

## Relationships between coral reef substrata and fish

P. Chabanet<sup>1,2</sup>, H. Ralambondrainy<sup>3</sup>, M. Amanieu<sup>1</sup>, G. Faure<sup>4</sup>, R. Galzin<sup>2</sup>

<sup>1</sup> Laboratoire d'Écologie marine, Université de La Réunion, BP 7151. 97715 St-Denis Messag Cedex 9. La Réunion, France

<sup>2</sup> Ecole Pratique des Hautes Etudes, URA 1453 CNRS, Université de Perpignan 66860 Perpignan Cedex, France

<sup>3</sup> Institut de Recherche en Mathématiques et Informatique Appliqués, Université de La Réunion, BP 7151. 97715 St-Denis Messag Cedex 9. La Réunion, France

<sup>4</sup> I.S.I.M. (Sciences et Techniques de l'eau), Université de Montpellier Place Eugène Bataillon. 34095 Montpellier cedex, France

Accepted: 26 July 1996

**Abstract.** The objective of this work is to identify which substrata characteristics (such as coral morphology, coral diversity, coral species richness, percentage coverage by live coral or by algae) influence the structure and abundance of fish communities. The study was carried out at Reunion Island, Indian Ocean, where six sites were sampled in two zones (reef flat and outer reef slope). Quantitative data were collected by visual census techniques, along a linear transect of 50 m for the substratum, and a belt of 50 × 2 m for the fish communities. Correspondence analysis (CA) and an optimising cluster analysis, called dynamic clustering method (DCM) were used to describe and compare fish assemblages with the benthic composition. The relationships between benthic and fish communities were examined using the classes revealed by the partitioning of the substratum with DCM. This partitioning allowed us to derive four classes of substratum: the non-disturbed reef flat, the non-disturbed outer reef slope, the perturbed reef habitat and the reef pass. The analysis of the partitioning based on the coral variables suggests that there are significant relationships between benthic and fish assemblages.

### Introduction

The complex architecture of coral reefs offers shelter to an extremely diverse fauna (Connell 1978). In most studies, the physical complexity of the reef substratum is positively correlated with the diversity of fish community, but not with fish abundance (e.g. Luckhurst and Luckhurst 1978; Talbot et al. 1978; Roberts and Ormond 1987). The biological nature of the substratum, i.e. coral species richness and/or live coral, had no influence on the diversity and abundance of fish communities in some studies (Luckhurst and Luckhurst 1978; Mc Manus et al. 1981; Bouchon et al. 1987; Roberts and Ormond 1987) while in others, these fish characteristics were positively correlated with live coral (Carpenter et al. 1981; Sano et al. 1984,

1987; Bell and Galzin 1984, 1988). The variability in the relationship between the fish and coral communities may be attributed to geomorphological, ecological and methodological factors.

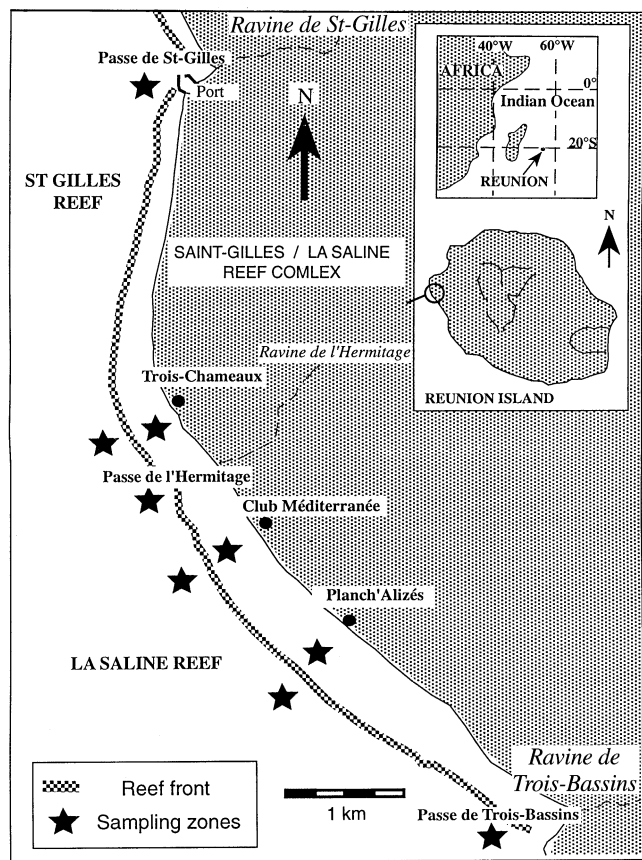
The objective of this study was to identify which characteristics of the substratum influence the structure (estimated by species richness and diversity) and abundance of fish communities at Reunion Island. To achieve this objective required the adoption of methods to identify relationships between two sets of heterogeneous attributes; those relating to the substratum and those associated with fish communities. We explain the use of the dynamic clustering method (Everitt 1974; Jain and Dubes 1988; Celeux et al. 1989) for this purpose.

### Materials and methods

#### *Study area*

This study was carried out on the high volcanic island of La Reunion located in the western Indian Ocean (21°07'S, 55°32'E) (Fig. 1). Coral reefs lie along the western coast which is the hottest and driest side of the island. Reefs are exposed to strong hydrodynamic conditions, mainly due to the southeast trade winds during the cool season (June–October) and to tropical cyclones during the hot season (November to May). Tides are semidiurnal and range from 0.1 m (neaps) to 0.9 m (springs) (Cuet et al. 1988).

The narrow (maximal width: 520 m) fringing coral reef forms a discontinuous belt along a 25 km section of the island's 210 km circumference. The reef's geomorphology has been previously described by Montaggioni and Faure (1980). From the open ocean towards the land, the reef can be divided into three parts: the outer slope, the reef flat, and the back reef. This study was conducted in the St-Gilles/La Saline reef complex which is the most developed reef of the island (9 km long). Sampling was carried out at six sites; Saint-Gilles, Trois-Chameaux, Passe de l'Hermitage, Club Méditerranée, Planch'Alizés and Passe de Trois-Bassins (Fig. 1). These sites were chosen for their physico-chemical features. Trois-Chameaux reef flat (an undisturbed site) is characterised by oligotrophic waters; Planch'Alizés and Club Méditerranée reef flat (disturbed sites) are subject to eutrophic waters (Cuet et al. 1988; Cuet 1989; Cuet 1994). This eutrophication results from urban development of catchment areas which has polluted the submarine groundwater discharge into reef waters (Cuet et al. 1988; Chabanet et al. 1995a). Live coral cover



**Fig. 1** Location of the studied sites on St-Gilles/La Saline reef complex, Reunion Island, SW Indian Ocean

is declining and benthic algal populations are increasing, apparently due to the combined effects of elevated nutrients and undergrazing (Cuet et al. 1988; Naim 1993; Chabanet 1994).

### Substrata and fish census

A total of 27 fish and benthic transects were surveyed. The surveys were carried out on the reef flat, the outer reef slope (average depth 18 m), and passes which are deeply cut into the reef caused by river runoff. In each of these 3 zones, 3 stations (benthic and fish transects) were censused (Fig. 1).

