PRESENT KNOWLEDGE OF THE STRUCTURE OF CORAL REEF FISH ASSEMBLAGES IN THE PACIFIC

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ABSTRACT

Assemblages of coral reef fish in the Pacific are characterized by a large number of species and a great variability of species composition, density, or biomass over time and space. There is a gradient across the Pacific of the number of coral reef species but the gradient is poorly reflected by the number of species on a given reef. There is also a gradient across the Pacific of the trophic and life-history structure of the coral reef species pools. The pools can be clustered into two major groups: the Western Pacific group, which can be subdivided into the Central Pacific, the Great Barrier Reef-New Caledonia region, and the Central-West Pacific; and the East and South Pacific group, which can be subdivided into the Hawaiian-Polynesian region and the Norfolk-Lord Howe-Kermadec region. Data are still insufficient to correlate the structures of these species pools to the structure of the reef fish assemblages from the various regions. Variability of the trophic structure or life-history strategies of reef fish assemblages is usually low at a large scale if species composition is considered. Variability is greater when the structures are considered in terms of density or biomass. At a small scale in time or space, variability of these structures is usually important. The main cause of variability is likely to be random recruitment of juveniles to reefs. Within a region, assemblages on widely separated reefs of a particular type share more similarities than assemblages on reefs near each other but of different types. Within a given type of reef, only a limited number of species are ubiquitous, and only certain species are restricted to particular parts of the reef. Density and biomass are much more variable than species diversity although the sampling of non-territorial species is often a major problem in assessing these population parameters. The present review indicates that improved knowledge of the structure of coral reef fish assemblages will require (1) the development of testable hypotheses on the generation and maintenance of the organisation of coral reef fish assemblages, (2) the collection of standard data from various parts of the Pacific, and (3) the development of data bases on the growth, reproduction, and behaviour of the main species.

INTRODUCTION

Coral reefs in the Pacific support a very large number of fish species, with approximately 4,000 species known to be present in the aggregate (Myers 1989). It is likely that these species are not distributed at random but are formed into assemblages that follow some kind of organisation. In order to understand how these reef fish assemblages function, it is necessary to *detect* and then to *explain* their organisation. Doherty and Williams (1988) have documented the various hypotheses now proposed to explain this organisation. I provide information on what has been detected about the organisation so far.

The character of what is detected is linked with the level of observation. Because the very high spatial and temporal variability of the fish populations in the assemblages make it difficult to detect any organisation at a small scale, it is mandatory to make observations at an adequately large scale. Otherwise, local variability blurs the observations to such a degree that it has often been concluded that the organisation underlying coral reef fish assemblages is very loose (Sale 1982). To facilitate understanding and analysis of the organisation, it is useful to partition it into what can be called structures. Because the structures are no more than analytical tools, there can be as many as are needed to answer our questions. The most frequently used structures are species structure, trophic structure, life-history structure, and space-utilisation structure. The main problem in using this approach is inadequacy of data. For instance, species structure implies the correct identification of each taxon; trophic structure requires knowledge of the diet of each species as well as the variations of diet with age or between different geographical locations; life-history strategy structure requires information on life-history traits (reproduction, growth, mortality . . .) of each species. At present, this kind of information, except for species identification, is limited and it is necessary to make many generalisations, which could lessen confidence in the results. Nevertheless, it is possible to detect the major trends described in this paper.

Explanation of assemblage organisation rests on both internal and external factors. Internal factors are linked to the traits of each species. Thus, larval dispersion, habitat or food preference of juveniles or adults, reproductive behaviour, and so forth may explain some of the characteristics of reef fish assemblages. Another internal factor is the available species pool. Given similar external factors but different species pools, different types of organisation may result. External factors are mainly physical and include temperature, salinity, currents, wave action, and turbidity as well as the nature of the substrate and the benthic organisms found there (coral, algae, invertebrates . . .). A major purpose behind the discovery of explanations of assemblage organisation is to be able to predict what kind of organisation would prevail under a given set of factors or what trajectory the organisation would follow if the factors are modified.

Although there are many sources of information on Pacific coral reef fish assemblages, only five areas have received more than superficial investigation: the Great Barrier Reef, Hawaii, French Polynesia, Micronesia (Guam, Saipan, Enewetak), and New Caledonia. Except for large scale variation, most of the present paper will centre on unpublished data from New Caledonia, with discussion of similar work done in other areas of the Pacific. I follow this approach because the New Caledonian data base is very extensive and covers most aspects of the organisation of reef fish assemblages. The only other work containing such detail is Galzin's (1985) for French Polynesia, though that study lacks biomass data.

LARGE GEOGRAPHICAL VARIATIONS

It is likely that the organisation of coral reef fish assemblages is in great part linked to the composition of the species pool available. This composition varies considerably across the Pacific, with the greatest diversity in the Indonesia-Philippines region. From this centre, there are two gradients of decline in species diversity. The sharpest gradient is eastward, the number of reef fish species declining from approximately 2,500 in the Philippines to 460 in Hawaii and 125 at Easter Island. The second path of decline is either northward or southward from the equator; this gradient is not as strong as the longitudinal one (Figure 1). How are these gradients in species richness reflected in the species diversity of fish assemblages for a given type of reef? The heterogenous information available from the literature (Table 1) suggests that there is no direct correlation between the diversity of fish observed on a reef and the number of species available to that reef.

Table 1a shows the variations in density and biomass estimates of coral reef fish across the Pacific. The existing data show no particular geographical trend. Excluding patch reefs, densities fluctuate between 0.2 and 11 fish/m^2, with most values between 1 and 5 fish/m^2. The range for biomass extends from 25 to 240 g/m^2, with most values between 80 and 200 g/m^2. Inshore or fringing reefs tends to have lower densities or biomass than middle lagoon or barrier reefs. The density and biomass estimates for patch reefs should be treated with caution because usually only the hard substrate is taken into account. If these estimates were calculated on the basis of all substrates present in a radius of 50m of these patch reefs, the densities or biomasses would be considerably lower. For example, in the Chesterfield islands, density estimates for patch reefs range from 5.6 to 127 fish/m^2 for hard substrates alone and from 0.15 to 1.5 fish/m^2 if all substrates are taken into account. These patch reefs are the refuge for many species that feed either in the water column (Caesionidae, Apogonidae, Holocentritidae, and a number of Pomacentridae) or on the nearby soft bottoms (Lutjanidae, Mullidae, Lethrinidae, and some Acanturidae). Also, a number of piscivores (Serranidae, Carangidae, and some Lutjanidae) forage on the fish concentrations formed on patch reefs but are usually found at much lower concentrations on extensive reef formations.

If there is no apparent relationship between fish-species richness of a given coral reef type and the species richness of the species pool available, there might still be a correlation between the composition of this species pool and the various structures observed for this assemblage. The first step in verifying this hypothesis is to look for cross-Pacific variations of the characteristics of the species pools. Trophic structure and life-history structure will be considered here. For 17 areas in the Pacific, reasonably accurate checklists of coral reef fishes were collected. For each of these checklists, data were gathered from the literature on the food habits and main life-history traits for as many of the species as possible. If no information was available on a particular species, data from the most closely related species were considered. Information was obtained on the diets or life-history traits of over 70 per cent of the species on the checklists.

Food items are divided into nine classes: fish, benthic macro-invertebrates, benthic micro-invertebrates, zooplankton, other plankton, macro-algae, micro-algae, coral, and detritus.

Table 1 : species diversity of coral reef fish assemblages in the Pacific. The number of species in the species pool are derived from figure 1. The first number gives the number of species, the second number is the sampled surface in m^2. In case of repetitive samplings of the same area or of undefined sampled area "ex" will be noted for the surface.

* : estimated
for the references see end of Table 1a

Area	Number of pool species		Type of Reef				Method
		Inshore/ Fringeing	Patch	Middle lagoon	Barrier	Outer	
Midway (1)	460		135 ex				Visual
Midway (1)	460		82 310 m^2				Rotenone
Hawaii (2)	460	155-187 ex					Visual
Hawaii (3)	460		76-81 1500 m^2				Rotenone
Hawaii (4)	460	81-84 1000-2000 m^2					Visual
Hawaii (5)	460		77 1800 m^2				Rotenone
Fanning (17)	550*	26 ex	62-102 ex	127 ex	88 ex	110 ex	Visual
Moorea (6)	630	54 ex		100-107 ex	160 ex	156 ex	Visual
Mataiva (7)	630			6-25 500 m^2	27-30 500 m^2		Visual
Tonga (8)	800*			46 1000 m^2			Visual
Chesterfield (11)	800	54-114 400 m^2	53-80 80-170 m^2				Visual
Chesterield (11)	800	112-132 500 m^2	117-145 80-170 m^2				Rotenone
GBR (13)	860		9-38 3-28 m^2				Visual
GBR (16)	860		25-50 50 m^2	30-75 50 m^2			Explosive
Saipan (14)	870	90 2000 m^2	74 2000 m^2		60-77 2000 m^2	61-86 2000 m^2	Visual
Guam (15)	870	80-119 ex					Visual
New Caledonia (9)	1200	168-252 ex		204-264 ex	201-219 ex		Visual
New Caledonia (10)	1200	35-53 1000 m^2		98-140 1000 m^2	120-135 1000 m^2		Visual
New Caledonia (10)	1200	106 600 m^2	50-120 40-150 m^2	224 600 m^2	227 600 m^2		Rotenone
GBR (12)	1300	110 1500 m^2		201 1500 m^2	163 1500 m^2		Explosive

Table 1a : Estimates of density and biomass for some reef types across the Pacific.

