

The Fish Communities of a Coral Reef Transect¹

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ABSTRACT: As a contribution to the discussion on the causes of the high fish species diversity found on coral reefs, a coast-to-sea transect has been studied in the lagoon of Moorea Island (French Polynesia) in order to uncover the spatial scales at which recurrent assemblages (i.e., communities) can be identified. The transect was divided into 22 stations where fishes were sampled. According to the null hypothesis (chaos), the fish species should be distributed at random along the transect. This was tested first by a method of constrained clustering that performs a statistical test of cluster fusion, based on a null hypothesis that corresponds to chaos. Groups of stations were found with, at most, a 5% chance of resulting from a random distribution of species among the groups. The distribution of species among the stations provided a second test of the null hypothesis; the observed number of ubiquitous species was found to be significantly smaller than expected under the hypothesis of chaos and, in the same way, the species limited to a single group of stations were found to be significantly more numerous than expected under chaos. Both patterns are consistent with reports from other reefs of the Indo-Pacific.

TRADITIONAL EXPLANATIONS OF the high diversity encountered within coral reef fish communities state that, like other tropical systems, coral reefs are equilibrational systems in which species compete for, and partition, a number of limiting resources. For example, Smith (1977, 1978) suggests that living space is a limiting factor which imposes a regular and predictable structure on reef-fish assemblages. This view can be termed the theory of "order."

Sale (1984) argues that the predictions from this theory must be tested against a null hypothesis (H_0) stating that there is no pattern other than that of a random redistribution of individuals and species within each generation, among resources which have patchy distributions. This theme has been developed in a

number of papers (Sale 1974, 1977, 1978 ...); it has been referred to by various authors as the "chaos" hypothesis. The main argument is that, although reef fishes are habitat specialists with regard to broadly defined habitats within the reef, the allocation of space within habitat occurs through a chance process that Sale calls a "lottery" for living space (Sale 1977, 1978).

This paper reports on a program of observations designed to uncover the spatial scale at which community structure can be identified. This program is actually a part of a larger research program aimed at measuring the stability and variability of fish communities on coral reefs in the Pacific Ocean (French Polynesia). Using statistical methods that take chaos as their null hypothesis, the fish community will be shown to be significantly structured in space following the major habitats discernable on the reef.

This paper contributes further to the discussion on the causes of the high fish species diversity on coral reefs, in directly testing predictions from chaos theory (H_0) as to the number of ubiquitous species and the number of area-typical species on the reef. Unfortunately, our program of observations is not

¹ Manuscript accepted April 1987.

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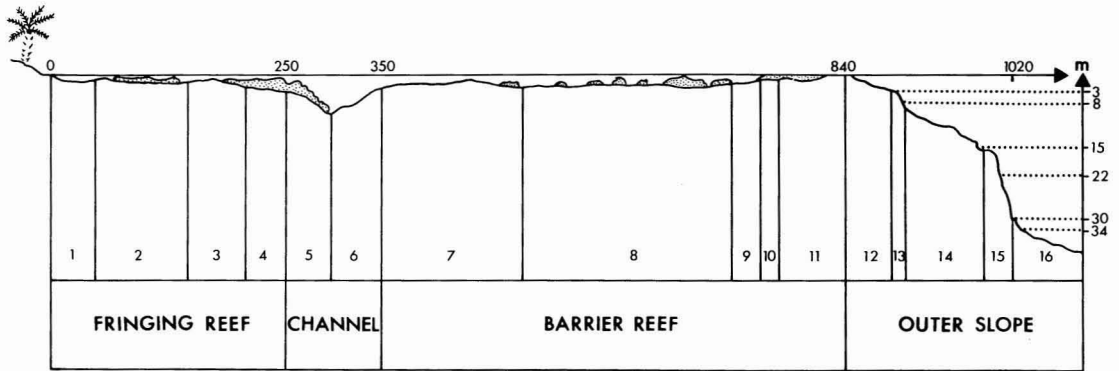


FIGURE 1. Geomorphological description of the Tiahura reef transect. The section numbers correspond to:

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|-----------------------------------|----------------------------------|
| 1—Sandy accumulation | 9—Scattered detritic zone |
| 2—Reef flat with microatolls | 10—Coral heads area |
| 3—Dying filling-up reef flat | 11—Outer biogenic ridge |
| 4—Coral head | 12—Furrowed platform |
| 5—Channel coral slope | 13—Precipitous slope |
| 6—Channel sandy slope | 14—Buttresses and valleys |
| 7—Coral sand area | 15—Outer slope spurs and grooves |
| 8—Reef flat with scattered corals | 16—Sandy area |

appropriate to test the theory of lottery; as shown by Sale (1977), predictions from lottery theory could primarily be tested from a sampling through time.