Sampling was carried out by visual observations, snorkelling on the reef flat and scuba diving on the outer slope. A 50 m long line was positioned along depth contours. Substrata and ichthyological data were collected on different days. First, the line was used as a line intercept transect to record the position and extent of benthic organisms (hard and soft live corals, algae, sponges) and abiotic substrata (Loya 1972, 1978). Scleractinian corals were identified to species, while algae were recorded as 'fleshy', 'calcareous' or 'turf'. The other benthic categories used were 'soft corals' and 'sponges'. Second, the line transect was used as the centre of a 50 × 2 m belt transect for counting reef fishes using the abundance groupings technique of Harmelin-Vivien and Harmelin (1975): 1, 2–5, 6–10, 11–30, 31–50, 51–100; etc. In this study, we divided the second class into two (2 and 3–5) because pair behaviour plays an important role in reef environments (Bouchon-Navaro 1980, 1981). A series of transverses of each transect was conducted: the first passage was divided into 10 m intervals, for two types of census performed in succession; one from a fixed point to count escaping fish and one performed whilst slowly swimming along the line in order to count species which were immobile or slow. Acanthuridae and Pomacentridae, which were particularly abundant, were counted on the

second and third passages, respectively. To account for temporal variability, these procedures were repeated three times per transect.

Visual census methods for assessing reef fish populations underestimate the real populations (Harmelin-Vivien et al. 1985; Kulbicki 1988). Nevertheless, these methods do provide a good basis for comparison between areas (McCormick and Choat 1987). In this study, some families such as Labridae were excluded from the census. We also did not count species which were seen only occasionally during the census, like night-hunting species (Holocentridae, Apogonidae, Muraenidae, Scorpaenidae), species that live in the reef framework (Blennidae, Gobiidae) and those occupying the outer slope water column (Caesionidae, Carangidae). The following families were included during fish census: Serranidae, Haemulidae, Lutjanidae, Lethrinidae, Pentapodidae, Kyphosidae, Mullidae, Pomacanthidae, Chaetodontidae, Cirrhitidae, Pomacentridae, Scaridae, Acanthuridae, Zanclidae, Siganiidae, Balistidae, Monacanthidae, Ostraciidae, Tetraodontidae and Diodontidae.

The sampling took place from January 1991 to February 1992 and was interrupted during the austral winter (June to October 1991) because of unsuitable wave conditions. On each site, a census of benthic and fish communities was undertaken at two of the three stations during the first period (January to June) and the third station during the second period (October to February). It took between 4 to 10 days to sample one station (1 benthic transect + 3 fish replicates).

### Substrata and fish variables

Several summary variables were also calculated at each station. They included coral species richness, coral abundance (number of coral colonies per station), average size of coral colonies, diversity (Shannon-Weaver index), coverage of the substratum: % live coral, % of sand and rubble, % algae and % coverage of three coral growth forms (branching, massive and encrusting). Soft coral and sponges were excluded because they represented a very low coverage on the transect. Branching corals included all of those species whose growth forms provided shelter for the studied fishes. The coverage of branching coral colonies was also considered to be an index of structural complexity of the substratum.

For the fish community, the following parameters were determined for each transect: species richness, diversity (Shannon-Weaver index), total abundance; and abundance of the following trophic groups: herbivores, omnivores, sessile Invertebrate browsers, carnivores (including piscivores) and plankton feeders (after Hiatt and Strasburg 1960; Hobson 1974; Harmelin-Vivien 1979).

### Data analysis

To analyse the relationships between benthic and fish communities, correspondence analysis (CA) (Benzecri and Benzecri 1976; Greenacre 1984) was applied on two contingency tables, one for the 96 substratum variables and stations, and one for the 98 fish species and stations. Second, we adopted a strategy based on discriminant analysis (Fisher 1936) which we refer to as dynamic clustering method (DCM). The goal of DCM is to find classes of stations based on the summary substratum attributes. Then, for each class, summary tables of the associated fish assemblages are constructed. DCM is a variant of the *K*-means clustering algorithm (Everitt 1974; Jain and Dubes 1988; Celeux et al. 1989) in which the number of classes *k* is defined a priori. A 'good' choice of *k* provides classes which are internally homogeneous, but well separated faunistically from each other (Huber and Levin 1976; Milligan and Cooper 1985). The dissimilarity measure was the normalised distance measure *d* (Milligan and Cooper 1985). This measure was chosen because it is independent of the amplitude of variables and the units used to measure them.

The analyses we used are based on the following procedure. Let  $g_1, \dots, g_k$  be the gravity centres (prototypes) of the clusters  $C_1, \dots, C_k$  of an partition  $P$ . The centre of gravity of the set of

observations is  $g$ . The heterogeneity between classes was expressed as the interclass inertia, which is the average distance between the centres of gravity of the  $k$  clusters:

$$\text{INTER}(P) = \sum_{1 \leq r \leq k} p_r d^2(g_r, g)$$

where  $p_r$  is the weight of cluster  $C_r$  ( $p_r =$  number of class observation divided by the total number of observations).

The measure of homogeneity (*Hom*) within class  $C_r$  is the average of proximities between  $g_r$  and the class observations:

$$\text{Hom}(C_r) = \sum \{p_i d^2(o_i, g_r) | o_i \in C_r\}$$

where  $p_i$  is the weight associated to the  $i$ 'th observation  $o_i$  ( $p_i = 1/\text{total number of observations}$ ).

The quality of partition  $P$  is given by the following criterion (called intraclass inertia) which is the sum of the homogeneity of each class:

$$\text{INTRA}(P) = \sum_{1 \leq r \leq k} \text{Hom}(C_r)$$

If  $\text{INTRA}(P2) > \text{INTRA}(P1)$ , the partition  $P1$  should be preferred to  $P2$  because its clusters are globally more concentrated than partition  $P2$  ones. The DCM algorithm is an optimisation method which selects a 'good' partition and minimises the intraclass inertia or maximises the interclass inertia. From an initial partition chosen haphazardly, an iterative process is used to find a partition for which

the quality criterion takes its optimum. For the DCM, a specific procedure based on the concept of 'strong patterns' is available (Celeux et al. 1989). A strong pattern is a set of observations that are always classified together during the different trials. We also added the constraint of having at least four observations in each cluster.

Cluster interpretation was performed using the index  $dd$ , which is the contribution of a variable to determining a cluster.

$$dd = (m_j^r - m_j) / \sigma_j$$

where  $m_j^r$  is the mean of the variable in the class  $C_r$ ;  $m_j$  is the mean of the variable in the population; and  $\sigma_j$  is the standard-deviation of the variable in the population. If  $|dd|$  is greater than 1, the variable mean in the class differs significantly from the variable mean in the population.