D : density in fish / m^2 B : biomass in g / m^2
* : value estimated from the data presented
+ : values for hard substrate only

Location	Inshore/ Fringeing		Patch reef		Middle Lagoon		Barrier reef		Outer reef		Method
	D	B	D	B	D	B	D	B	D	B	
Midway (1)			$10.9/13^{+*}$								Rotenone
Midway (1)			$1.4/10.3^{+*}$								Visual
Hawaii (2)	0.8/1.8										Visual
Hawaii (3)	3.1	106									Rotenone
Hawaii (4)	1.6/2.2										Visual
Hawaii (5)			2.6	102							Rotenone
Moorea (6)	2.7				1.4/1.5				2.2/5.8		Visual
Mataiva (7)					0.2/0.5		0.7				Visual
Chesterfield	2.0/3.2	37/43	$5.6/127^{+}$	$400/1400^{+}$							Rotenone
(11)	1.2/3.3	90/200									Visual
	3.3/5.3	110/231									Vis.+Rot.
GBR (13)			15.5^{+*}								Visual
GBR (16)						17/195					Explosive
GBR (12)	7	92			8.4	237			3.2	156	Explosive
PNG (18)	2.6/4										Visual
Guam (15)	1.3/5.3										Visual
New Caledonia											
(9)	2.2/5.8	61/155			1/11	81/218	1.1/3.7	120			Visual
(10)	0.86	25			3.4	301	3.4	244			Visual
(10)	1.06	28			2.5	95	2.8	151			Rotenone

References
1 - Schroeder 1989
2 - Hayes et al. 1982
3 - Brock et al., 1979
4 - Walsh, 1983
5 - Wass, 1967
6 - Galzin, 1985
7 - Galzin et al., 1990
8 - Zann et al., 1984
9 - Kulbicki, unpub.
10 - Kulbicki et al., 1991
11 - Kulbicki et al., 1990
12 -Williams and Hatcher, 1983
13 - Sale and Douglas, 1984
14 - Amesbury et al., 1979
15 - Molina, 1981, 1982
16 - Talbot and Goldman, 1972
17 - Chase and Eckert, 1974
18 - Birkeland and Amesbury, 1987

A discussion of this classification along with the findings for the species from New Caledonia are given by Kulbicki *et al.* (in prep.). Species were also grouped into six life-history classes according to the criteria given in Table 2. This life-history classification remains tentative because precise biological data are still lacking on most species. However, because the categories are broad, there will not be many misclassifications.

Figure 2 gives the distribution of the trophic composition of the checklists analysed. A cluster analysis (Figure 4a) indicates that these checklists may be grouped into two major clusters: the Western Pacific group, which extends from Papua New Guinea to Samoa and from Japan to the south of the Great Barrier Reef; and the other cluster, which includes the southern coral reefs (Lord Howe, Norfolk, Kermadec) and the Central Pacific islands (Polynesia, Johnson Atoll, Hawaii, Easter Island). To further divide these groups, in the west there is a major subgroup extending from Japan to Fiji and from New Guinea to the Marshall Islands. A second subgroup shows an antitropical association between Belau and the Great Barrier Reef and New Caledonia. Eastwards, there is a similar antitropical association between the Hawaiian Islands and the southern islands (Norfolk, Lord Howe, Kermadec, and Easter Island).

Table 2 : life history strategies of fish from coral reef fish assemblages.
life length can be considered as life expectancy (L50 after recruitment)

CLASS	SIZE	REPRODUCTION	BEHAVIOR	GROWTH	MORTALITY LIFE LENGTH
1	Large to very large > 50 cm usually > 1m	Very late in life Usually > 70% maximum size at first reproduction often ovoviviparous low gonado-somatic index	almost never schools except for reproduction	Very slow specially after reproduction	Very low > 12 years
2	Medium to large > 30cm usually >50cm	late in life Usually > 70% maximum size at first reproduction low gonado-somatic index	seldom schools often territorial	slow after first reproduction. Often rapid initial growth	low 7-12 years
3	Small to medium < 30 cm	late in life usually > 70 % maximum size at first reproduction medium gonado-somatic index	seldom schools often territorial	slow after first Initial growth often fast	low 7 to 12 years
4	Medium to large > 30 cm	2-3 years old at first reproduction high gonado-somatic index	often schools seldom territorial simple sexual behavior	rapid initially or through life	medium 3 to 7 years
5	Small to medium < 30 cm	1-3 years old at first reproduction high gonado-somatic index	often schools may be territorial sexual behavior may be complex	rapid initially	medium 3 to 7 years
6	Small to medium < 30 cm	very early in life very high gonado-somatic index	most species school simple sexual behavior	very fast	high 0.5 to 3 years

Figure 3 shows the distribution of life-history strategies of reef fishes across the Pacific. Similarly to the situation with trophic structure, a cluster analysis (Figure 4b) shows that there is a major difference between the western Pacific and the eastern and southern Pacific. In the western area are two subgroups, one encompassing the Great Barrier Reef, New Caledonia, New Guinea, and Belau to the west, and the other subgroup extending from Japan to Rapa. In the eastern and southern areas, no subgroups can be defined.

Cluster analysis of the combined information from life-history and trophic structures reveals remarkable geographical associations (Figure 5). Well marked is the separation between the western Pacific species pools of coral reef fishes and those of the eastern and southern Pacific. Within the boundaries of each of these areas, several subgroups can be defined. In the west, the three subgroups are the Great Barrier Reef region (the Great Barrier Reef and New Caledonia), the Central West Pacific (Japan to Fiji and Papua New Guinea to the Carolines), and a central Pacific area from the Marshalls to Samoa. In the south, the New Zealand group (Lord Howe, Norfolk, Kermadec) is separated from the eastern group of Polynesian archipelagoes.

This examination suggests that the species pools show significant differences across the Pacific. But are such differences reflected at the reef level? In other words, are the variations

in trophic or life-history structures between a coral reef fish assemblage in Polynesia and on the Great Barrier Reef linked to any extent to the variations of their species pools or to other factors. To answer this question would require a comparative study of similar types of reef under similar conditions in several areas of the Pacific. Such data are not now available. In any case, as will be shown in this paper, there is no simple answer because of the extreme variability of these structures in time and space -- a variability that has resulted in diametrically opposite conclusions being drawn from different levels of observation.

REGIONAL VARIATIONS

Coral reef fish assemblages in the Pacific have been studied at the regional level in French Polynesia, the Great Barrier Reef, and New Caledonia. Information is also available on other locations such as the Hawaiian islands, Guam, and Saipan, but these data are not designed for regional comparison.

The regional studies have shown that within a region the structure of a reef fish assemblage is mainly dependent on the type of reef or on the reef's position. Thus, Galzin (1985) in French Polynesia found greater similarity among assemblages on similar types of reef from five different islands than among different reef types of a single island. On the Great Barrier Reef, the work of Williams (1982), Russ (1984), and Williams and Hatcher (1983) indicates that the structure of reef fish assemblages had greater affinities among reefs of a similar type on a north-south gradient than among reefs of different types at the same latitude. Kulbicki (unpub. data) demonstrates that the structure of reef fish assemblages is linked to the position of the reef in the lagoon and therefore to the reef type (Figures 6 to 9).

However, depending on the type of data one analyses, the differences in structure between various reef fish assemblages may vary considerably, as is illustrated by data on the structure of reef fish assemblages in New Caledonia. Consideration of the trophic or life-history-strategy structures in terms of species (Figures 6a, 6b) shows that there is little variation across the lagoon either on a coast-to-barrier-reef axis or a north-south axis. Figures 7a and 7b show that in terms of density these structures are very different from the ones for species (Figures 6a, 6b), with gradients of the importance of the various trophic or life-history strategy classes along a coast-to-barrier-reef axis and a north-south axis. In terms of biomass, Figures 8a and 8b indicate different structures from those observed for density or species composition. As with Figures 7a and 7b, there are gradients along the coast-barrier-reef axis and the north-south axis but they involve different trophic or life-history-strategy classes. Combining trophic and life-history structures results in different clusterings depending on whether it is density, biomass, or species being considered (Figure 9). A similar result was found by Kulbicki and Wantiez (1990) for soft-bottom communities. Detailed analysis of the data presented in Figures 6 to 9 indicates that the species, trophic, or life-history-strategy structures are much more stable between reefs than are density or biomass structures. This is so simply because a major change in species composition requires more disturbance than a change in density or biomass. Consequently, the detection of a difference between reef-fish assemblages in the trophic or life-history structures at the species level is likely to reflect larger dissimilarities in the functioning of these assemblages than would a similar difference at the density or biomass level.

