species pair. Associations between 11 positively associated pairs and between 5 negatively associated pairs are explainable in terms of similar or dissimilar habitat preferences. Only 1 negatively associated pair of species (*Apogon angustata–Labroides dimidiatus*) was significantly associated by habitat, suggesting possible negative interaction, although the nature of this is not clear. Four pairs of species that were significantly positively associated had significantly different habitat associations, suggesting possible positive interaction between species. In 3 of these cases (*Apogon angustata–Apogon* sp. 1, *A. angustata–Acanthochromis polyacanthus*, *Apogon* sp. 1–*A. polyacanthus*) the species commonly occurred together as juveniles in large mixed schools and it is possible that their association is mutually beneficial, providing some measures of protection from predators (e.g., Ehrlich and Ehrlich 1973). The fourth case involved 2 species of goby, *Ptereleotris microlepis* and *Valencienna longipinnis*. Both species inhabit the periphery of reefs. *Ptereleotris microlepis* swims in small groups above the bottom and *Valencienna longipinnis* lives in burrows in the sand. When threatened by predators, *P. microlepis* seeks shelter in the holes of *V. longipinnis* and possibly benefits from this commensal relationship similar to that of other sand-dwelling gobies (Poulson 1978).

Juvenile settlement

Patterns of settlement on replicate reefs.—To examine patterns of settlement in identical reefs, we compared the numbers of individuals of each species which settled on replicates of each reef type. Total numbers of newly arrived juveniles of each species were summed for the various reefs, and numbers of individuals on replicate reefs were compared using Morisita's (1959) index of dispersion, I_δ, to test for departure from randomness. Because there were fewer censuses for replicates from the winter set, we considered recruitment only over the period, August 1972–May 1974. We also eliminated all rare species. Because the minimum number of individuals needed for there to be a 95% expectation that all 4 replicates would be settled by at least 1 individual is 16, we excluded all cases where fewer than this number were recruited.

Examining the numbers of species that were significantly nonrandom or randomly distributed among replicates for each of the reef types (Table 6), we see that, for any particular reef type, at least two thirds of species which settled in sufficient numbers for testing, showed significant nonrandom patterns of distribution ($I_\delta > 1$, $P < .05$).

Habitat preferences.—Habitat selection by newly settling juveniles was tested by examining the recruit-

ment of each species to the different reef types. Data from both reef sets were combined and for each species we summed the numbers of newly arrived juveniles which occurred on each of the 4 reef types. Numbers of individuals on the different reefs were compared using the Kolmogorov-Smirnov test for goodness-of-fit (Siegal 1956). Rare species, with <16 individuals recruited, were eliminated from testing. Of the 45 testable species, 24 (53.3%) occurred in numbers that were not significantly different from that expected by chance ($P > .05$), while 21 species (46.7%) showed significant differences between reefs in the numbers of individuals which settled ($P < .05$). These results indicate that a significant proportion of species, nearly a half of those tested, show some habitat preference.

Intraspecific interactions.—The clumped nature of recruitment to replicates, irrespective of reef type, suggests social factors may be important in settlement. Two possible explanations are that larvae actively aggregate in the plankton and settle together and/or that there is some kind of social facilitation of settlement. We have no information on the presettlement behavior of fish larvae, but the latter possibility can be tested by comparing numbers of individuals recruited with numbers of individuals of that species present in the preceding census. Data were sufficient to test this relationship for 28 species. Sixteen species (57.1%) showed no significant relationship (Spearman r, ns, $P > .05$), while the remaining 12 (42.9%) all showed a significant positive correlation ($P < .05$) between numbers of individuals present and subsequent recruitment. None of the species tested showed any negative relationship. These results suggest that for some species at least, the presence of conspecifics may facilitate further settlement by individuals of the same species.