## Results

### Correspondence analysis

#### Benthic communities

The correspondence analysis revealed striking differences in the benthic composition of different zones. Axes 1,

**Table 1** Summary table of results obtained with correspondance analysis on substrata variables. Variables are ordered in decreasing absolute contribution values. A: axis 1; B: axis 2; C: axis 3

A	Reef flat stations Variables	C <sup>a</sup>	AC <sup>b</sup>	RC <sup>c</sup>	Outer reef slope stations Variables	C <sup>a</sup>	AC <sup>b</sup>	RC <sup>c</sup>
	Rubble	1.2	16.7	75.5	Soft corals	-0.8	5.6	57.6
	<i>Acropora pulchra</i>	1.5	13.5	35.4	<i>Porites lutea</i>	-0.9	5.6	35.4
	Macroalgae	0.8	11.6	35.1	Turf	-0.5	5.5	24.8
	<i>Synarea iwayamaensis</i>	1.3	6.5	56.9	<i>Astreopora myriophthalma</i>	-0.8	2.7	61.2
	<i>Montipora circumvallata</i>	1.1	5.6	38.3	Blocks	-0.8	3.0	13.2
	<i>Acropora pharaonis</i>	1.6	3.6	33.3	Sand	-0.4	2.5	10.8
	<i>Acropora digitifera</i>	1.4	0.1	32.3	Volcanic substratum	-1.1	1.1	10.7
	<i>Acropora humilis</i>	1.5	0.8	33.5				
	<i>Porites nigrescens</i>	1.2	0.6	54.3				
B	Undisturbed stations Variables	C <sup>a</sup>	AC <sup>b</sup>	RC <sup>c</sup>	Disturbed stations Variables	C <sup>a</sup>	AC <sup>b</sup>	RC <sup>c</sup>
	<i>Acropora pulchra</i>	2.0	36.3	60.7	Macroalgae	-1.1	29.2	56.7
	<i>Acropora pharaonis</i>	2.1	9.3	57.3	Rubble	-0.5	5.0	14.5
	<i>Acropora digitifera</i>	1.9	2.7	56.6				
	<i>Acropora humilis</i>	1.9	2.2	59.3				
	<i>Acropora valida</i>	1.1	1.2	54.4				
	<i>Synarea iwayamaensis</i>	0.7	2.7	15.3				
	<i>Millepora excesea</i>	2.1	1.3	37.9				
C	Pass stations Variables	C <sup>a</sup>	AC <sup>b</sup>	RC <sup>c</sup>	Outer slope ss stations Variables	C <sup>a</sup>	AC <sup>b</sup>	RC <sup>c</sup>
	Sand	1.0	34.3	80.6	Turf	-0.1	6.9	16.7
	Blocks	1.9	32.9	76.9	Soft coral	-0.5	4.3	24.0
					<i>Porites lutea</i>	-0.6	4.3	16.0
					Volcanic substratum	-1.3	3.4	17.7

<sup>a</sup> coordinate on axis

<sup>b</sup> absolute contribution ( $\times 100$ )

<sup>c</sup> relative contribution

2 and 3 explained 60% of the total information (inertia) (Fig. 2), and thus summarise more than half of the information contained in the contingency array. Axis 1 (which explains 27.5% of the variation) separated the reef flat and the outer slope stations (Fig. 2A). The reef flat cluster was strongly characterised by the following variables: rubble, macroalgae, *Acropora pulchra* and *Synarea iwayamaensis*; the outer slope was characterised by soft corals, *Astreopora myriophthalma* and *Porites lutea* (Table 1A).

Axis 2 (17.5% of the variation) discriminated the reef flat into two groups: the undisturbed stations of Trois-Chameaux stations and the disturbed stations of Club Méditerranée and Planch'Alizés. The undisturbed stations were characterised by coral species, especially *Acropora sp* (*A. pulchra*, *A. pharaonis*, *A. digitifera*, *A. humilis*, *A. valida*) while the disturbed stations were best characterised by macroalgae (Table 1B).

Axis 3 (15% of the variation) split the outer reef slope stations into two groups: pass and outer slope (Fig. 2B). The outer slope stations were most characterised by soft corals, turf, *Porites lutea* and volcanic substratum. Pass stations were characterised mainly by sand and blocks (Table 1C).

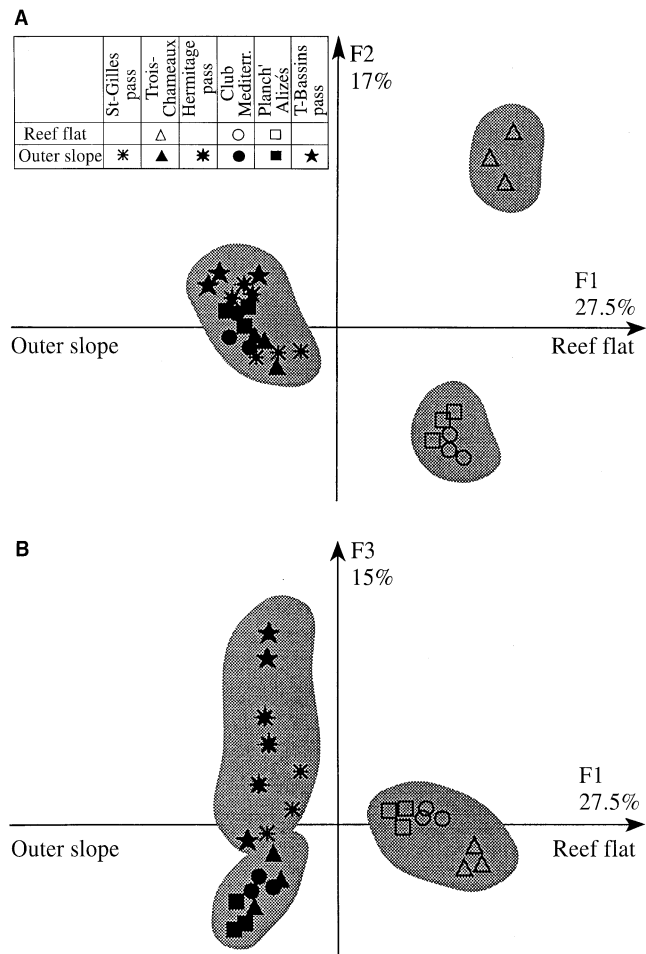


Fig. 2A, B Results of correspondence analysis (CA) on substrata variables. A first and second axes, B first and third axes

Fish communities

Similarly, fish assemblages varied greatly among zones and sites, as revealed by correspondence analysis. The first 3 axes of the CA for the 27 fish stations explained 47% of total inertia (Fig. 3).

On axis 1 (which explain 25% of the variation), the reef flat and the outer slope stations were opposed (Fig. 3A), in accordance with the trend observed for the benthic communities. The reef flat stations were characterised by *Acanthurus triostegus*, *Scarus sp*, *Stegastes limbatus* and *Plectroglyphidodon dicki*, while the outer reef slopes were characterised by two planktivorous damselfish: *Chromis nigrura* and *Chromis dimidiata* (Table 2A).

Axis 2 (12.5% of the variation) shows a discrimination between Passe de Trois-Bassins from the other outer slope stations. The discrimination was mainly caused by two gregarious species: *Gnathodentex aureolineatus* and *Mulloides vanicolensis*. The high relative contributions to axis 2 by these variables (respectively 92.5% and 93%) are due to the fact that these species occur in large schools. When the schooling fish were removed from the analysis, axis 2 (9% of the variation) split the reef flat stations into the disturbed stations of Club Méditerranée and the undisturbed stations of Trois-Chameaux (Fig. 3B).