MATERIAL AND METHODS

Study Area

A coast-to-sea transect, 1020 m long, was established at "Tiahura" in the lagoon located at the northwest end of the high volcanic Moorea Island (149°50'W, 17°30'S) in French Polynesia. The geomorphology of the transect is as follows (Figure 1):

—The fringing reef, 250 m wide from the beach, is shallow (less than 1.5 m). The coral sand beach (1) is followed by a zone of detritic sediments (2), including several microatolls, considerably degraded and colonized by algae. This is followed by a highly crumbled, dying reef flat (3) which is being filled in. Following is a zone of coral patches (4), some isolated from one another, others aggregated in large coral heads.

—The channel, 9 m deep and 100 m wide, is colonized by coral constructions on the beachward slope (5), while the seaward slope is gently sloping and sandy (6).

—The barrier reef, 490 m wide, begins with a zone of fine coral sand (7) covered by 2.5 m of water or less, at high tide. Then comes a reef flat (8) with sparsely distributed coral patches, increasing in number towards the ocean; these coral patches grow on the old coral limestone bench which is covered, outside the patches, by a few centimeters of sand. This is followed by an area scattered with pebbles and detritus (9), preceding a zone of coral masses closing into a coral table (10). The barrier reef ends with a slightly elevated zone of limestone (11), supporting a mixed reef ridge.

—The outer slope begins with a furrowed, upper platform (12), with 0 to 3 m of water at high tide, followed by a sharp slope (13) 3 to 8 m in depth. The next zone is subhorizontal (14), sloping gently from 8 to 14 m, with coral buttresses and valleys. From 14 to 30 m deep, the slope is sharp again, with spurs and grooves (15). Zone no. 16 is an area of strewn coral sand, which ends at a depth of 65 m, at a sharp slope towards the abyss.

Sampling

The transect was divided into 22 sampling stations. On the reef, each station was 50 m long (Figure 2), except for station 17, the last

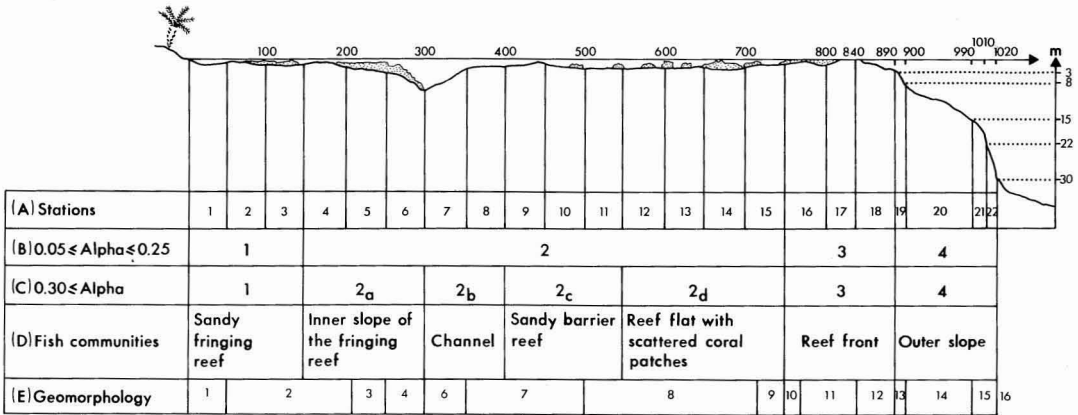


FIGURE 2. Profile of the Tiahura reef transect, showing (A) The 22 sampling stations. (B) The four groups of stations obtained by constrained clustering. (C) The seven groups of stations obtained also by constrained clustering. (D) The corresponding fish community names. (E) The geomorphology; the 16 sections are described in the legend of Figure 1.

one of the barrier reef, which was only 40 m long. On the outer slope, stations were divided at depths of 3, 8, 15, 22, and 30 m, following Harmelin-Vivien and Bouchon-Navaro (1983), who described fish distributions on that slope.