Effects of established fishes on recruitment.—Initial rates of recruitment to the winter-laid reefs during the first 6 mo of colonization were significantly higher than those for the summer-laid set during the same period (2-way analysis of variance comparing numbers of individuals, sets × months: differences between sets significant, $F_{1,5} = 4.23$, $P < .05$). Because the only difference between the sets was that the older summer-laid reefs were inhabited mainly by adult fishes whereas the newly laid winter reefs were populated by juveniles, the data suggest adult fishes may have been limiting the numbers of juveniles which were able to settle.

To examine this effect on individual species, we compared monthly immigration rates of individuals of each species on the 2 sets of reefs. If there is significant adverse interspecific interaction between newly settling juveniles and already established adults we might expect rates of immigration for those species to be significantly lower on older reefs. However, the presence of adults might facilitate settlement by juveniles of some species and, in this case, immigration rates would be expectedly higher on older reefs. Table 7 summarizes the number of species which showed immigration rates that were significantly higher, lower, or which were not significantly different on the new vs. older reefs during the initial period of recruitment to the new reefs (July 1972–January 1973).

TABLE 6. Numbers of species showing significant nonrandom and random distributions of individuals among replicates for the different reef types. Randomness was tested for by calculating the index of dispersion I_δ, and referring the quantity $[I_\delta(N - 1) + 4 - N]/3$ to tables of F with $n_1 = 3$, $n_2 = \infty$, $P < .05$ (Morisita 1959)

	Distribution of individuals among replicates	
Reef type	Nonrandom ($I_\delta > 1$)	Random ($I_\delta \approx 1$)
Plain reefs	17	4
Small-holed	14	3
Medium-holed	15	3
Large-holed	19	7

A total of 64 species were recruited to the 2 sets of reefs over the 6-mo period. Rates of immigration, however, were significantly higher on new reefs for only 9 species (Table 4, t-test, $P < .05$); 2 species showed significantly higher rates of immigration to older reefs; and 1 species showed significantly higher rates of immigration to both new and old reefs at different times. We conclude from this that for most species, interspecific interactions between adults and newly settling juveniles are unimportant, the apparent overall disparity in immigration rates between the 2 reef sets being due mainly to a few species which settled more heavily on some new reefs.

Changes in community structure through time

To examine temporal changes in community structure we calculated mean between-census similarities (Coefficient of Community). These values are shown for each consecutive monthly census in Table 8. The data suggest there are substantial changes in community structure between censuses. Similarity values are consistently low for both sets of reefs, and in no case does the mean between-census similarity exceed >.500.

Species equilibrium.—To establish whether a species equilibrium was approached during the period of observation of the reefs, we used 2 criteria (Schoener 1974). In the first method, the colonization curves for each set of reefs were arbitrarily divided into 2 sections, censuses up to 6 mo and those afterwards. For each part of the curves, the relationship between average number of species per reef and time was approximated using a linear regression, the data from the 8 reefs in each set being treated as replicate observations and analysis of variance carried out to test for

TABLE 7. Comparison of recruitment to newly established reefs (winter-laid set) with that to older reefs (summer-laid set) at monthly intervals over the same period (July 1972–January 1973). Immigration rates for each species were compared for each set using Student's t-test. The numbers of species showing significantly greater ($I_a > I_b$) or lesser ($I_a < I_b$) rates of immigration ($P < .05$), or no significant difference ($I_a = I_b$) in immigration ($P > .05$) to new vs. old reefs are shown

		Census period					
		Jul–Aug	Aug–Sep	Sep–Oct	Oct–Nov	Nov–Dec	Dec–Jan
Number of	$I_a > I_b$	0	3	3	3	1	2
species	$I_a < I_b$	0	1	2	0	0	0
where	$I_a = I_b$	30	21	27	24	35	39

heterogeneity among the means (Sokal and Rohlf 1969). To test for equilibrium conditions we determined whether the first part of the curve rose more steeply and was significantly different from the second part. Because we made only 2 censuses during the first 6 mo of the summer set, this test was only possible for the winter set.