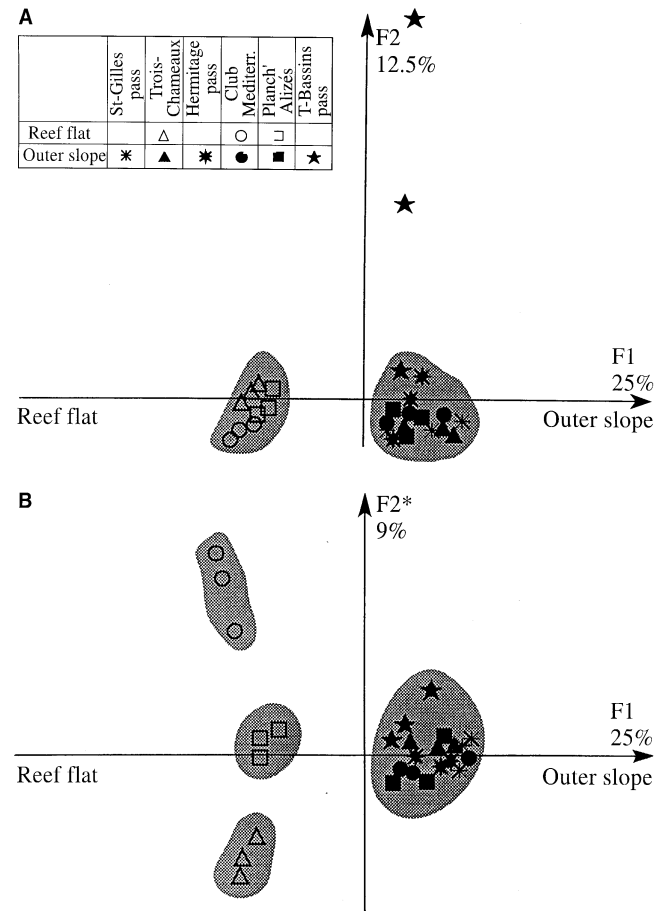


Fig. 3A, B Results of correspondence analysis (CA) on fish variables. A first and second axes; B first and second axes with exclusion of *Gnathodentex aureolineatus* and *Mulloides vanicolensis* (F2\*)

Planch'Alizés stations, which are also disturbed, were in an intermediate position between Trois-Châteaux and Club Méditerranée. The undisturbed stations were characterised by *Chaetodon trifasciatus*, *Plectroglyphidodon* sp (*P. dicki*, *P. leucozonus*, *P. johnstonianus*) and *Abudedefduf sparoides*. The disturbed stations, represented mainly by Club Méditerranée, were characterised by *Acanthurus triostegus*, *Rhinecanthus aculeatus* and *Chaetodon lunula* (Table 2B).

The correspondence analysis gives a first impression of the relationships between benthic and fish communities.

Clearly, the groupings of stations depend on whether data on benthos or fish are considered. For example, on the reef flat, three groups of fish communities were distinguished while only two groups of benthic communities were differentiated (Trois-Châteaux opposed to Club Méditerranée and Planch'Alizés). On the outer reef slope, benthic communities were differentiated (outer slope and reef pass) while fish communities were more homogeneous. These observations show that the fish communities do not map in a simple manner onto benthic communities.

**Table 2** Summary table of results obtained with correspondence analysis on fish variables. Variables are ordered in decreasing absolute contribution values. A: axis 1; B: axis 3

A				B			
Reef flat stations				Outer reef slope stations			
Variables	C <sup>a</sup>	AC <sup>b</sup>	RC <sup>c</sup>	Variables	C <sup>a</sup>	AC <sup>b</sup>	RC <sup>c</sup>
<i>Acanthurus triostegus</i>	-1.3	9.3	38.9	<i>Chromis nigrura</i>	0.9	21.7	62.1
<i>Scarus</i> sp	-0.8	8.8	45.8	<i>Chromis dimlotata</i>	0.8	5.1	43.4
<i>Stegastes limbatus</i>	-1.3	7.7	57.5	<i>Cirrhiothys oxycephalus</i>	0.8	1.3	51.2
<i>Plectroglyphidodon dicki</i>	-1.3	6.3	31.1				
<i>Chrysiptera glauca</i>	-1.4	3.8	36.2				
<i>Ctenochaetus striatus</i>	-0.6	2.9	19.3				
<i>Chaetodon trifasciatus</i>	-1.3	2.8	45.1				
<i>Stegastes fasciatus</i>	-0.1	2.6	36.6				
<i>Plectroglyphidodon leucozonus</i>	-1.2	2.4	44.4				
<i>Chrysiptera unimaculata</i>	-1.3	1.8	58.1				
B				A			
Disturbed stations				Undisturbed stations			
Variables	C <sup>a</sup>	AC <sup>b</sup>	RC <sup>c</sup>	Variables	C <sup>a</sup>	AC <sup>b</sup>	RC <sup>c</sup>
<i>Acanthurus triostegus</i>	1.4	26.5	42.2	<i>Plectroglyphidodon dicki</i>	-1.5	22.8	42.4
<i>Rhinecanthus aculeatus</i>	2.2	4.8	56.4	<i>Chaetodon trifasciatus</i>	-0.1	6.1	36.8
<i>Chrysiptera glauca</i>	0.9	4.1	14.6	<i>Plectroglyphidodon leucozonus</i>	-0.1	4.2	29.3
<i>Stegastes fasciatus</i>	0.7	3.5	18.6	<i>Abudedefduf sparoides</i>	-1.2	3.9	23.6
<i>Chaetodon lunula</i>	1.6	2.5	47.0	<i>Plectroglyphidodon johnstonianus</i>	-0.7	3.2	28.2
<i>Chaetodon auriga</i>	1.1	1.5	23.3	<i>Chaetodon trifascialis</i>	-1.7	2.4	29.9
				<i>Oxymonacanthus longirostris</i>	-2.1	1.6	14.9

<sup>a</sup> coordinate on axis

<sup>b</sup> absolute contribution ( $\times 100$ )