Table 3 gives some idea of the variations observed in trophic structure on several reef types across the Pacific. Although disparate methodologies make comparisons between regions difficult, it is clear that at the species level there are only a few differences between regions or reefs of different types. In all cases, the invertebrate feeders are the most important group. The highest contribution to density is given by plankton feeders in the Great Barrier Reef-New Caledonia region, and by invertebrate feeders in Hawaii -- and probably also in French

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Table 3 : trophic structure of 5 types of reef across the Pacific. All numbers are percentages.
S : species D : density B : biomass
* : estimated ** : value given by Parrish et al. (1986)

Location	Trophic Groups	Fringeing			Inner			Middle			Barrier			Patch		
		S	D	B	S	D	B	S	D	B	S	D	B	S	D	B
GBR	Piscivores				13	2	11	10	1	6	3	1	2			
(Williams and	Invert. feed.				63	7	34	51	6	12	55	6	26			
Hatcher, 1983)	Plankton feed.				13	88	45	23	90	71	25	67	43			
	Algae feeders				12	4	9	15	3	11	17	22	29			
New Caledonia	Piscivores	10	4	9	12	2	9	12	5	9	10	3	10			
Kulbicki (unpubl.)	Invert. feed.	52	17	32	49	18	27	51	21	30	53	23	36			
	Plankton feed.	14	59	21	16	55	26	14	51	33	11	48	9			
	Algae feeders	24	20	38	23	25	38	23	23	28	26	26	45			
Chesterfield	Piscivores	9	4	9										12	4	24
Kulbicki et al.	Invert. feed.	56	46	32										54	33	24
(1990)	Plankton feed.	12	23	12										17	50	31
	Algae feeders	23	27	47										17	13	21
Moorea	Large carnivores		2									5				
Galzin (1985)	Small diurnal carn.		8									30				
	Plankton feeders		3									2				
	Sessile invert.		7									9				
	Omnivores		52									5				
	Algae feeders		27									49				
Hawaii	Piscivores**													18	4	8
Brock et al.	Invert. feeders													53	62	18
(1979)	Plankton feeders													12	22	59
	Algae feeders													13	11	13
	Omnivores													3	1	2
NW Hawaii	Piscivores													16*	6*	19*
Parrish et al.	Invert. feeders														70*	
(1985, 1986)	Plankton feeders														8*	
	Algae feeders														16*	

Polynesia, where the "omnivore" category of Galzin (1985) consists mainly of invertebrate feeders. On the Great Barrier Reef, most of the biomass is accounted for by plankton feeders, whereas in New Caledonia, depending on the type of reef, it is either the algae feeders or the plankton feeders that are the most important trophic group in terms of biomass. In the eastern Pacific, the only information is provided by Brock *et al.* (1979), who indicate that plankton feeders had the highest biomass on the coral patch they studied.

WITHIN-REEF VARIATIONS

A single reef usually contains several zones. Moving from the windward to the leeward side, the usual, though not invariable, sequence is an outer reef, a reef crest, a lagoon, and a back reef. As a general rule, the density and diversity are greatest on the back reef and least on the reef crest (Goldman and Talbot 1976; Harmelin-Vivien 1977, 1989; Russ 1984; Galzin 1985). The difference is linked to wave activity, habitat diversity, and coral cover. Habitat diversity usually decreases with depth. The number of species restricted to one zone of the reef is usually low (5-15 per cent); similarly, ubiquitous species are rather rare (4-8 per cent). Birkeland and Amesbury (1988) and Thollet *et al.* (1991) have indicated that coral reef fish assemblages are usually not much influenced by nearby assemblages such as soft-bottom or mangrove-fish communities. Across a reef there are noticeable changes in the trophic structure (Goldman and Talbot 1976; Harmelin-Vivien 1989; Galzin 1985) and, as at the regional level, species trophic composition is fairly stable compared with density or biomass trophic composition. Usually plankton feeders are mainly found on the outer reefs and leeward side of the reefs, algae feeders prefer the reef flats and leeward side, whereas the piscivores and invertebrate feeders show no special distribution. Species composition and trophic structure change with depth, with grazers' diversity and density decreasing with depth (Galzin 1985; Harmelin-Vivien 1989).

Studies of the species composition of isolated patch reefs indicate marked differences in species composition, density, and biomass -- a diversity that has been mainly explained by random recruitment (Sale and Douglas 1984). It seems that in most instances, these small and relatively isolated reefs are not a system by themselves; the fish found on a patch reef do not represent an assemblage just as a bird assemblage often cannot be supported by an isolated tree.

LONG-TERM VARIATIONS

The few studies that have been done of long-term variations of coral reef assemblages show that over an area at least the size of an entire reef, changes at the species level or density level are not very important. This suggests that at these scales, coral reef assemblages show some stability. For instance, Galzin *et al.* (1990) at Mataiva in French Polynesia found no change over an eight-year period for the total number of species per habitat, the number of species per area unit, or for density (all species pooled). The classification of zones according to their fish assemblage remained the same over the eight years. Williams (1985), looking at the effects of *Acanthaster* on fish assemblages on the Great Barrier Reef, found that, at a given time, variations within reefs was 2-29 per cent and between reefs was 46-82 per cent but that, for a given reef, variation through time of only 0.5 per cent. This study used a log scale, however, which is a rather coarse measure. Hobson (1983), using a limited number of samples, found no difference in densities of the ten major species after two years in Midway and three years in Kona Bay (Hawaii). Also in Hawaii, Brock *et al.* (1979) poisoned a reef twice, 11 years apart. Of the total of 112 species, 40 per cent were common between the two surveys. Density, biomass, and trophic structure remained similar. In a study that covered 23 months before a big storm over an Hawaiian reef and 16 months afterwards, Walsh (1983) found no decrease in abundance or species richness although he noticed some changes in the abundance of a few species.

There are also examples of changes over the long term and on a large scale. Galzin (1985) found in Mooréa (French Polynesia) that between 1976 and 1983, fish density increased 39 per cent on the fringing reef and 47 per cent on the barrier reef. During the same period, there had been a decrease in coral cover and an increase in algae cover, which were likely responsible for an increase in Labridae and Scaridae and a decrease in Chaetodontidae and Pomacentridae. In New Caledonia, the grouping of data into two periods of three years between 1985 and 1991 (Figure 10) indicates that on a regional basis there was no change in species composition but that the density of short-lived species (life-history classes 5 and 6 on Table 2), which are mainly plankton and microalgal feeders, had decreased drastically. Figure 10 also shows that the biomass of fish in life-history-strategy classes 2 and 5 had decreased between 1985-88 and 1989-91 whereas those of class 4 had increased. Because fish of class 2 are the most valuable commercially, they had been subjected to a great increase in fishing pressure during that period. At the moment, no explanation has been found for the variations of fish in classes 4 and 5.

Studies on patch reefs (Sale and Douglas 1984; Schroeder 1989) have shown important changes over time in species composition and density. The changes are attributed to large variations in recruitment, but most of the species taken into account during these studies are of life-history-strategy classes 4, 5, and 6 (Table 2). There is little evidence that similar changes occur for fish in strategy classes 1, 2, or 3 because their densities on patch reefs are usually too low for statistical comparison. Moreover, most of these species have a range that covers a larger area than a single patch reef. As already noted, most isolated patch reefs may not represent a sufficient unit of observation for the study of reef fish assemblages.

SHORT-TERM VARIATIONS

Coral reef fish assemblages show fluctuations of species composition, density, and biomass over short periods of time. In French Polynesia, Galzin (1985) examined three types of reefs over a 15-month period. On fringing reefs there were between 36 and 49 species per survey; 25 of these were permanent and formed 80 per cent of the density. On the barrier reef the number of fish species per survey fluctuated more (33 to 55 species), with 21 permanent species forming 74 per cent of the density. On the outer reef the surveys varied from 45 to 69 species, of which 36 were permanent and formed 94 per cent of the density. Variations in density were highest on the outer reef and lowest on the fringing reef. A seasonal trend, which Galzin attributed to recruitment, appeared successively on the outer reef, barrier reef, and fringing reef. Molina (1982), who studied two of Guam's fringing reefs over a 15-month period, noted a marked increase in recruitment-related density. Carnivores had a peak in abundance - linked to recruitment - between April and June, whilst herbivores increased in abundance between October and December. The carnivores tended to show such peaks on the deepest stations (18 and 30 m), whilst herbivores had similar peaks on the shallowest stations (5 and 9 m). In New Caledonia, Kulbicki *et al.* (1991) have looked at the variations in species composition, density, and biomass of three different reef types (fringing, middle lagoon, and barrier) over a 12-month period (Figure 11). The number of species per station was fairly constant, as was overall density. In contrast, biomass and average weight showed marked variations, without any apparent pattern -- although the investigators believe that much of the fluctuation is related to non-resident species. The trophic structure was fairly stable with regard to species of invertebrate and algae feeders except on the fringing reef. Such stability was not apparent at the density or biomass levels, perhaps because of the variations in abundance on the transects of non-resident species. This emphasizes the significance of sample size (1,500 m^2 on each reef in this case) in that coral reef fish assemblages show such a diversity in space and time.

Variations of coral reef fish assemblages are known to occur at even shorter time scales, *e.g.*, monthly, daily, day/night. Galzin's (1985) investigations of this matter indicate that there are definite trends in the activity, and therefore the detectability, of most reef fish species. These trends are linked to the lunar cycle. There are also important differences between the fish active at night and during the day. Differences during daytime can be linked to tidal cycles. The trophic composition of the species active during the day and at night is also different. Algae feeders are all diurnal whereas a large percentage of the invertebrate feeders are nocturnal. All these variations in fish activity point yet again to the need for comprehensive sampling in the study of coral reef fish assemblages if we are to have more than a quite incomplete understanding of the assemblages.

CONCLUSIONS

Coral reef fish assemblages are derived from species pools that themselves show important variations across the Pacific in species numbers and in trophic and life-history-strategy organisation. The data now available are insufficient to determine the influence of these species pools on the structure of any particular coral reef assemblage.

The structure of coral reef fish assemblages show little variation at a large scale, either in time or space. Thus, reefs of a given type or morphology will support assemblages with comparable characteristics. On a long-term basis and at the scale of a reef, changes in species composition, density, or biomass are usually minor compared with the variations observed at a lower level, where species composition, density, biomass, or trophic structure are indeed heterogeneous and show significant variations through time -- variations that are mainly attributed to random recruitment.

The number of species found in a given assemblage depends on the type of reef, with the lowest diversity usually being found nearshore and the greatest diversity in the middle lagoon. Barrier reefs and outer reefs have intermediate values. This number of species is fairly stable over time. Within a given reef type, a limited number of species are ubiquitous (<20 per cent), and similarly few species are found in only one part of the reef (<10 per cent). Density and biomass are much more variable than diversity, but the sampling of non-territorial species is often a major problem in assessing these quantities. Trophic structure is usually very stable within a region when considered at the species level. Invertebrate feeders are the most diverse trophic group in coral reef fish assemblages across the Pacific. In the western Pacific, the plankton feeders tend to be the most abundant. The most important trophic group in terms of biomass varies with the region, the type of reef, and over time in such a way that no particular trend can be detected.