The regression for the winter set over the first 6 mo showed a steep slope (b = 2.18, ±0.21, 95% confidence limits) and the data show a good fit to a straight line ($F_{4,42} = 1.571$, $P > .1$). By comparison, the slope for the remainder of the curve was not significantly different from 0 (b = 0.35, ±0.43, 95% confidence limits), although deviations about the regression were highly significant ($F_{9,77} = 64.472$, $P < .001$) indicating a poor fit to a straight line. For the summer set, the slope for the second part of the curve was just significantly different from 0 (b = 0.16, ±0.08, 95% confidence limits), but again the regression showed a poor fit to a straight line ($F_{19,147} = 17.057$, $P < .001$). These results can be interpreted as showing a significant difference between the 2 parts of the colonization curves, with species being added at a slower rate after 6 mo, but the poor fit of both sets of data after 6 mo, however, suggest only equivocal support for a species equilibrium.

As a second, more powerful test for species equilibrium, we calculated immigration rates (I) and extinction rates (E) for each census period by comparing the species present in successive censuses. Species not present in the preceding census were considered immigrants, and species absent were considered to have become extinct. Colonization rates (C) were obtained by taking the difference between immigration and extinction rates (I–E) over the sample period (Schoener 1974). Theoretically, a plot of colonization rate against time should yield a decreasing curve which approaches 0 as equilibrium is attained (Schoener 1974). Inspection of the colonization-rate curves for the artificial reefs (Fig. 5) suggests that this equilibrium condition was not achieved on either the summer- or winter-laid reefs. The colonization rates of both sets show a strong seasonal pattern, with reefs generally showing a net loss of species in winter and a net gain in summer.

Species turnover and persistence.—Species turnover was measured by calculating the numbers of species lost and gained between censuses and expressing these according to the formula given by Smith (1975) for calculating faunal resemblance between samples:

$$T_{ov} = \tfrac{1}{2}\left(\frac{l}{n_j} + \frac{g}{n_k}\right) \times 100\%,$$

where l is the number of species lost between census j and k, and g is the number gained, and n_j and n_k are the numbers of species in censuses j and k. Because unseen losses and gains cannot be measured, the estimate of turnover is a minimum one.

Mean turnover values for consecutive monthly censuses for the 2 sets of reefs are given in Table 9. As a measure of turnover, T_{ov} is sensitive to numbers of species, consequently for the initial censuses of the winter set, when only small numbers of species were present, percent turnover appears much higher than in subsequent censuses. Ignoring this initial period, mean between-census turnover showed a pattern which ranged from ≈17% of species per month in winter to ≈39% in summer.

Species persistence (P) was taken as the period be-

TABLE 8. Mean between-census similarity values (Coefficient of Community) calculated for consecutive monthly censuses, for the 2 sets of artificial reefs

	1972									1973					1974	
	Apr–May	May–Jun	Jun–Jul	Jul–Aug	Aug–Sep	Sep–Oct	Oct–Nov	Nov–Dec	Dec–Jan	Apr–May	Jul–Aug	Aug–Sep	Sep–Oct	Oct–Nov	Jan–Jan	Feb–Mar
Summer set	.283	.163	.192	.253	.252	.275	.270	.355	.375	.223	.185	.143	.248	.217	.189	.194
Winter set	. . .	. . .	. . .	. . .	.465	.392	.256	.232	.395	.260	.266	.178	.250	.316	.309	.215