<sup>c</sup> relative contribution

**Table 3** Mean and standard deviation per census of substrata variables in the four class determined by DCM

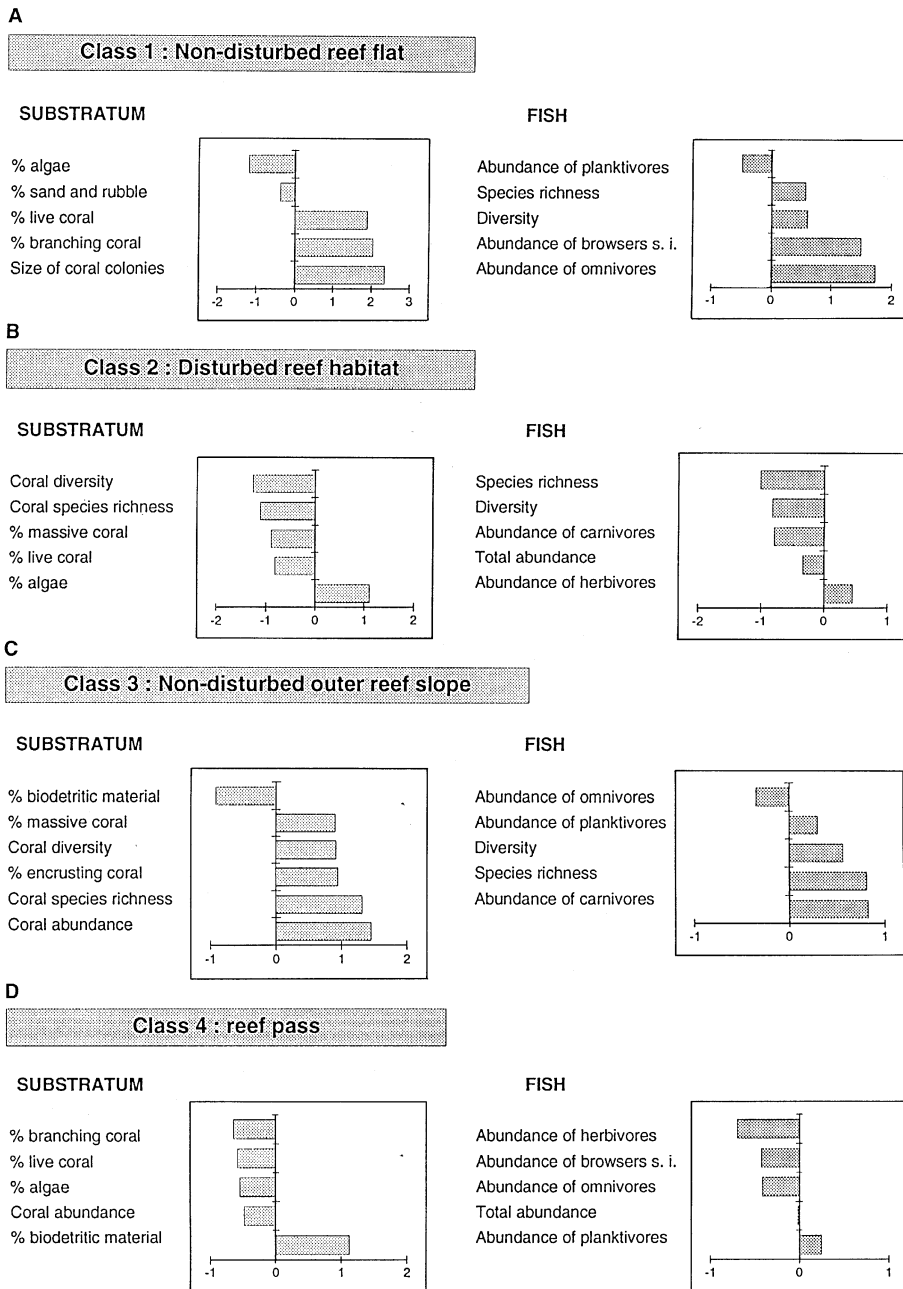
	Class 1		Class 2		Class 3		Class 4	
	Population mean	Cluster mean	Cluster mean	Cluster mean	Cluster mean	Cluster mean	Cluster mean	
Coral species richness	20 $\pm$ 7.6	30 $\pm$ 2.6	12 $\pm$ 3.9	20 $\pm$ 2.7	19 $\pm$ 3.5			
Coral abundance	69 $\pm$ 27	110 $\pm$ 12	49 $\pm$ 9.9	56 $\pm$ 17	64 $\pm$ 2.7			
Mean size of coral colonies (cm)	22 $\pm$ 12	19 $\pm$ 2.8	16 $\pm$ 2.5	18 $\pm$ 1.4	51 $\pm$ 2.8			
Diversity (Shannon)	3.6 $\pm$ 0.63	4.2 $\pm$ 0.23	2.8 $\pm$ 0.48	3.8 $\pm$ 0.18	3.6 $\pm$ 0.28			
% live coral ( $\times 100$ )	31 $\pm$ 19	40 $\pm$ 8.4	16 $\pm$ 4.7	20 $\pm$ 6.2	66 $\pm$ 1.9			
% biodetrital material ( $\times 100$ )	33 $\pm$ 20	14 $\pm$ 4.3	30 $\pm$ 12	56 $\pm$ 19	25 $\pm$ 4.1			
% algae ( $\times 100$ )	30 $\pm$ 20	31 $\pm$ 11	52 $\pm$ 10	20 $\pm$ 14	7 $\pm$ 4.6			
% branching coral ( $\times 100$ )	11 $\pm$ 15	8 $\pm$ 1.9	8.1 $\pm$ 4.8	1.4 $\pm$ 0.09	42 $\pm$ 18			
% massive coral ( $\times 100$ )	19 $\pm$ 13	31 $\pm$ 7.8	7.4 $\pm$ 5.9	18 $\pm$ 6.5	23 $\pm$ 19			
% encrusting coral ( $\times 100$ )	0.96 $\pm$ 0.79	1.7 $\pm$ 0.45	0.62 $\pm$ 0.86	0.62 $\pm$ 0.48	1 $\pm$ 0.71			

*Dynamic clustering method*

The DCM optimisation procedure suggested four classes, corresponding to the non-disturbed reef flat, the non-disturbed outer reef slope, the perturbed reef habitat and the reef pass. Means and standard-deviations of the ten substrata variables in each class are shown in Table 3, and the contribution of selected substrata and ichthyological variables to the index *dd* are shown in Fig. 4. The histograms in Fig. 4 indicate the extent to which variables contribution is below or above the overall mean contribution for that variable. Thus, if the contribution is around 0, it does not significantly differ from the average in this class. The interpretation of the classes are as follows:

**Class 1: non-disturbed reef flat (4 stations).** The three reef flat stations at Trois-Chameaux (undisturbed site) were grouped with one on the edge of Passe de Trois-Bassins. This class (Fig. 4A) is characterised by positive contributions of three coral variables (large colony size, high percentage of living coral, especially branching coral) and by a few ichthyological variables (especially omnivorous fish, and browsers on sessile Invertebrates). The high contribution of coral morphology and coral size (*dd* > 2) reflect the importance of physical structure in this type of environment. This class typifies a 'luxuriant' coral reef environment found mostly in shallow waters.

**Class 2: disturbed reef habitat (8 stations).** Six of the eight stations were located on the reef flats of Club Méditerranée



**Fig. 4A–D** Results of the clustering analysis (DCM) on substrata and fish variables. Each variable is characterised by its degree of participation to the class = index *dd* reported on histograms. *s.i.*: sessile invertebrates. **A** class 1; **B** class 2; **C** class 3; **D** class 4

and Planch' Alizés (perturbed zones) and two on Trois-Châteaux outer slope. These stations are characterised by a high algae coverage and a low live coral cover. This class (Fig. 4B) has high abundance of both algae and herbivorous fishes, but otherwise has sparse and not very diverse coral and fish communities.

Class 3: non-disturbed outer reef slope (7 stations). This class (Fig. 4C) is characterised by a large number of species and coral colonies, a high coral diversity and a high percentage of massive and encrusting corals. This rich and diverse coral environment is associated with an equally diverse fish population, predominantly carnivorous and planktivorous species. In contrast to class 1, the other unperturbed unit, this is a deep water class with abundant massive corals.

Class 4: reef pass (8 stations). This unit contained all except one pass station. This class is characterised by a high percentage of sand and rubble material, and by abundant plankton feeding fish. Apart from this, it is the absence of coral and ichthyological variables which characterise this class (Fig. 4D). This environment is therefore poor in coral and algae, in contrast to class 2 stations which have abundant algae.