Sampling was carried out from 1 October to 18 November 1982 using two complementary techniques (Smith and Tyler 1972; Galzin 1979). The presence or absence of each of 280 species was noted for all 22 stations. First, visual observations were made during randomly directed 45 min swims within each station by a trained observer (R.G.) while snorkel or scuba diving. Station 1 is too shallow for diving and was sampled by net fishing, supplemented with visual observations under calm surface conditions. Secondly, single coral patches of about 0.5 m³ were selected within each station and poisoned with rotenone by a diver (R.G.) who expelled the solution from a plastic bag at the base of the patch. The fish, which were usually nocturnal or crack-inhabiting species, were then collected with a fine-meshed hand net.

Numerical Analysis

The sampling described above was designed to test the null hypothesis that the fish community is not structured in space on the reef (chaos theory). It will first be analysed using a

statistical method described as "chronological clustering" by Legendre et al. (1985). This method partitions multi-species data series into homogeneous segments, following hierarchical agglomeration. The method is said to be "constrained" in that only samples or segments of samples that are adjacent along the series are allowed to cluster. The present paper extends this method to space series. Cuts in the data series are produced only when the null hypothesis is rejected by a randomization statistical test, at the Alpha-level of significance. The null hypothesis states that the two groups tested do actually form a single group. This statistical hypothesis seems appropriate for testing the ecological null hypothesis of chaos, since Legendre et al. (1985) have shown that the null hypothesis is rejected by the randomization test with a frequency Alpha, when applied to randomly generated data (corresponding to chaos), in a Monte Carlo simulation. Connectedness of 50% was used for the intermediate-link linkage agglomeration that precedes the test of cluster fusion. The similarity matrices subjected to constrained clustering were computed among stations from the species presence and absence data, using the binary coefficients of Jaccard and of Kulczynski; on similarity coefficients, see for instance Legendre and Legendre (1983). The statistical tests of predictions from the null hypothesis of chaos, for the

number of ubiquitous species and for the numbers of species characterizing each group of stations, are described with the Results.

RESULTS

Both the Jaccard and the Kulczynski coefficients of similarity produced exactly the same partitioning of the 22-sample space series into groups, for all the Alpha-levels considered. At the Alpha = 5% level of significance, four major groups of stations were found. They are shown in Figure 2B. As recommended by Legendre et al. (1985), larger Alpha-levels were tried in order to find finer partitions. The partition of the data series remains exactly the same for all Alpha-levels of significance from 5% to 25%. When Alpha reaches 30%, a finer partition is found (Figure 2C). This seven-group solution is nested in the four-group partition, although this is not a property of this clustering method; this shows the robustness of the four-group solution, since the seven-group partition brings only a refinement to the large central group 2. The seven groups were found at all Alpha-levels between 30% and 50% (the largest Alpha-level used in this study), which shows again the stability of the seven-group partition. The four fish communities can be characterized as follows (Figure 2D):

- I—Sandy fringing reef community
- II—Lagoon community:
 - (a) Inner slope of the fringing reef
 - (b) Channel
 - (c) Sandy barrier reef
 - (d) Reef flat with scattered coral patches
- III—Reef front community
- IV—Outer slope community.

A posteriori tests were performed among the seven groups of stations in order to detect affinities between non-adjacent segments of the partition. Using the same randomization test as the clustering procedure does, significant relationships were found between segments 2a and 2c on the one hand (the probability of the null hypothesis of fusion was

80%) and between segments 2a and 3 on the other (the probability of H_0 was 40%).

Forty-six families are represented among the 280 fish species recorded along the transect. The most important are the Labridae (40 species), the Pomacentridae (25), the Chaetodontidae (19), the Acanthuridae (19), the Apogonidae (14) and the Scaridae (13).