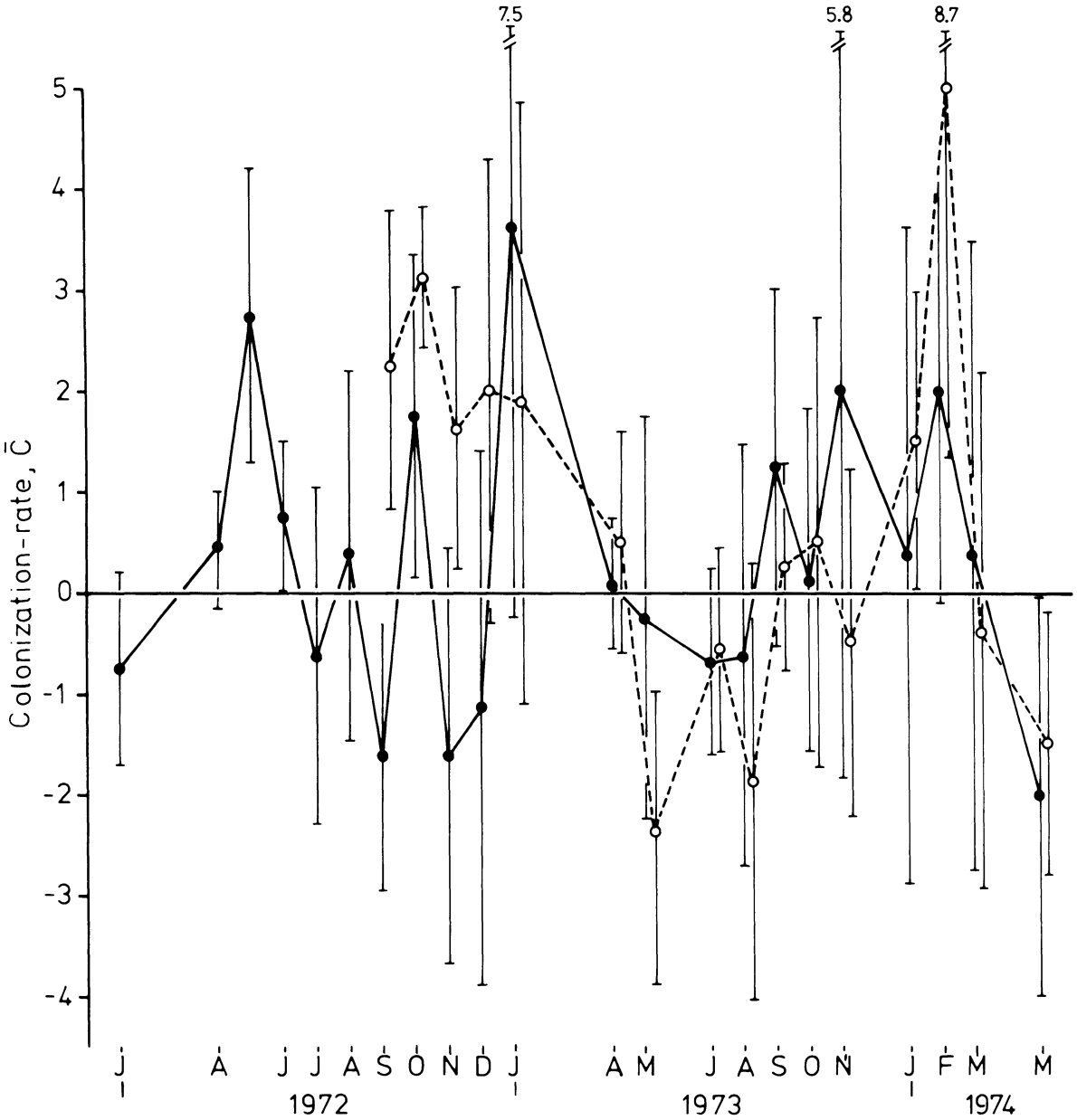

FIG. 5. Colonization-rate curves for the summer (solid line) and winter-laid reefs (dotted line), September 1972–May 1974. Colonization rates were obtained by taking the difference between immigration rates (I) and extinction rates (E) for consecutive censuses. Values plotted are the mean colonization rates ($\bar{C}$) for each period. Vertical bars indicate 95% confidence limits.

tween immigration of a species to a reef and its extinction. For any 1 reef, however, a species might immigrate and become extinct a number of times. We therefore calculated mean persistence ($\bar{P}$) of a species as the average period of occurrence on all reefs, and maximum persistence (P_{max}) as the longest period that a species occurred on any of the reefs. For most species, survivorship is low. Frequencies of P_{max} for different species are shown in Table 10. Although there is some bias in estimating P_{max} due to the different periods of observation on the 2 sets of reefs, most species persisted for a maximum period of only a few months, well short of the lesser 23-mo period of observation of the winter set. Sixty-five species (61.9%) were present for <6 mo; only 19 species (18.1%) persisted for a maximum of 12 mo or more; and only 1 species lasted for 27 mo. These results are further evidence of the lack of any persistent species equilibrium. Additional evidence of nonequilibrium conditions are suggested by an analysis of the times