To improve our knowledge of the structure of coral reef fish assemblages, the following three approaches should be considered:

1. develop *testable* hypotheses about the generation and maintenance of the organisation of coral reef fish assemblages;

2. gather *standardized* information on species composition, density, and biomass of assemblages associated with selected types of reefs across the Pacific; and

3. develop databases on the life-history traits of Pacific coral reef fishes, in particular on growth, diet, age or size at first reproduction, reproductive effort, and recruitment patterns.

At present, the only hypotheses ruling the organisation of these assemblages have to do with the type of recruitment of coral reef fishes, food, and space allocation. It is unlikely that so few hypotheses can support all the contradictory information that has already been gathered on the assemblages. Other ideas need to be tested. For instance, to what extent is the organisation of these assemblages linked to the species pool available? Is there a unit of observation at which the structure of these assemblages show some stability? And so forth. To answer such questions it will be necessary to compare reefs from different regions of the Pacific. At present, such comparisons are difficult because of disparity in research methods. In addition, many regions of the Pacific have not yet been sampled so that any biogeographic study on the variation of the structure of fish assemblages can only be incomplete. To attribute a given structure to an assemblage requires data on the biology of all its species, whereas now our knowledge of the biology of coral reef fish remains limited, especially on growth, reproduction, and behaviour. Such studies are of course very time consuming and may be less attractive to the scientific community than broader theoretical studies. Unfortunately, it is difficult to build a house with only mortar (hypotheses) and no bricks (biological data).

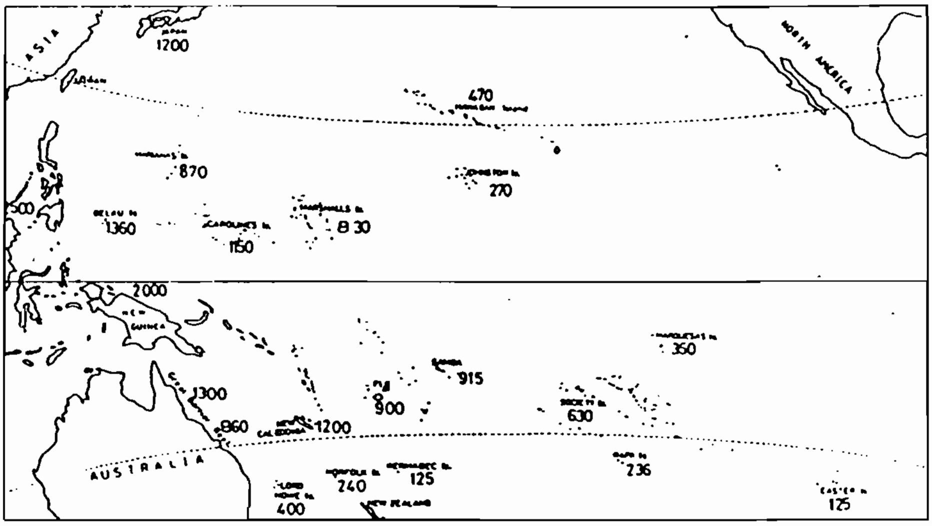


Figure 1 : Distribution of the number of reef fish species across the Pacific (adapted from Myers, 1989).

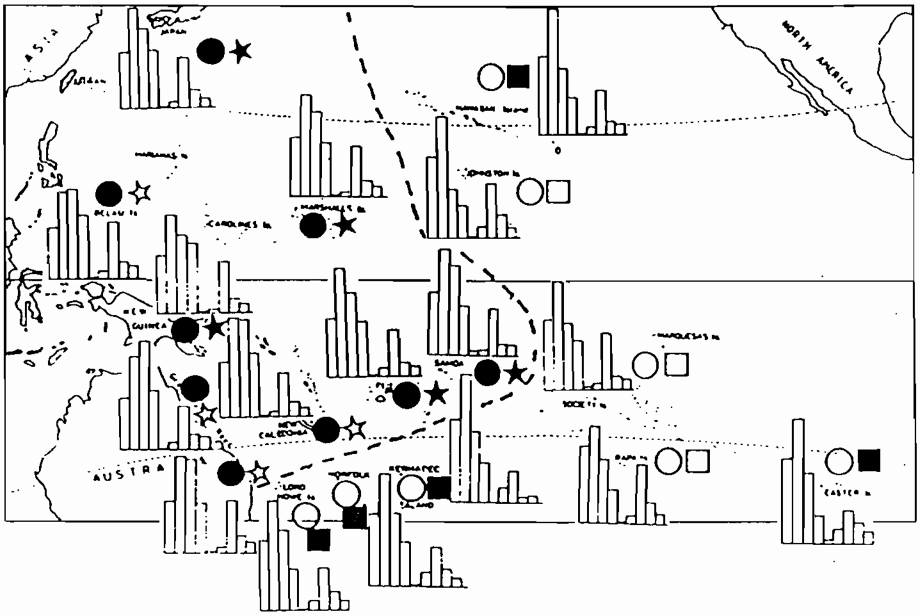


Figure 2 : trophic structure of the coral reef fish species pools across the Pacific. There are nine classes on each histogramm, from left to right : piscivores, macroinvertebrate feeders, microinvertebrate feeders, zooplankton feeders, other plankton feeders, macroalgae feeders, microalgae feeders, corallivores and detritus feeders. The symbols next to the histogramms are derived from the cluster analysis shown on figure 4a.

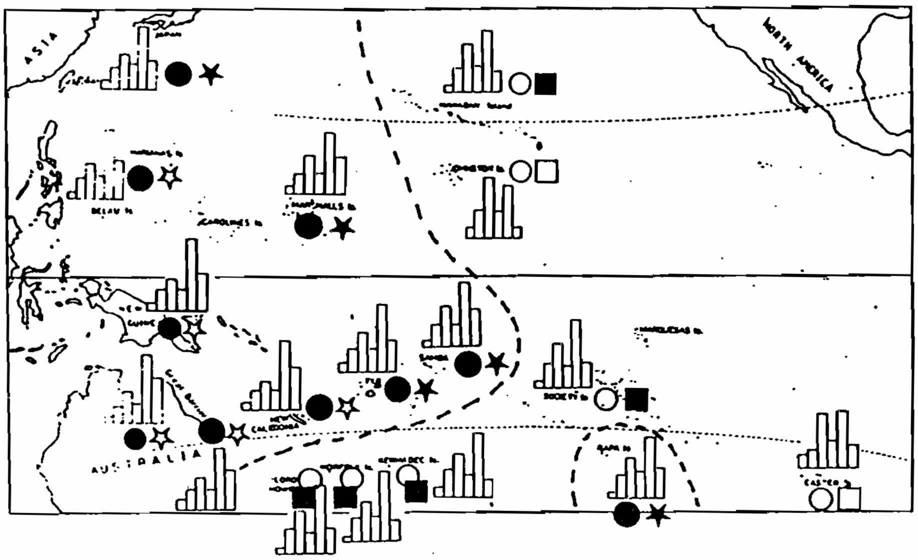


Figure 3 : Life history strategy structure of the coral reef fish species pools across the Pacific. The six classes on each histogramm are from left to right the classes 1 to 6 of table 2. The symbols next to each histogramm are derived from the cluster analysis illustrated on figure 4b.