Contingency tables comparing the presence/absence of each species to the 7-group classification of stations show that the Acanthurid *Ctenochaetus striatus* is found at all 22 sampling stations of the transect, while five other species show up in each of the seven groups of stations (*Pseudopenaeus multifasciatus*, *Chaetodon vagabundus*, *Stegastes nigricans*, *Stethojulis interrupta* and *Acanthurus triostegus*), giving a total of six ubiquitous species (2%). On the other hand, 15 species (5%) were found at least once in each of the four major groups of stations 1 to 4. A direct prediction from the hypothesis of chaos was tested as follows: under the hypotheses of random distribution among stations, and of independence of adjoining stations, the probability of presence of each species at least once in each group of stations (ubiquity) was computed. These probabilities were calculated from the hypergeometric distribution, taking as probability p the actual proportion of stations occupied by each given species (the hypergeometric distribution was used instead of the binomial, because we are sampling without replacement from a finite population). Assuming that the species are not associated to one another, the probabilities of ubiquity for each of the 280 species were combined by summing. The expected number of ubiquitous species is 36 for the 7-group classification of stations, and 67 for the 4-group classification. The differences between observed and expected numbers of ubiquitous species are very highly significant ($p < 0.001$), using a Pearson's chi-square test or a G-test of goodness of fit, or by computing the confidence intervals of the observed proportions of ubiquitous species.

On the other hand, only 28 species are limited to a single habitat, considering the 4-group classification. Only the species present in at least half of the stations of any

given group are counted here. Two species are found in a majority of stations of the fringing reef (group 1) and nowhere else: *Pseudocheilinus tetrataenia* (Labridae) and *Amblygobius decussatus* (Gobiidae). Three species characterize the lagoon (group 2): the Acanthurid *Acanthurus nigricauda*, the Ostraciantid *Ostracion cubicus*, and the Tetraodontid *Canthigaster valentini*. Five species are typical of the reef front (group 3): *Platybelone argala* (Belontiidae), *Crenimugil crenilabis* (Mugilidae), *Kyphosus vaigiensis* (Kyphosidae), *Cirripectes variolosus* (Blenniidae), and *Acanthurus guttatus* (Acanthuridae). Finally, 18 species are found in a majority of the stations of the outer slope (group 4) and nowhere else: 1 Muraenid, 1 Synodontid, 3 Serranids, 2 Lutjanids, 1 Pomacentrid, 1 Pomacentrid, 2 Labrids, 1 Scarid, 1 Eleotrid, 4 Acanthurids, and 1 Balistid. Using the same method as above, the number of species expected to characterize a majority of stations of each group, while being found nowhere else, was computed under assumptions corresponding to chaos theory. For groups of stations 1 to 4, these values are respectively 0.090, 0.008, 0.090 and 0.006. A Pearson's chi-square test, or a G-test of goodness of fit, shows the observed numbers of typical species (reported above) to be significantly different ($p < 0.001$), and larger than these expectations, thus allowing us to reject the null hypothesis corresponding to chaos.

DISCUSSION AND CONCLUSIONS

The major finding of this study is that the fish assemblages display more order than is consistent with a null model based on random distributions, and that most of this "order" can be explained by predictable associations between species and habitats.

Comparison of the fish communities, identified above by constrained clustering, with the geomorphology of the transect shows interesting relationships (Figure 2). The fringing reef community occupies the shallow sandy section (1 and 2) of the fringing reef. The community found on the inner slope of the fringing reef penetrates far deeper into the fringing reef (sections 3 to 5) than would be

expected from the geomorphology; this is due to the channel water influence, described above, and the consequent vitality of corals in these sections. To the fish, the channel itself is the sandy part, found in geomorphologic section 6 and a part of section 7. On the barrier reef, the fish communities of the sandy barrier reef and of the coral patches (2c and 2d) fit almost exactly geomorphologic sections 7 to 9; detritic zone 9 does not bear a characteristic fish community. This is followed for the fish by a well-identified reef front community, found in geomorphologic zones 10 to 12, and an outer slope community occupying zones 13 to 15. No sampling took place in zone 16.

The similarity of the communities of the inner slope of the fringing reef (2a), of the sandy barrier reef (2c), and of the reef front (3), is of particular interest. The affinity between these three reef sections may be due to water circulation on the reef. Each of these three sections seems to act as a "reef front," and it would be interesting to test the hypothesis that these "fronts" receive the planktonic fish larvae first, directly from the ocean. According to this hypothesis, other sections of the reef would then be colonized afterwards, by the fish that have settled on these "fronts."