TABLE 9. Mean percentage turnover ($\overline{T}_{ov}$) of species between consecutive monthly censuses on the 2 sets of artificial reefs. Species turnover was measured as:

$$\overline{T}_{ov} = \tfrac{1}{2}\left(\frac{l}{n_j} + \frac{g}{n_k}\right) \times 100\%,$$

where l is the number of species lost, and g is the number gained between censuses, and n_j and n_k are the number of species in censuses j and k

	1972									1973					1974	
	Apr–May	May–Jun	Jun–Jul	Jul–Aug	Aug–Sep	Sep–Oct	Oct–Nov	Nov–Dec	Dec–Jan	Apr–May	Jun–Aug	Aug–Sep	Sep–Oct	Oct–Nov	Jan–Feb	Feb–Mar
Summer set	28.3	16.3	19.2	25.3	25.1	27.5	27.0	35.5	37.5	22.3	18.5	14.3	24.8	21.7	18.9	19.4
Winter set	...	...	...	...	46.5	39.2	25.6	23.2	39.5	25.8	26.6	17.8	25.0	31.6	30.9	21.5

of persistence of species present in early vs later censuses. One prediction of the species equilibrium model is that with time there is a gradual accumulation of longer lived, more persistent species (Wilson 1969).

We took the mean times of persistence ($\overline{P}$) of each species as an estimate of the probability of survivorship and compared the frequencies of $\overline{P}$ for the species present at different census intervals (Table 11). Ranked frequencies show a high degree of agreement between censuses (Kendall Coefficient of Concordance, for the summer set, $W = .816$, $P < .05$; for the winter set $W = .709$, $P < .05$) indicating no significant shift in community structure towards longer-lived, more persistent species.

DISCUSSION

Almost all recruitment to the artificial reefs was by juvenile fishes newly settled from the plankton. Notable exceptions to this rule were some predatory fishes that took up temporary residence on some reefs, and also gobies which recruited mainly as subadults and adult individuals. Randall (1963), Bussing (1972), Gunderman and Popper (1975), and Nolan (1975) also observed colonization of new and defaunated reefs was mainly by juvenile fishes.

Settlement by juveniles at One Tree Reef is markedly seasonal. The majority of reef fishes in this part of the Great Barrier Reef have fairly long breeding seasons that extend over 5–6 mo from ≈September to May (e.g., Sale 1970, 1971, 1974; Keenleyside 1972; Robertson 1973, 1974; Goeden 1974; Russell et al. 1974, 1977). Over this period, spawning occurs more or less continually and most species produce numerous clutches of young. Recruitment of juveniles, however, shows a marked peak in January–February, this corresponding to the period of highest temperatures (Russell et al. 1977). During winter, recruitment of newly metamorphosed juveniles is negligible, although there is some colonization by older juveniles and subadults, suggesting perhaps some redispersal of earlier settled individuals (Russell et al. 1974). However, these tend to be mostly solitary migrants and their arrival has little effect on numbers of individuals present in winter.

The distinct annual temperature regime (20°–28°C) at the southern end of the Great Barrier Reef (Brandon 1973) may well impose a pattern of seasonal breeding and recruitment that is much more marked than in more equatorial regions. However, near the northern end of the Barrier Reef, at Lizard Island (Lat. 14°40′S) recruitment also is strongly seasonal (Anderson, *personal observations*), and there is evidence from elsewhere (Erdman 1956, 1976; Munro et al. 1973; Powles 1975; Watson and Leis 1974; Luckhurst and Luckhurst 1977) which shows breeding and recruitment in tropical reef fishes follow similar seasonal patterns, albeit at different times of year. These patterns may be linked with local seasonal changes in food availability for larvae and newly settled juveniles (Russell et al. 1977), or with factors such as annual or semiannual changes in current flow and direction (Watson and Leis 1974), possibly as a mechanism for increased local retention of larvae.