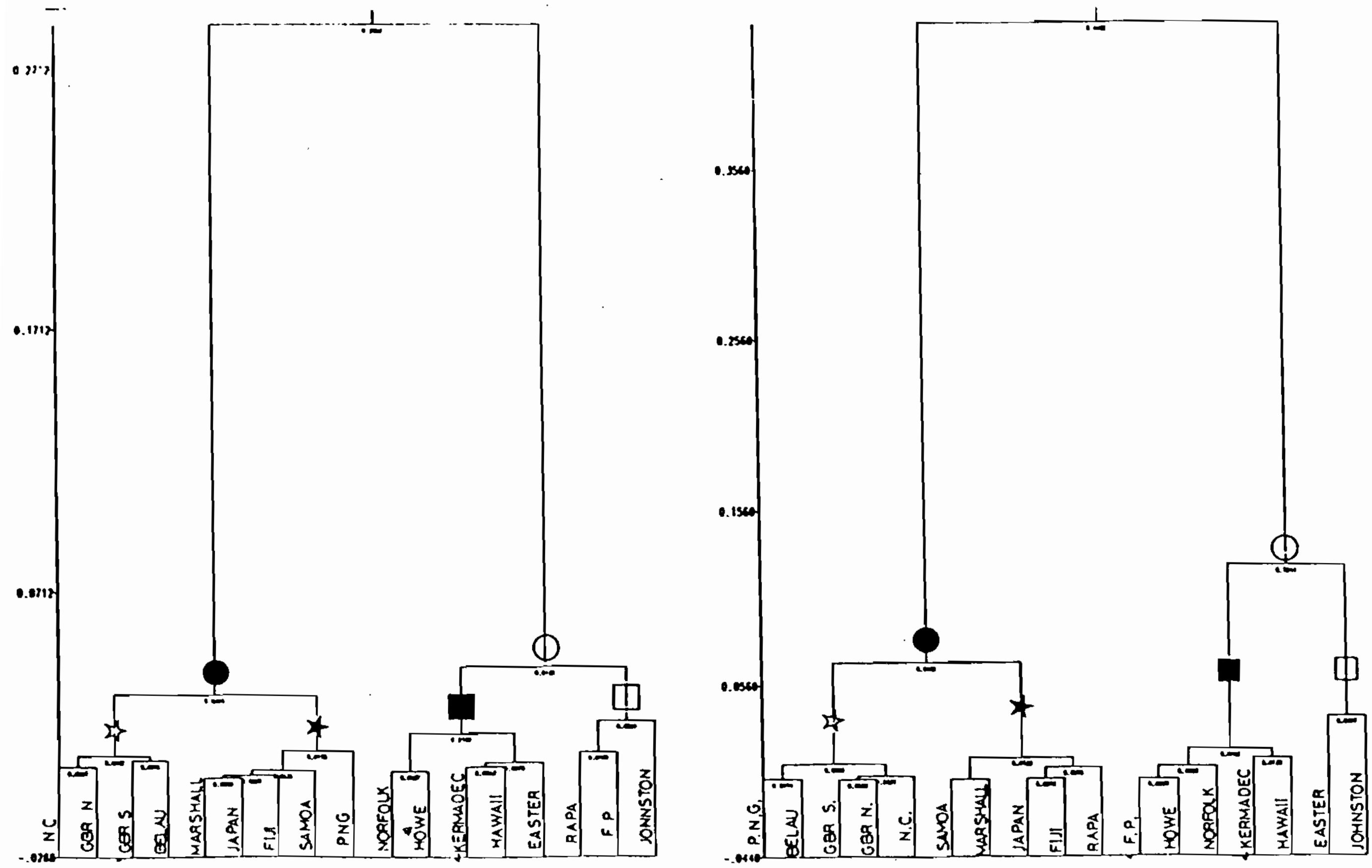
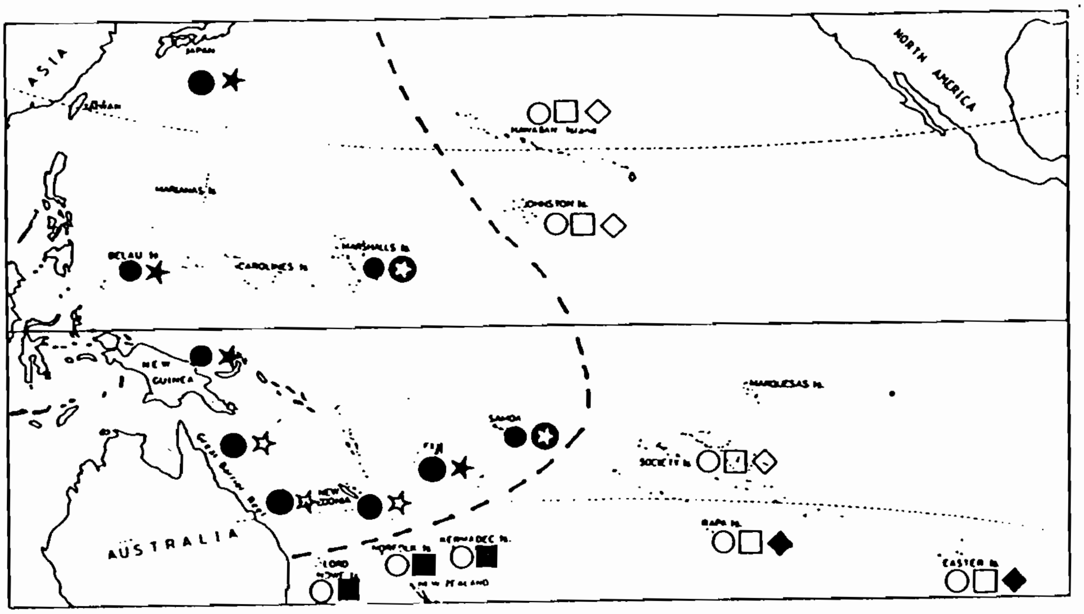


Figure 4 : a) Cluster analysis of the trophic structures of 17 species pools across the Pacific
b) Cluster analysis of the life history strategy structure of 17 species pools across the Pacific



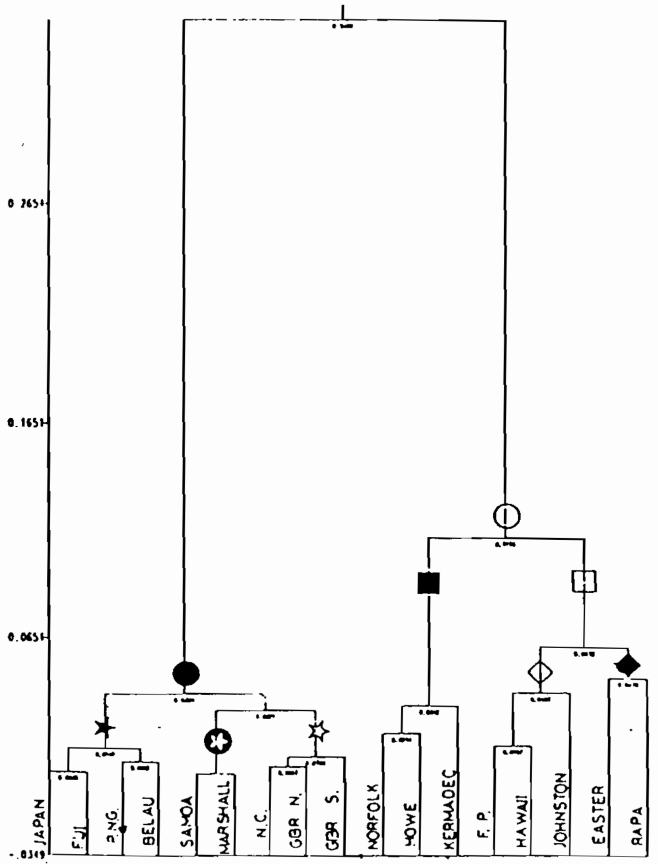
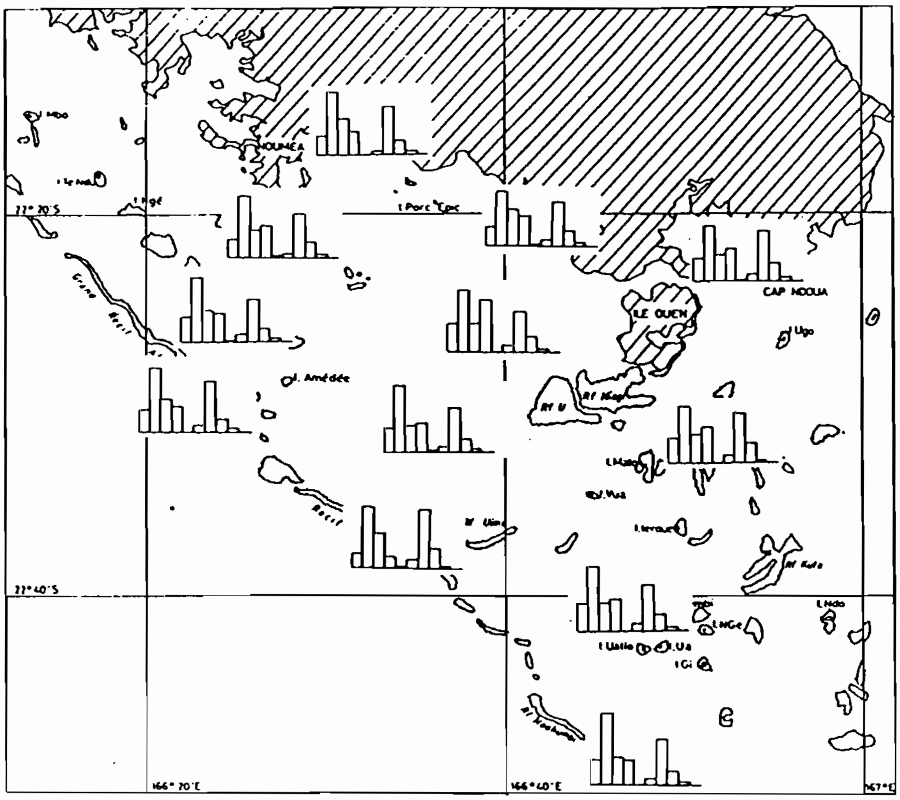
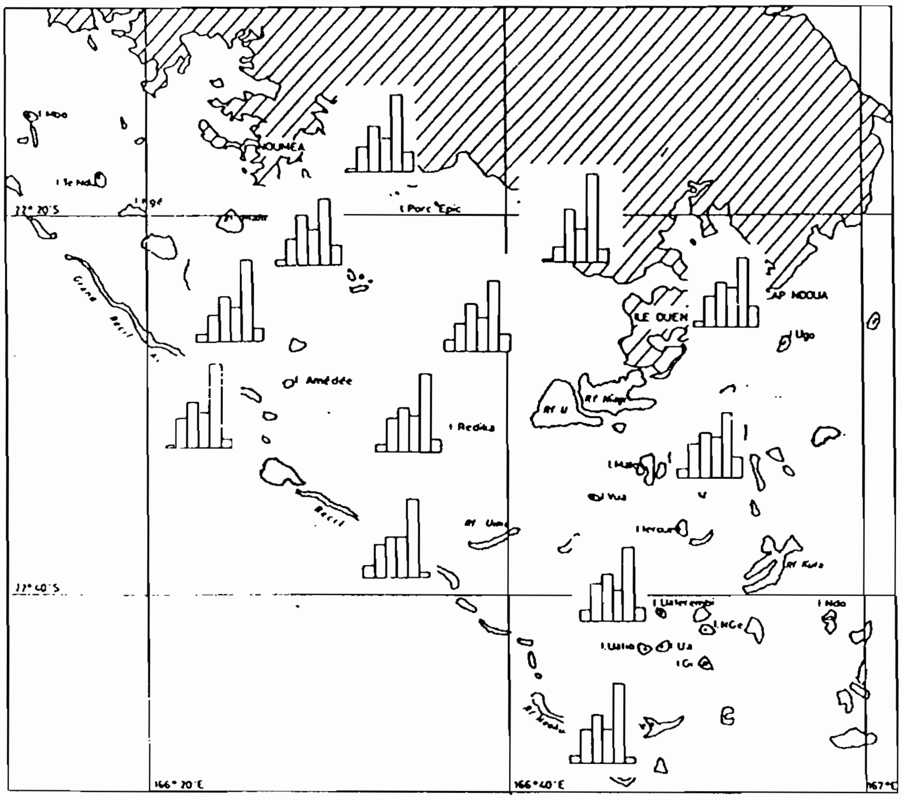


Figure 5 : Cluster analysis of the combination of the trophic and life history strategy structures of 17 species pools across the Pacific.