## Discussion and conclusions

### *Data analysis*

The relationship between benthic and fish assemblages was investigated using two different approaches: an ordination (CA) and a clustering method (DCM). CA was performed on two set of data (substratum type and fish) to avoid two problems. First, the number of variables (96 substrata + 98 fish variables) is too high compared to the number of observations (27). Second, both the benthic and fish data are heterogeneous. Consequently, canonical correlation analysis (Caroll and Chang 1970), which is a constrained ordination that explores direct correlations between two sets of numerical variables measured on a set of observations, was not suitable as a means of analysing the relationship between substrata and fish variables.

This lead us to use summary characteristics and clustering methods. The clustering method we presented (DCM) compares favourably with hierarchical clustering methods (e.g. average linkage, Wards method), which impose a nested structure on data, and are very rigid in their assignment of stations to clusters. Partitioning clustering methods such as DCM do not impose any hierarchical constraints on the clusters formed. Moreover, unlike hierarchical methods which require a large amount of subjectivity in their choice and interpretation, DCM is an optimisation method that identifies a 'good' partitioning. By the optimisation of two statistical criteria (intra- and interclass variances or inertias), DCM provides a statistically more robust solution.

DCM were used with summary substrata characteristics to find the 'best' partition of the stations into groups. This procedure suggested four types of benthic assemblages: the non-disturbed reef flat, the non-disturbed outer

reef slope, the reef pass and the disturbed reef habitat. Imposing the same partitioning on the fish variables suggests a number of relationships between profiles of substratum and types of fish species, which are discussed later. DCM also has the advantage that it provides a categorical variable partition  $P$ , which quantifies the strength of the link between the two sets of variables.

### *Relationship between substrata and fish variables*

Species richness and diversity of fish assemblages were correlated with many coral variables such as architectural complexity (or coverage of branching coral), diversity, species richness, abundance, size of colony, coverage of living coral, coverage of massive and encrusting coral. Other studies have also demonstrated correlations between architectural complexity of the substratum and fish populations (Luckhurst and Luckhurst 1978; Talbot et al. 1978; Gladfelter et al. 1980; Carpenter et al. 1981; Sano et al. 1984, 1987; Roberts and Ormond 1987; Hixon and Beets 1989; Grigg 1993; Galzin et al. 1994). Sale and Douglas (1984) considered this relationship to be valid only for sedentary or territorial fish species. Nevertheless, it appears that a highly complex environment allows the habitat to be shared by many species (Barbault 1992). As a consequence, destruction of the habitat, caused by a great diminution in the coverage by branching corals (Naim 1993), may lead to a reduction in the number of fish species (Letourneur 1992; Chabanet et al. 1995b).

The relationship between species richness of the fish assemblage and the diversity or abundance of coral is less apparent in the literature than habitat complexity due to the difficulties of coral classification. Certain authors (Williams 1986; Sano et al. 1987; Galzin et al. 1994) consider that a large variety of living corals support more specialist fish species by increasing the variety of microhabitats (Barbault 1992). This hypothesis is supported in the present study.

Various studies have also shown that the coverage by living coral has a positive influence on the species richness of fish (Carpenter et al. 1981; Sano et al. 1984, 1987; Bell and Galzin 1984, 1988). However, other authors (Luckhurst and Luckhurst 1978; Roberts and Ormond 1987; Mac Manus et al. 1981) have found no correlation. One of the reasons for this difference may stem from the influence of depth: the aforementioned authors worked in shallow waters (< 3 m), in contrast to the others whose samples were taken at greater depths, as deep as 40 m. It appears that the correlation between species richness of fish and the coverage by living coral is greater on the reef flat than on the outer slope, but it remains significant when data from all zones are pooled (Chabanet 1994).

In the analysis of the relationships between fish abundance and live coral cover, our results also highlighted the importance of geomorphological zones and the degree of perturbation of the reef environment. However, the density of fish was apparently limited by the percentage of live coral cover only on disturbed sites (see Fig. 4B). As mentioned previously, some authors (Carpenter et al. 1981; Sano et al. 1984, 1987; Bell and Galzin 1984, 1988) found the correlation between these characteristics to be signifi-

cant, whereas others (Luckhurst and Luckhurst 1978; Roberts and Ormond 1987) did not. The relationship between the abundance of fishes and the coverage by living coral may be stronger in shallow water because fish there remain in closer physical proximity to the substratum. The correlation between the abundance of fish and the species diversity of the coral was only significant in disturbed environments (see Fig. 4B). An environment with low coral diversity can therefore limit fish abundance. The physical complexity of the substratum was correlated to fish abundance only in few studies (Sano et al. 1984, 1987; Alcalá and Gomez 1985; Samoily 1988) perhaps because fish density is dependant upon numerous additional factors (e.g. competition, predation), which may intensify with an increase in the number of species.

The relationship between the abundance of herbivorous fishes and algal cover was weak. According to some authors, herbivores are more numerous in environments rich in algae (Galzin 1985; Letourneur 1992) whereas other studies have found no correlation (Sano et al. 1984; Wellington and Victor 1985; Williams 1986; Chabanet et al. 1995). The discrepancy between those results may be due to numerous factors, such as the territorial behaviour of certain herbivorous species, strong interspecific competition for a common resource (Robertson and Polunin 1981; Sano et al. 1984; Robertson and Gaines 1986), recruitment limitation (Doherty and Williams 1988), or diet preference. The complexity of this relationship is due, in part, to the diversity of food consumed by herbivores. Their diet includes algae, but also sediment, detritus and fish faeces (Robertson 1982; Jones 1991; Choat 1991).

The densities of omnivores and browsers of sessile Invertebrates were correlated with the percentage of living, branched coral in non-perturbed reef flat sites (Fig. 4A). The trophic classes most dependent on the structural complexity will be those which use the substratum for food and for shelter. On coral reefs, these trophic types are represented mainly by the Pomacentridae (omnivores) and the Chaetodontidae (sessile Invertebrate feeders). As the majority of the Pomacentridae are small, territorial, or live close to the substratum, they appear to be influenced the most by the morphological characteristics of the substratum (Roberts and Ormond 1987). Damselfish use coral more as a habitat than as a food resource (Sano et al. 1984, 1987; Jones 1991). In contrast, it appears that living coral is used more as a food resource by the Chaetodontidae, in which the majority of species are corallivores (Harmelin-Vivien 1979; Harmelin-Vivien and Bouchon-Navaro 1981, 1983). Various authors (Sano et al. 1984, 1987; Bell and Galzin 1984; Williams 1986; Bouchon-Navaro et al. 1985; White 1988; Bouchon-Navaro and Bouchon 1989; Roberts et al. 1992, Chabanet and Letourneur 1995; Chabanet et al. 1995) have in fact, found a positive correlation between the abundance of Chaetodontidae and percentage of living coral. However, in some cases (Bell et al. 1985; Roberts and Ormond 1987; Roberts et al. 1988; Fowler 1990), this correlation was poor, suggested that these populations of butterflyfish may have been limited more by recruitment than by food availability.

There was no clear relationship between the abundance of carnivorous and planktivorous fishes and substratum

variables (Fig. 4C, D). This suggested that carnivores and planktivores abundance may be responding to other aspects of the biotic and abiotic environment which characterise the outer reef slope, including the reef pass. Elsewhere, the density of planktivorous fishes has been related to the speed of currents, which transport plankton onto the reef (Hobson and Chess 1978; Thresher 1983). The density of carnivorous fish (Lutjanidae, Serranidae) may also be affected by their own predators, including humans (Mc Manus et al. 1981).