Our data also indicate that, in addition to seasonally varying recruitment, there is little year-to-year constancy in recruitment. We observed 3 or 4-fold differences in numbers of species settling in the same months in different years, and up to a 10-fold difference in the numbers of individuals that settled from year to year (Russell et al. 1977). Similar differences in larval abundance and in recruitment in consecutive years are also reported by Powles (1975) and Luck-

TABLE 10. The numbers of species that persisted for a maximum period (P_{max}) of ≤1,2,3 ... >24 mo. P_{max} taken as the longest period that a species occurred on any of the reefs, data from both reefs combined

≤	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16–24	>24
	18	11	18	6	3	6	4	...	7	4	...	6	3	4	2	3	1

hurst and Luckhurst (1977). Allen (1972) suggests that such periodic "blooms" may occur in some coral reef fishes in seasons when favorable environmental conditions enhance recruitment survival. Whether due to irregularities in breeding, differing environmental conditions, or to chance factors in dispersal, such differences serve to highlight an important element of unpredictability in the recruitment of individual species from year to year.

Our analysis of spatial variation in reef fish community structure is also consistent with a high degree of local unpredictability in juvenile recruitment. The data show a high between-reef variability in species composition that is not readily explainable in terms just of habitat differences. Likewise, species-species interactions seem insufficient to account for the observed differences between reefs.

Sale and Dybdahl (1975) found that most of the species they studied showed little evidence of microhabitat specialization, and concluded that chance factors were overwhelmingly important in determining the distribution of species. Our settlement data, however, indicate that, while a majority of species appear to be opportunistic in their choice of habitat, a nonetheless significant proportion (nearly half) of species do show habitat selection, at least of the type and scale investigated. Our data further suggest intraspecific interactions may be important in determining patterns of settlement of at least some species.

Temporal variation in community structure on our artificial reefs was exceedingly high. Mean between-census similarity values for both sets of reefs indicated significant changes in community structure from 1 census to the next. Species turnover rates showed a turnover of ≈17% of species per month in winter, ranging up to ≈39% in summer, suggesting once again strong seasonal change in community structure. Maximum times of persistence for most species was <12 mo and for many individuals, survivorship was of the order of only a few months. Over a full year, the data suggest there is a turnover of most species in the community.

Predation probably accounts for much of the high turnover losses. We base our evidence of this mainly on observation. During censusing we frequently observed instances of predation, particularly by roving and transient predators (*Synodus variegatus*, *Epinephelus* spp., *Caranx* sp., *Carangoides* sp.) which preyed mainly on the smaller schooling fishes (especially juvenile apogonids and pomacentrids). A number of resident species (*Gymnothorax flavimarginatus*, *G. favigineus*, *Scorpaenodes guamensis*, *Dendrochirus zebra*, *Dendroscorpaena* sp., *Pterois volitans*, *Cephalopholis pachycentron*, *Diploprion bifasciatum*, *Epinephelus merra*, *Sphyraenella chrysotaenia*, *Parapercis polyopthalma*) are also mostly piscivorous and probably contributed additionally to predation losses.

Emigration losses appeared to involve only a relatively few species and, in terms of numbers of individuals, are probably unimportant. We could attribute emigration losses mainly to a change in behavior and habitat requirements as the fishes grew from juveniles to adults.