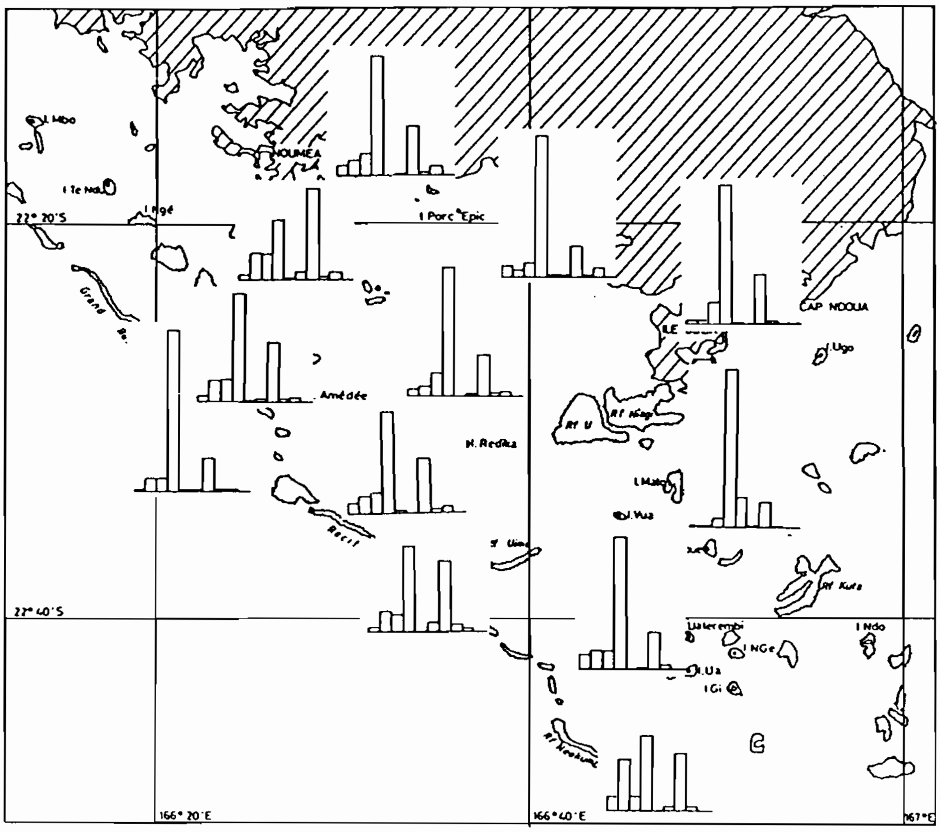
SPECIES TROPHIC



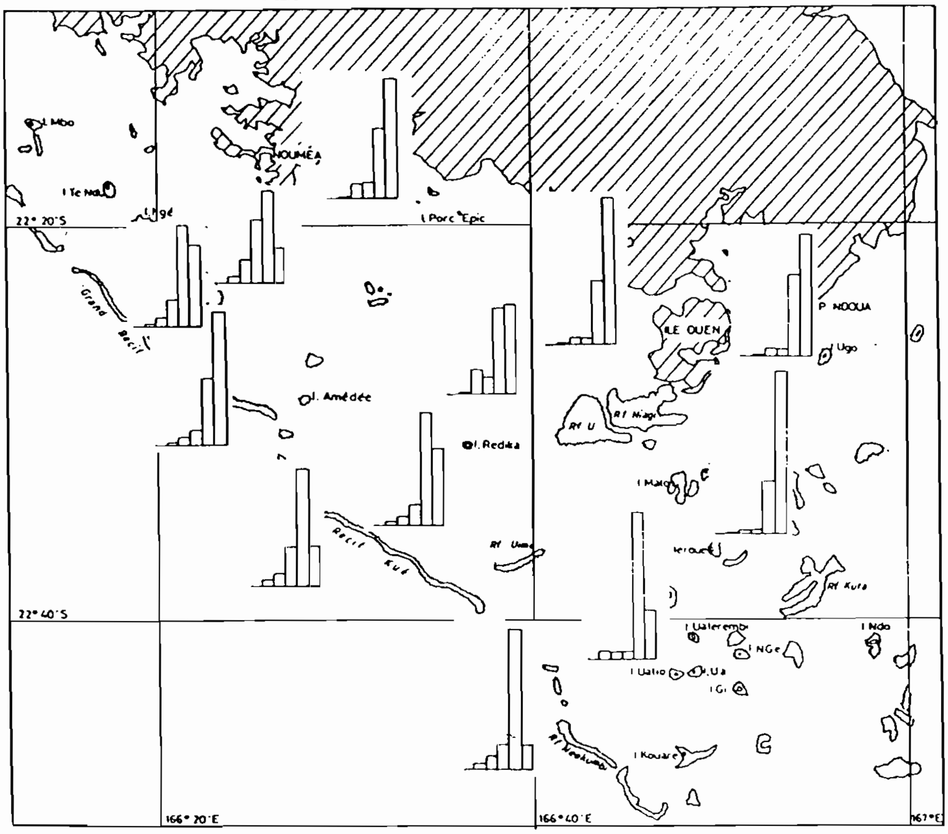
SPECIES LIFE HISTORY

Figure 6 : a) distribution of the trophic structure of coral reef fish assemblages at the species level across the S.W. lagoon of New Caledonia (approx. 2400 square nautical miles). The histogramms are arranged as on figure 2. Each histogramm is the average of 20 stations sampled over an area of 200 square nautical miles.

b) distribution of the life history strategy structure of coral reef fish assemblages at the species level across the S.W. lagoon of New Caledonia