Among the factors responsible for the partitioning of the Tiahura reef transect into four major communities, the percentage of living coral has been found to be of prime importance by Bell and Galzin (1984). This same variable has also been found by Sale (1984) to be a significant predictor of the number of fish species found on a patch reef, together with the reef surface area. Hydrodynamic activity is here another important factor, as shown by the *a posteriori* clustering of station groups 2a, 2c and 3, described above, because these reef sections seem to behave as reef fronts. The same phenomenon has recently been pointed out by other workers (Williams 1982, Williams and Hatcher 1983, Russ 1984). This finding also agrees with the theory of Legendre and Demers (1985) concerning the importance of ergoclines (transition zones from high to low levels of auxiliary energy) in the dynamics of ecosystems.

As far as we know, only two other papers present data comparable to ours: the work of

Goldman and Talbot (1976) on One Tree Island Reef, in the Great Barrier Reef System of Australia, and that of Harmelin-Vivien (1979) on the Tulear reefs in Madagascar. The partition of the reef into five major habitats, considered by Goldman and Talbot, is given by the geomorphology, while Harmelin-Vivien used non-constrained hierarchical clustering of the [species x zones] data matrix to recognize three major fish communities. Despite the differences in methods, these authors' results are quite comparable to ours in terms of ubiquitous species, and of species limited to a single habitat (Table 1). For the species limited to one habitat, the above-mentioned authors had counted all species present at least once in any given habitat and absent from all others. The figures given in Table 1 for the present study's data follow this rule, instead of the "species found in a majority of stations of any one habitat" rule that was used above for the statistical test.

With regard to chaos theory: three statistical tests of hypotheses, each with a null hypothesis corresponding to chaos, have shown the disagreement of our observations with chaos theory. These are: (1) A partition of the transect into four major groups has been evidenced by constrained clustering. This method of clustering, which respects the spatial relationship of the stations with each other within the ecological continuum, shows differences between the successive groups at the Alpha = 5% level of significance; this means that the structure that has been evidenced has at most a 5% chance to be the result of random allocation of species among those four groups. (2) The number of ubiquitous species is significantly smaller ($p < 0.001$) than the number of ubiquitous species that should have been observed if the species had been distributed at random among the stations on the transect, supposing that adjacent stations are independent. (3) The species limited to only one of the four groups of stations are significantly more numerous ($p < 0.001$) than what would have been expected from the same hypotheses. Data available in the literature indicate that fish species show comparable distribution patterns on other reefs (Table 1).

It could be argued, of course, that chaos

TABLE 1

COMPARISON OF THREE CORAL REEFS IN THE INDO-PACIFIC AREA, FOR PERCENTAGES OF UBIQUITOUS SPECIES AND OF SPECIES RESTRICTED TO A SINGLE HABITAT

REEF	PARTITION OF THE REEF	TOTAL NUMBER OF SPECIES	% UBIQUITOUS SPECIES	% SPECIES RESTRICTED TO ONE HABITAT	% SPECIES RESTRICTED TO OUTER SLOPE	REFERENCE
One Tree Island (Australia)	5 sections	395	6.6	47.6	15.4	Goldman and Talbot (1976)
Tulear (Madagascar)	3 sections	552	8.2	44.0	14.5	Harmelin-Vivien (1979)
Tiahura (Polynesia)	4 sections	280	5.4	45.0	14.6	Present study

does not necessarily imply the independence of adjacent stations, as was used in the hypergeometric simulations leading to tests (2) and (3) above. Even in that case, test (1) still holds, since it was constructed to take the spatial adjacency of samples into account.

One should finally notice that after rejecting chaos as the explanation of ichthyological diversity along the Tiahura reef transect, one is not left with a single alternative hypothesis. Specific tests have to be designed to decide among various alternative theories. For instance, we need to look at the patterns of settlement and juvenile survivorship of the coral reef fishes. Several authors (Williams 1980, Doherty 1982 and 1983, Victor 1983) have proposed that population abundances within habitats are primarily determined by recruitment from the pelagic larval phase. In addition, finer observations at the microhabitat level are needed to define the affinity or exclusion relationships among species resulting possibly from their co-adaptation. Finally, longer-term studies are needed to measure the stability of communities and of the environment.

The original [species x stations] data table is available from the authors.

ACKNOWLEDGMENTS

Contribution No. 311 of the Group d'Écologie des Eaux douces, Université de Montréal. We are grateful to J. D. Bell, P. J. Doherty, M. L. Harmelin-Vivien, P. J. Sale, and two anonymous referees, for valuable discussions and comments. This study was supported by the Centre National de la Recherche Scientifique (CNRS/RCP 806).

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