TABLE 11. Comparison of the mean persistence times ($\bar{P}$) of species present at different census intervals. Mean persistence ($\bar{P}$) calculated as the average period a species occurred over all reefs. Numbers of species with $P \leq$ 1–19, 2–2.9 ... 5–5.9, >6.0 mo compared using Kendall's Coefficient of Concordance, W

		Mean persistence ($\bar{P}$) in months					
	Census	≤1–1.9	2–2.9	3–3.9	4–4.9	5–5.9	>6.0
Summer set	2 wk	1	11	9	1	0	3
	4 mo	1	8	10	2	2	2
	7 mo	2	9	8	2	1	4
	12 mo	2	14	10	2	4	4
	24 mo	2	12	10	3	3	2
	32 mo	2	12	9	2	2	2
Winter set	1 mo	1	2	2	0	1	1
	6 mo	1	13	9	2	2	1
	12 mo	3	13	10	2	2	0
	22 mo	3	13	10	2	2	0

Mortality due to storm-induced habitat disruption also appears insignificant. Despite their catastrophic effects on coral reefs (Glynn et al. 1965; Stoddart 1969; Connell 1974, 1978), tropical cyclones are comparatively infrequent and their impact on reef fishes appears to be minimal, particularly in sheltered areas such as the lagoon at One Tree Reef. In the Capricorn Group region only 18 tropical cyclones have been recorded in the period July 1909–June 1975 (Lourensz 1977), giving a mean frequency of 1 major storm every 3.7 yr. During the present study we experienced only 1 tropical cyclone (Cyclone Emily), the centre of which passed close to One Tree Island on 2 April 1972. Despite strong winds of up to 135 km/h and heavy seas, with waves up to 1.5 m height breaking in the lagoon (S. Domm, *personal communication*), damage to the artificial reefs was limited to collapse of only a few blocks and there was no noticeable effect on the fishes.

Our colonization data fail to exhibit convincing evidence that an equilibrium number of species is approached. Species equilibrium theory predicts either a monotonic increase in numbers of species until equilibrium is reached (MacArthur and Wilson 1967) or an initial rapid build-up of species to a higher level "noninteractive" peak, followed by a sharp decline to a more enduring but lower "interactive" equilibrium number of species, in which competition and/or predation reduces the number of species which are able to coexist (Simberloff and Wilson 1969). Over more substantial time intervals (several years), there may be a gradual increase in the number of species to an "assortative" equilibrium of longer-lived, more-persistent species (Wilson 1969). Though we might expect

that, on small isolated areas of reef, where space is at a premium, initial colonizers might monopolize that space and preclude further colonization, leading to an early equilibrium, this is not always the case. Schoener (1974) concluded that the colonization data for a number of marine benthic communities failed to show a species equilibrium because the pool of potential colonizers relative to the number of species in the community was large and this led to continued growth of the community. On our artificial reefs, the pool of colonizing species also was large relative to the maximum number of species which occurred at a particular time on any 1 reef, yet our data do not suggest any significant increase in species numbers with time. Rather, the colonization rate curves show a strong periodic component, so that in winter there is a net loss of species and, in summer, a net gain. Because of this seasonally varying pattern, we see the development of an equilibrium number of species as being largely short-circuited.

Successional changes in the reefs' biota are unlikely to alter this pattern. During the present study such changes were relatively minor in their effect on the fish assemblages. During the 1st yr, there was early settlement of the reefs by oysters (*Crassostrea amosa*) and after the 2nd yr, limited patchy colonization by alcyonarians (*Xenia elongata*) and small branching corals (*Pocillopora, Seriatopora*). Only the arrival of blennies could be correlated with any of these changes. As a group, blennies did not occur in any numbers on the reefs until the 2nd yr and it is likely that their successful settlement was associated with the availability of dead oyster shells which are used as shelter and nest sites by these fishes. Although we might expect further succession of corals and other organisms to result in additional settlement by other habitat specialists (e.g., coral-dwelling gobies, anemone fishes), there are comparatively few such species and any significant long-term increase in the numbers of fish species or a shift towards longer-lived, more stable assemblages is unlikely.

We would predict that, in the long term, because of the continual intercession of predation and other losses and because recolonization is so markedly seasonal and also largely unpredictable, the development of any persistent species equilibrium is unlikely. This view contrasts sharply with generally held ideas of stability of coral reef fish communities (Smith and Tyler 1973*a*, 1973*b*; Smith 1975). We suspect that observations on the apparent stability of reef fish assemblages derive at least partly from observations at much larger intervals than ours. Estimates of turnover are dependent on the census period, and censuses at long intervals may drastically underestimate real turnover (Diamond and May 1977). For example, Smith and Tyler (1973*b*) base their conclusion that there is little variation in species composition of 'benthic residents' on a Bahamas patch reef, on censuses made at 6-mo intervals. Nolan (1975), however, in study similar to ours, found considerable variation in species numbers and in species composition on Enewetak patch reefs censused at intervals of 2–4 mo.