In conclusion, DCM has been useful for generating hypotheses on relationship between the two sets of variables related to benthic and fish communities. This method identifies groups not constrained by hierarchies, and those groups are determinate by a clustering criterion which optimise the partition. Through the interpretation of this partition, we have found that among the different substratum characteristics, it is primarily coral variables which are correlated with the richness and diversity of fish assemblages (i.e. Fig. 4A, C). This result highlight the importance of coral vitality to maintaining a rich and diverse fish community. Fish abundance was also correlated with some coral variables (diversity, species richness, % live and massive corals) but only on disturbed sites (i.e. Fig. 4B). The inconsistency between substrata and fish relationships on coral reefs reported in the literature may be due to the diverse methodologies that have been used (e.g. the spatial scale of sampling, choice of study site, method of evaluation). These relationships can also vary according to the behaviour of the fish families that are studied (sedentary or wandering), or the period during which sampling is effected. It would be interesting to compare our Reunion results with those from other studies carried out on different coral reefs. Such comparisons would require long term studies in a variety of environments, to better understand the complicated functioning of coral reef ecosystems.

*Acknowledgements.* This research was supported by the Conseil Régional of La Reunion, by the D. R. E. D. (French Ministry of National Education) and by URA 1453 CNRS. This paper constitutes a portion of the senior author's PhD thesis at the Laboratory of Marine Ecology, University of Reunion Island. We are grateful to Drs O. Naim, Y. Letourneur, C. Conand and P. Legendre for critically reviewing an early draft of the article. We thank also Dr C.A. Payet (IREMIA) for his help on correspondence analysis and K. Longworth for valuable improvements to the English. Great thanks are also expressed to Dr T. Done for his valuable suggestions on later drafts, and to the anonymous reviewers for their constructive comments on the manuscript.

## References

- Alcalá AC, Gomez ED (1985) Fish yields of coral reefs in the central Philippines. Proc 5th Int Coral Reef Symp 5: 521–524
- Barbault TR (1992) Hétérogénéité spatiale, variabilité temporelle et peuplements. In: *Ecologie des peuplements: structure, dynamique et évolution*. Masson, pp 141–163
- Bell JD, Galzin R (1984) Influence of live coral cover on a coral reef fish communities. *Mar Ecol Prog Ser* 15: 265–274
- Bell JD, Galzin R (1988) Distribution of coral and fish in the lagoon at Mataiva: potential for increase through mining? Proc 6th Int Coral Reef Symp 2: 347–352



- Bell JD, Harmelin-Vivien ML, Galzin R (1985) Large scale spatial variation in abundance of butterflyfishes (Chaetodontidae) on Polynesian reefs. *Proc 5th Int Coral Reef Symp* 5:421–426
- Benzecri JP, Benzecri F (1976) *Pratique de l'analyse des données. I: Analyse des correspondances, exposé élémentaire*. Dunod, Paris
- Bouchon C, Bouchon-Navaro Y, Louis M, Laborel J (1987) Influence of the degradation of coral assemblages on the fish communities of Martinique (French West Indies). *Proc 38th Congr Gulf and Carib Fish Inst*: 453–468
- Bouchon-Navaro Y (1980) Quantitative distribution of the Chaetodontidae on a fringing reef of the Jordanian coast (Gulf of Aqaba, Red Sea). *Tethys* 9 (3):247–251
- Bouchon-Navaro Y (1981) Quantitative distribution of the Chaetodontidae on a reef of Moorea Island (French Polynesia). *J Exp Mar. Biol Ecol* 55:145–157
- Bouchon-Navaro Y, Bouchon C (1989) Correlations between chaetodontid fishes and coral communities of the Gulf of Aqaba (Red Sea). *Environ Biol Fish* 25 (1–3):47–60
- Bouchon-Navaro Y, Bouchon C, Harmelin-Vivien ML (1985) Impact of coral degradation on a chaetodontid fish assemblage (Moorea, French Polynesia). *Proc 5th Int Coral Reef Symp* 5:427–432
- Carpenter KE, Miclat RI, Albaladejo VD, Corpuz VT (1981) The influence of substrate structure on the local abundance and diversity of Philippine reef fishes. *Proc 4th Int Coral Reef Symp* 2:497–502
- Carroll JD, Chang JJ (1970) Analysis of individual difference in multidimensional scaling via an N-way generalization of "Eckart-Young" decomposition. *Psychometrica* 35:283–319
- Celeux G, Diday E, Govaert G, Lechevallier Y, Ralambondrainy H (1989) *Classification automatique des données*. Bordas, Paris
- Chabanet P (1994) *Etude des relations entre les peuplements benthiques et les peuplements ichthyologiques sur le complexe récifal de St-Gilles/La Saline (Ile de la Réunion)*. Thèse de Doct Univ Aix-Marseille III, 263 pp
- Chabanet P, Letourneur Y (1995) Spatial pattern of size distribution of four fish species on Reunion coral reef flats. *Hydrobiologia* 300/301:299–308
- Chabanet P, Join JL, Cuet P, Naim O (1995a) Spatial variability in submarine groundwater discharge (SDG) occurrence and benthic and fish communities patterns on St-Gilles/La Saline reef: a tentative interpretation through an hydrogeological model (Reunion island). *Int Soc Reef Stud, Ann Meeting Newcastle (Abst)*
- Chabanet P, Dufour V, Galzin R (1995b) Impact of disturbance on reef fish communities in Reunion Island (Indian Ocean). *J Exp Mar Biol Ecol* 188:29–48
- Choat JH (1991) The biology of herbivorous fishes on coral reefs. In: Sale PF (ed) *The ecology of fishes on coral reef*. Academic Press, San Diego, pp 120–155
- Connell JH (1978) Diversity in tropical rain forest and coral reefs. *Science* 199:1302–1310
- Cuet P (1994) Sources de l'enrichissement en sels nutritifs de l'écosystème récifal à La Réunion: impact des eaux souterraines. In: Coudray J, Bouguerra ML (eds) *Environment en milieu tropical*. ESTEM Paris, pp 105–110
- Cuet P, Naim O, Faure G, Conan JY (1988) Nutrient-rich groundwater impact on benthic communities of la Saline fringing reef (Reunion Island): Preliminary results. *Proc 6th Int Coral Reef Symp* 2:207–212
- Doherty PT, Williams DMcB (1988) The replenishment of coral reef fish populations. *Oceanogr Mar Biol* 26:487–551
- Everitt BS (1974) *Cluster analysis*. Heinemann, London
- Fisher RA (1936) The use of multiple measurements in taxonomic problems. *Ann Eug* 7:179–188
- Fowler AJ (1990) Spatial and temporal patterns of distribution and abundance of chaetodontid fishes at One Tree Reef, southern GBR. *Mar Ecol Prog Ser* 64:39–53
- Galzin R (1985) *Ecologie des poissons récifaux de polynésie Française*. Thèse es Sciences, Univ Montpellier, 170 pp
- Galzin R, Planes S, Dufour V, Salvat B (1994) Variation in diversity of coral reef fish between French Polynesian atolls. *Coral Reefs* 13:175–180
- Gladfelter W, Ogden J, Gladfelter E (1980) Similarity and diversity among coral reef communities: a comparison between tropical western Atlantic (Virgin Islands) and tropical central Pacific (Marshall Island) patch reefs. *Ecology* 61 (5):1156–1168
- Greenacre M (1984) *Theory and applications of correspondance analysis*. Academic press, New York
- Grigg RW (1993) Effects of sewage discharge, fishing pressure and habitat complexity on coral reef ecosystems in Hawaii. *Proc Int Symp on Biodiversity and adaptative strategies of coral reef organisms, Japan, Abstr*
- Harmelin-Vivien ML (1979) *Ichtyofaune des récifs coralliens de Tulear: écologie et relations trophiques*. Thèse es Sciences, Aix-Marseille, II 165 pp
- Harmelin-Vivien ML, Bouchon-Navaro Y (1981) Trophic relationship among Chaetodontid fishes in the Gulf of Aqaba (Red Sea). *Proc 5th Int Coral Reef Symp* 2:537–544
- Harmelin-Vivien ML, Bouchon-Navaro Y (1983) Feeding diets and significance of coral feeding among Chaetodontid fishes in Moorea (French polynesia). *Coral Reefs* 2:119–127
- Harmelin-Vivien ML, Harmelin JG (1975) *Présentation d'une méthode d'évaluation in situ de la faune ichthyologique*. *Trav Sci Parc Nation Port-Cros* 1:47–52
- Harmelin-Vivien M, Harmelin J, Chauvet C, Duval C, Galzin R, Lejeune P, Bamabé G, Blanc F, Chevalier R, Duclerc J, Lasserre G (1985) *Evaluation visuelle des peuplements et populations de poissons: méthodes et problèmes*. *Rev Ecol Terre Vie* 40:467–539
- Hiatt WR, Stasburg DW (1960) Ecological relationship of the fish fauna on coral reefs of the Marshall Islands. *Ecol Monogr* 30 (1):65–127
- Hixon MA, Beets JP (1989) Shelter characteristics and Caribbean fish assemblages: experiments with artificial reefs. *Bull Mar Sci* 44:666–680
- Hobson ES (1974) Feeding relationships of teleostean fishes on coral reefs in Kona, Hawaii. *Fish Bull* 72:915–1031
- Hobson ES, Chess JR (1978) Trophic relationships among fishes and plankton in the lagoon at Enewetak Atoll, Marshall Islands. *Fish Bull* 76:133–153
- Huber L, Levin JR (1976) A general statistical framework for assessing categorical clustering in free recall. *Psych Bull* 83:1072–1080
- Jain AK, Dubes RC (1988) *Algorithms for clustering data*. Prentice-Hall, New Jersey
- Jones GP (1991) Postrecruitment processes in the ecology of coral reef fish populations: a multifactorial perspective. In: Sale PF (ed) *The ecology of fishes on coral reef*. Academic Press, San Diego, pp 294–328
- Kulbicki M (1988) Pattern in the trophic structure of fish populations across the SW lagoon of New Caledonia. *Proc 6th Intern Coral Reef Congr* 2:89–94
- Letourneur Y (1992) *Dynamique des peuplements Ichthyologiques des platiers récifaux de l'île de La Réunion*. Thèse de Doct, Univ Aix-Marseille II, 244 pp
- Loya Y (1972) Community structure and species diversity of hermatypic corals at Eilat, Red Sea. *Mar Biol* 13 (2):100–123
- Loya Y (1978) Plotless and transect methods. *Unesco Monogr Oceanogr Method* 5:197–217
- Luckhurst B, Luckhurst K (1978) Analysis of the influence of substrate variables on coral reef communities. *Mar Biol* 49:317–323
- McCormick MI, Choat JH (1987) Estimating total abundance of a large temperate reef fish using visual strip-transect. *Mar Biol* 96:469–478
- Mc Manus J, Miclat R, Palaganas V (1981) Coral and fish community structure of Sombrero Island at Batangas, Philippines. *Proc 4th Int Coral Reef Symp* 2:271–280
- Milligan GW, Cooper MC (1985) An examination of procedures for determining the number of clusters in a data set. *Psychometrica* 50 (2):159–179
- Montaggioni L, Faure G (1980) *Les récifs coralliens des Mascareignes (O. Indien)*. Collections des travaux du Centre Universitaire, Université française de l'Océan Indien