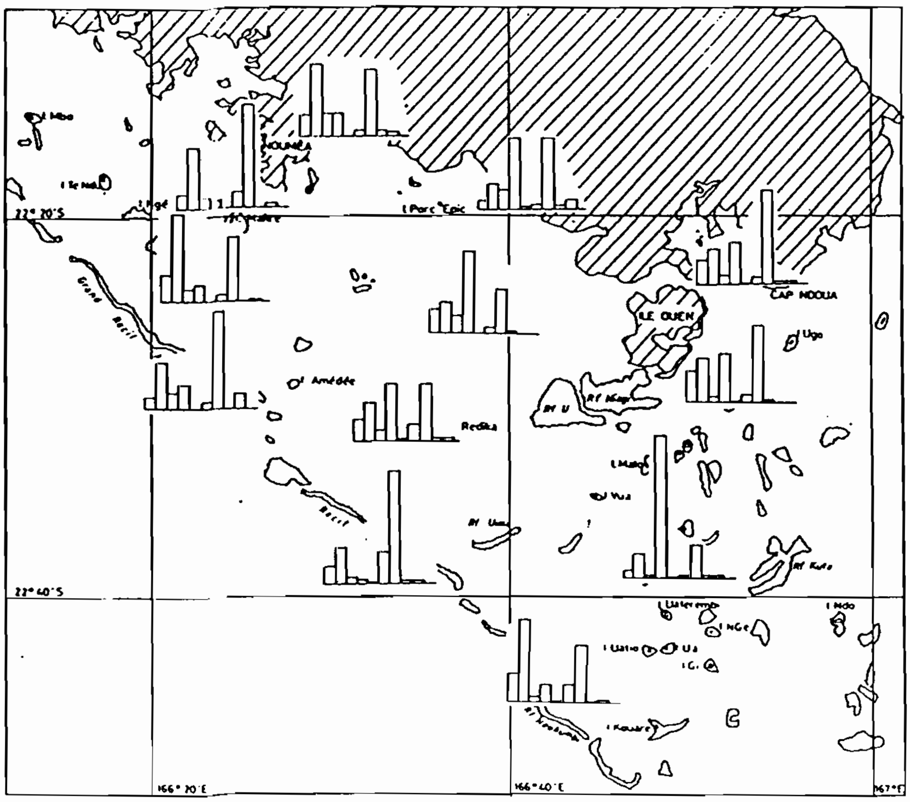
DENSITY TROPHIC



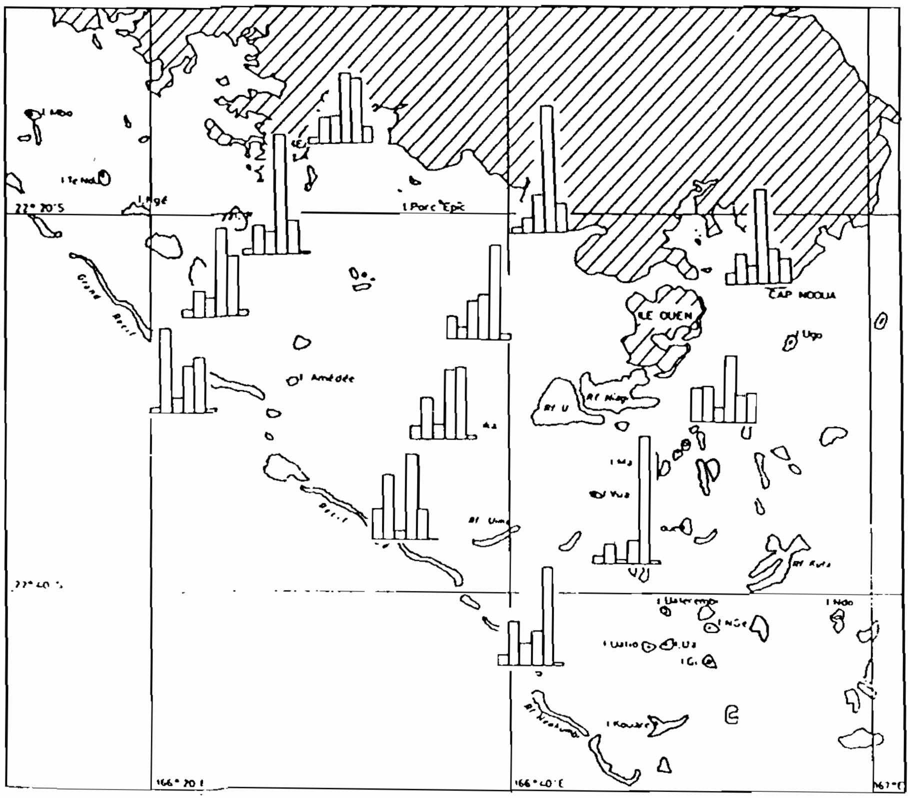
DENSITY LIFE HISTORY

Figure 7 : a) distribution of the trophic structure of coral reef fish assemblages at the density level across the S.W. lagoon of New Caledonia

b) distribution of the life history strategy structure of coral reef fish assemblages at the density level across the S.W. lagoon of New Caledonia



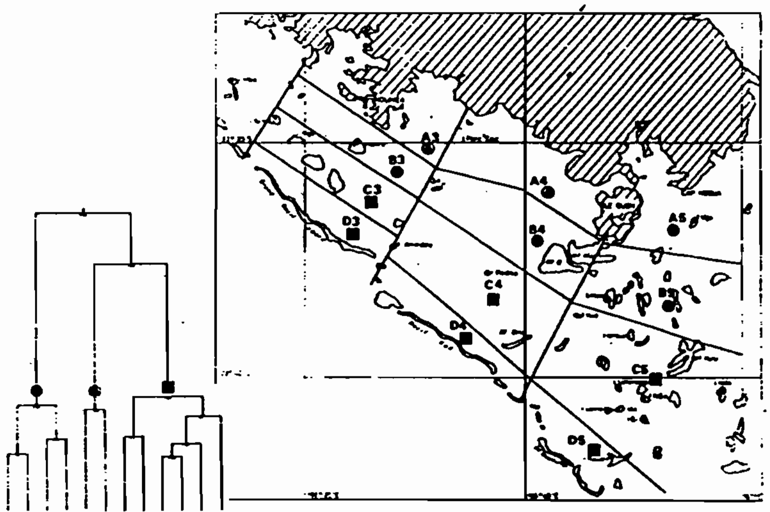
BIOMASS TROPHIC



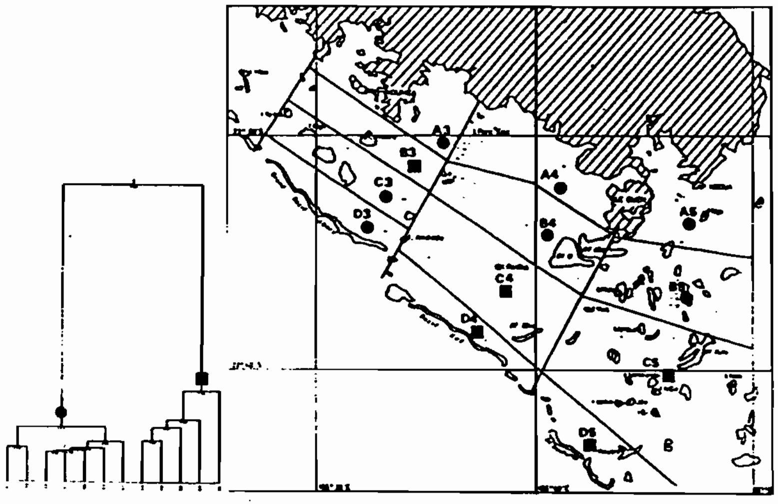
BIOMASS LIFE HISTORY

Figure 8 :a) distribution of the trophic structure of coral reef fish assemblages at the biomass level across the S.W. lagoon of New Caledonia

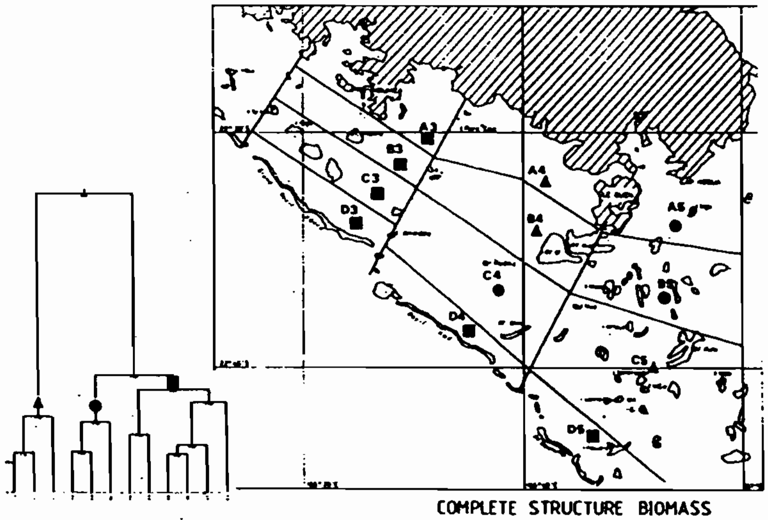
b) distribution of the life history strategy structure of coral reef fish assemblages at the biomass level across the S.W. lagoon of New Caledonia



COMPLETE STRUCTURE SPECIES



COMPLETE STRUCTURE DENSITY



COMPLETE STRUCTURE BIOMASS

Figure 9 : cluster analysis of the combination of trophic and life history strategy structures of coral reef fish assemblages at the species, density and biomass levels on the S.W. lagoon of New Caledonia

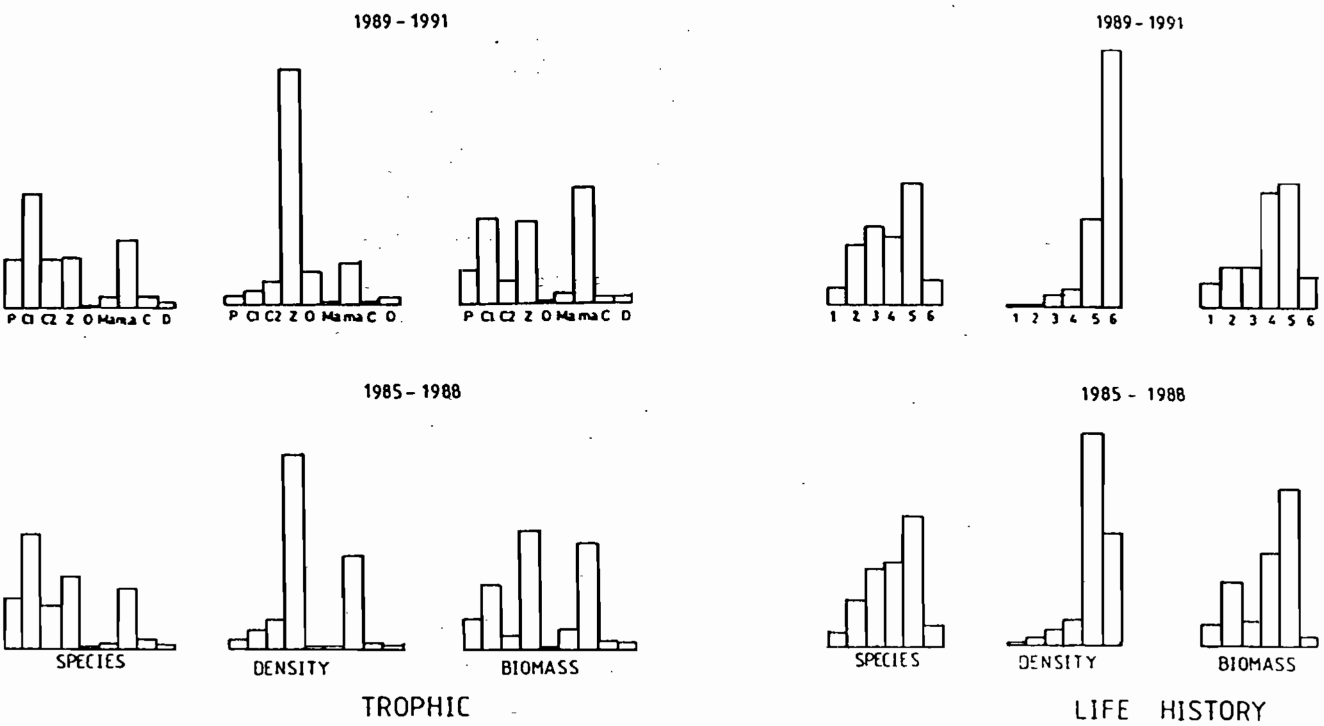


Figure 10 : temporal variations of the trophic and life history strategy structures of coral reef fish assemblages in the S.W. lagoon of New Caledonia. Trophic groups are arranged in the same order as on figure 2 and life history strategy groups are in the same order as on figure 3.