Sale (1977) has hypothesized that variability in species composition, both in time and space, is the result largely of chance patterns of colonization. He argues that recruitment occurs on a 'first-come-first-served' basis and that local diversity is a function of the number of species available and their relative abundance at the time of settling. This model makes 2 critical assumptions. First, recruitment to a site is assumed to be independent of the structure of the resident fish community at that site. This assumption is difficult to test. However, larvae of most species have at least a short oceanic-pelagic dispersive period and may be transported to areas considerable distances from those in which they are spawned. Thus, it seems that chance factors are likely to exert a significant influence on recruitment success, and our own data evidence a high degree of unpredictability in recruitment of individual species from year to year (Russell et al. 1977).

The second assumption—that species are more or less equal in their abilities to obtain space and that no one species has a competitive advantage—is only partially supported by our data. Our results indicate that, for most species, settlement on identical sites is nonrandom, some species differ in their abilities to colonize different sorts of space, and that for a few species, social interactions may be important in determining patterns of settlement. These results suggest the process of colonization is not entirely stochastic and may be much more complex than Sale's (1977) model assumes.

The real question at issue, however, is not whether colonization is largely a chance process or whether species are more or less equal in their abilities to obtain and hold space, but whether population interactions are ever sufficient for the community to reach an ordered state. Our results suggest that communities of small patch reef fishes are highly unstable and that a persistent species equilibrium may never be attained. We can envisage patch reef fish communities as spatio-temporal mosaics, the component patches of which are in continual flux. Recent theoretical work (Levins and Culver 1971, Horn and MacArthur 1972, Levin 1974, Slatkin 1974, Roughgarden and Feldman 1975) suggests that this kind of instability on a local scale may allow more species to occur together than would otherwise be permitted. Work by Levin and Paine (1974, 1975) and Connell (1978) further suggests that the level of local 'disturbance' of communities may be an important factor in the maintenance of diversity. They argue that localized, unpredictable disturbance, in the form of extinctions due to natural catastrophe, predation, or other chance events, interrupts the local march to and survival of equilibrium, thereby permit-

ting utilization of resources by a much larger number of species than would otherwise be able to coexist.

This hypothesis, the 'intermediate disturbance' model of Connell (1978), predicts that highest diversity will be maintained at intermediate levels of disturbance. If this is so, then the rather simple shelter characteristics of our artificial reefs may have resulted in much higher predation rates and thus higher turnover than would naturally occur on small patch reefs with greater shelter. We would expect, then, that natural reefs might show a higher diversity. Nolan's (1975) results also support this: he found artificial reefs had a higher turnover and supported fewer species than natural reefs, and was able to demonstrate experimentally an increase in the numbers of species on artificial reefs by providing additional shelter. By caging to exclude some predators, we might expect reefs to show an initial increase in diversity, and by excluding all predators, eventually a much reduced diversity. Experiments presently being carried out by 1 of us (G. R. V. Anderson) at Lizard Island indicate a significant increase in the numbers of species on artificial reefs caged to exclude larger roving predators. Similar experiments with natural patch reefs carried out by Nolan (1975), although mostly unsuccessful, also showed an increase in diversity. While further experiments clearly are needed, these results are consistent with the idea that diversity is highest at intermediate levels of disturbance (predation). They also substantiate our conclusion that predation is an important factor in determining community structure.

We suggest that reef fish populations are maintained in a nonequilibrium state principally by predation and the seasonally varying, uncertain nature of recruitment, and that by preventing monopolization of resources by any 1 species, these factors contribute to the high within-habitat diversity of coral reef fish communities.

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