- Naim O (1993) Seasonal responses of a fringing reef community eutrophication (Reunion Island, Western Indian Ocean). *Mar Ecol Prog Ser* 99: 307–315
- Roberts CM, Ormond RF (1987) Habitat complexity and coral reef diversity and abundance on Red Sea fringing reefs. *Mar Ecol Prog Ser* 41: 1–8
- Roberts CM, Ormond RF, Shepherd AR (1988) The usefulness of butterflyfishes as environmental indicators on coral reef. *Proc 6th Int Coral Reef Symp* 2: 331–336
- Roberts CM, Dawson Shepherd AR, Ormond RF (1992) Large-scale variation in assemblage structure of Red Sea butterflyfishes and angelfishes. *J Biogeogr* 19: 239–250
- Robertson DR (1982) Fish feces as fish food on Pacific coral reef. *Mar Ecol Prog Ser* 7: 253–265
- Robertson DR, Polunin NV (1981) Coexistence: Symbiotic sharing of feeding territories and algal food by some coral reef fishes from the western Indian Ocean. *Mar Biol* 62: 185–195
- Robertson DR, Gaines SD (1986) Interference competition structures habitat use in a local assemblage of coral reef surgeonfishes. *Ecology* 67 (5): 1372–1383
- Sale PF, Douglas WA (1984) Temporal variability in the community structure of fish on coral patch reefs and the relation of community structure to reef structure. *Ecology* 65 (2): 409–422
- Samoilys MA (1988) Abundance and species richness of coral reef fish on the Kenyan coast: the effects of protective management and fishing. *Proc 6th Int Coral Reef Symp* 2: 261–266
- Sano M, Shimizu M, Nose Y (1984) Changes in structure of coral reef fish communities by destruction of hermatypic corals: observational and experimental views. *Pac Sci* 38 (1): 51–79
- Sano M, Shimizu M, Nose Y (1987) Long-term effects of destruction of hermatypic corals by *Acanthaster planci* infestation on reef fish communities at Iriomote Island, Japan. *Mar Ecol Prog Ser* 37: 191–199
- Talbot FH, Russel BC, Anderson GR (1978) Coral reef fishes communities: unstable high-diversity systems? *Ecol Monogr*: 425–440
- Thresher RE (1983) Environmental correlates of the distribution of planktivorous fishes in the One Tree Reef Lagoon. *Mar Ecol Prog Ser* 10: 137–145
- Wellington GM, Victor BC (1985) El nino mass coral mortality: a test of resource limitation in a coral reef damselfish population. *Oecologia* 68: 15–19
- White AT (1988) *Chaetodon* occurrence relative to coral reef habitat in the Philippines with the implication for reef assessment. *Proc 6th Int Coral Reef Symp* 2: 427–432
- Williams DMcB (1986) Temporal variation in the structure of reef slope fish communities (central Great Barrier Reef) : short-term effect of *Acanthaster planci* infestation. *Mar Ecol Prog Ser* 28: 157–164