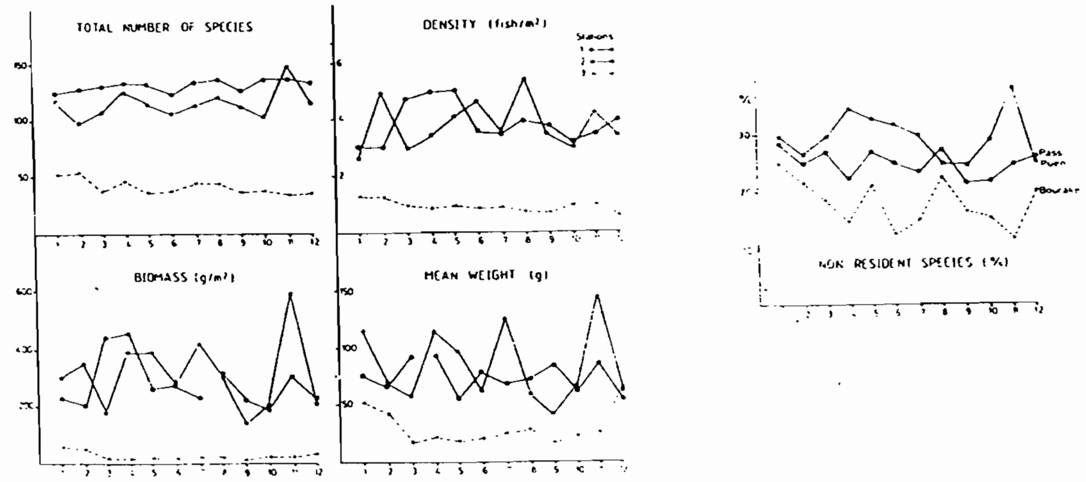


Figure 11 : annual variations of the species number, density, biomass, mean weight and percentage of non-resident species on three reefs in the S.W. lagoon of New Caledonia. Months are on the X axis. Station 1 (Bourake) is a fringeing reef, station 2 (Puen) is a middle lagoon reef and station 3 (Passe) is on the Barrier reef.

REFERENCES

Amesbury, S.S., Lassuy, D.R., Myers, R.F., and Tyndzik, V. 1979. A survey of the fish resources of Saipan Lagoon. *University of Guam Marine Laboratory Technical Report* 52.

Birkeland, C. and Amesbury, S.S. 1988. Fish-transect surveys to determine the influences of neighboring habitats in fish community structure in the tropical Pacific. *Co-operation for Environmental Protection in the Pacific.* UNEP Regional Seas Reports and Studies No. 97: 195-202.

Brock, R.E., Lewis, C. and Wass, R.C. 1979. Stability and structure of a fish community on a coral patch reef in Hawaii. *Marine Biology* 54: 281-292.

Chase, E.H. and Eckert, D.B. 1974 Ecological aspects of the distributions of fishes at Fanning Island. *Pacific Science* 28(3): 297-317.

Doherty, P.J. and Williams, D.McB. 1988. Are local populations of coral reef fishes equilibrial assemblages? The empirical data base. *Proceedings 6th International Coral Reef Symposium* (Australia) 1: 131-139.

Galzin, R. 1985. Ecologie des poissons récifaux de Polynésie Française. Ph.D. thesis, University of Montpellier.

Galzin, R., Bell, J., and Lefèvre, A. 1990. Etude interannuelle du peuplement ichthyologique du lagon de l'atoll de Mataiva en Polynésie Française. *Cybium* 14(4): 313-322.

Goldman, B. and Talbot, F.H. 1976. Aspects of the ecology of coral reef fishes. Pages 125-154 in O.A. Jones and R. Endean (eds.), *Biology and Geology of Coral Reefs.* (Vol. III Biology 2) Academic Press, New York.

Harmelin-Vivien, M. 1977. Ecological distributions of fishes on the outer slope of Tulear Reef (Madagascar). *Proceedings 3rd International Coral Reef Symposium* 1: 289-296.

Harmelin-Vivien, M. 1989. Reef fish community structure: an Indo-Pacific comparison. Pages 22-60 in M. Harmelin-Vivien and F. Bourlière (eds.), *Vertebrates in Complex Tropical Systems.* (Ecological Studies 69) Springer-Verlag, New York.

Hayes, T.A., Hourigan, T.F., Jazwinski, S.C., Johnson, S.R., Parish, J.D., and Walsh, D.J. 1982. The coastal resources, fisheries and fishery ecology of Puako, West Hawaii. *Hawaii Cooperative Fishery Research Unit Technical Report* 82 (1).

Hobson, E.S. 1983. The structure of reef fish communities in the Hawaiian archipelago. *Proceedings of the Symposium on Status of Resource Investigations in the Northwestern Hawaiian Islands-UNIHI Seagrant-MR* 84 (1): 101-122.

Kulbicki, M., Doherty, P., Randall, J.E., Bargibant, G., Menou, J.L., Mou Tham, G. and Tirard, P. 1990. La campagne CORAIL 1 du N.O. CORIOLIS aux îles Chesterfield. Données préliminaires sur les peuplements ichthyologiques. *ORSTOM Nouméa Océanographie Rapport Scientifique et Technique* 57.

Kulbicki, M. and Wantiez, L. 1990. Variations in the fish catch composition in the Bay of St. Vincent, New Caledonia, as determined by experimental trawling. *Australian Journal of Freshwater and Marine Resources* 41: 121-144.

Kulbicki, M., Mou Tham, G., Randall, J.E., and Rivaton, J. 1991. Suivi mensuel des peuplements ichthyologiques des récifs coralliens dans le lagon SW de Nouvelle Calédonie. *ORSTOM Nouméa Océanographie Rapport Scientifique et Technique* 61.

Kulbicki, M., Parrish, J., Thollot, P., and Wantiez, L. (in prep.) Main food types of lagoon fishes from New Caledonia.

Molina, M.E. 1981. Reef fish population investigations through the use of permanent transects. *Guam Department of Agriculture - Aquatic and Wildlife Resources Annual Report*: 50-67.

Molina, M.E. 1982. Reef fish population investigations through the use of permanent transects. *Guam Department of Agriculture - Aquatic and Wildlife Resources Annual Report*. Pp. 88-128.

Myers, R.F. 1989. *Micronesian Reef Fishes*. Coral Graphics, Guam.

Parrish, J.D., Callahan, M.W., and Norris, J.E. 1985. Fish trophic relationships that structure reef communities. *Proceedings 5th International Coral Reef Symposium* (Tahiti, French Polynesia) 4: 73-78.

Parrish, J.D., Morris, J.E., Callahan, M.W., Callahan, J.K., Magarifuji, E.J., and Schroeder, R. 1986. Piscivory in a coral reef community. Pages 285-297 C.A. Simenstad and G.M. Caillet (eds.), *Contemporary Studies in Fish Feeding*. Junk, Dorchdrecht, The Netherlands.

Russ, G. 1984. The distribution and abundance of herbivorous fishes in the Central Great Barrier Reef. I - Levels of variability across the entire continental shelf; II - Patterns of zonation in mid-shelf and outershelf reefs. *Marine Ecology Progress Series* 20: 23-34; 35-44.

Sale, P.F. 1982. The structure and dynamics of coral reef fish communities. Pages 241-253 in D. Pauly and G.I. Murphy (eds.), *Theory and Management of Tropical Fisheries.* (ICLARM Conference Proceedings 9.) CSIRO, Cronulla, Australia.

Sale, P.F. and Douglas, W.A. 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.

Schroeder, R.E. 1989. The ecology of patch reef fishes in a subtropical Pacific atoll. Recruitment variations, community structure and effects of fishing predators. Ph.D. thesis, University of Hawaii.

Talbot, F.H. and Goldman, B. 1972. A preliminary report on the diversity and feeding relationships of the reef fishes of One Tree Island, Great Barrier Reef. Pp. 425-443 on C. Mukundan and C.S. Gopinadha Pillai (eds.), *Proceedings of the Symposium on Corals and Coral Reefs.* Marine Biological Association of India, Cochin.

Thollot, P., Kulbicki, M, and Wantiez,L. 1991. Temporal patterns of species composition in three habitats of the St Vincent Bay area (New Caledonia): coral reefs, soft bottoms and mangroves. *Proceedings International Soc. Reef Studies*: 127-137. (Nouméa, New Caledonia)

Walsh, W.J. 1983. Stability of a coral reef fish community following a catastrophic storm. *Coral Reefs* 2: 49-63.

Wass, R.C. 1967. Removal and repopulation of fishes of an isolated patch coral reef in Kaneohe Bay, Oahu, Hawaii. M.Sc. thesis, University of Hawaii.

Williams, D.McB. 1982. Patterns in the distribution of fish communities across the Central Great Barrier Reef. *Coral Reefs* 1: 35-43.

Williams, D.McB. 1885. Temporal variations in the structure of reef slope fish communities (Central Great Barrier Reef): short term effects of *Acanthaster* infestation. *Marine Ecology Progress Series* 28: 157-164.

Williams, D.McB. and Hatcher, A. 1983. Structure of fish communities on outer reef slopes of inshore, midlshelf and outershelf reefs on the Great Barrier Reef. *Marine Ecology Progress Series* 10: 239-250.

Zann, L.P., Kimmerer, W.J., and Brock, R.E. 1984. The ecology of Fanga 'Uta lagoon, Tongatapu, Tonga. *Seagrant Cooperative Report - Univ. of Hawaii - UNIHI - Seagrant - CR* 84-04.

Kulbicki Michel. (1992).

Present knowledge of the structure of coral reef fish assemblages in the Pacific.

In : Coastal resources and systems of the Pacific basin : investigation and steps toward protective management. Nairobi : UNEP, (147), 31-53.

(UNEP Regional Seas Reports and Studies ; 147).