Biogeography of reef fishes of the French Territories in the South Pacific

by

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ABSTRACT. - There are three French territories in the tropical Pacific with coral reefs: New Caledonia, Wallis and Futuna, French Polynesia. The reef fish species composition presently known from these three territories is described. Similarities in species composition were analysed within these territories as well as amongst territories. These checklists were then included in a biogeographical analysis of reef fish species composition based on 64 checklists presently available for the tropical Pacific. This analysis allowed the definition of 9 biogeographical regions. New Caledonia and Wallis were assigned to the same region, "South-West Pacific" which also included the Great Barrier Reef, Fiji, Tonga and Rotuma. French Polynesia was associated to the Cook Islands and Pitcairn-Ducie to form a "South Polynesia" region. Endemism was found to be low in most French territories (4.4% for New Caledonia with 3.3% for Grande Terre, 2.5% for Ouvea, 1.8% for Chesterfield; 0% for Wallis; 6.1% for French Polynesia with 8.3% in the Marquesas, 2.5% for Rapa, 1.9% for Society, 1.1% for Tuamotu, 1.1% for Australes and 0.4% for Gambier). Most endemic species were small, secretive and rare. The effects of 4 factors on the distribution of reef fish species were tested: distance to the biodiversity centre, island size, island isolation and latitude. Total diversity was significantly affected by island isolation ($p < 0.0001$), distance to the biodiversity centre ($p < 0.05$) and island size ($p < 0.05$). The effects of these factors were also tested on the relative importance of 17 major families. These factors had complex effects, but the major trends indicated that Labridae, Scaridae, Acanthuridae, Chaetodontidae, Mullidae, Serranidae, Pomacanthidae, Balistidae were primarily influenced by island size, Pomacentridae, Lutjanidae, Tetraodontidae and Caesionidae were mainly influenced by latitude and Haemulidae, Nemipteridae, Siganidae and Lethrinidae were mainly influenced by the distance to the biodiversity centre.

RÉSUMÉ. - Biogéographie des poissons récifaux des Territoires français du Pacifique Sud.

Il existe trois territoires français dans le Pacifique tropical : la Nouvelle-Calédonie, Wallis et Futuna, la Polynésie française. La composition spécifique des poissons de récif actuellement connus de ces territoires est décrite. Les similarités dans la composition spécifique sont analysées au sein de chaque territoire et entre territoires. Ces listes faunistiques sont ensuite incluses dans une analyse biogéographique portant sur 64 listes faunistiques actuellement disponibles pour le Pacifique tropical. Cette analyse a permis de définir neuf régions biogéographiques. La Nouvelle-Calédonie et Wallis font partie d'une même région le "Pacifique sud-ouest" qui comprend aussi la Grande Barrière de Corail, Fidji, Tonga et Rotuma. La Polynésie française a été associée aux îles Cook ainsi que Pitcairn et Ducie pour former la région "Polynésie Sud". L'endémisme est faible dans l'ensemble de ces territoires (4,4% pour la Nouvelle-Calédonie avec 3,3% pour la Grande Terre, 2,5% pour Uvéa, 1,8% pour Chesterfield ; 0% pour Wallis ; 6,1% pour la Polynésie française avec 8,3% aux Marquises, 2.5% pour Rapa, 1,9% pour les Sociétés, 1,1% pour Tuamotu, 1,1% pour Australes et 0,4% pour Gambier). La plupart des espèces endémiques y sont petites, cachées et rares. Les effets de quatre facteurs sur la distribution géographique des poissons de récif ont été testés : la distance au centre de biodiversité, la taille des îles, la latitude et le degré d'isolement des îles. La diversité totale était significativement affectée par le degré d'isolement ($p < 0,00001$), la distance au centre de biodiversité ($p < 0,05$) et la taille des îles ($p < 0,05$). Les effets de ces facteurs ont aussi été testés sur la contribution relative de 17 familles à la diversité totale. Ces facteurs ont des effets complexes, mais les principales tendances montrent que Labridae, Scaridae, Acanthuridae, Chaetodontidae, Mullidae, Serranidae, Pomacanthidae, Balistidae sont influencées en premier lieu par la taille de l'île, les Pomacentridae, Lutjanidae, Tetraodontidae et Caesionidae sont influencées surtout par la latitude et les Haemulidae, Nemipteridae, Siganidae et Lethrinidae par la distance au centre de biodiversité.

Key words. - Reef fish - Biogeography - Pacific - New Caledonia - French Polynesia - Wallis.

The tropical Pacific is the region with the highest marine fish diversity in the world. At present approximately 5,900 taxa are recorded from this area (Fishbase, Froese and Pauly, 2004) for the 0-100 m depth range, this number excluding oceanic pelagic species. Reef fishes make the bulk of the diversity of the coastal species found in the tropical Pacific, with more than 4,000 taxa affiliated with reefs. Our knowledge of the distribution of fish species in this region coincides with a sharp increase in the number of species described, as well as in the number of genus and family revisions in the last 25 years. However much remains to be done with still hundreds of species to be described in museum collections and probably many more waiting to be collected and many genera and families in need of revision. Collection of coastal fishes is very uneven in the Pacific, some areas such as Japan, Hawaii, Taiwan or the Great Barrier Reef being well sampled while others are still little explored, for instance Vanuatu, most of central Micronesia, many parts of the Solomon Islands or Papua.

There are three French Territories in the tropical Pacific:

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New Caledonia, Wallis and Futuna and French Polynesia. Fish sampling has been very uneven in these Territories. New Caledonia has probably received the most attention with many exploratory cruises by IRD (formally Orstom), the visit of many scientific teams, three published check lists (Rivaton *et al.*, 1989; Kulbicki *et al.*, 1994; Kulbicki and Williams, 1997) and several revisions of families or genera from this region (e.g. Fricke, 2000, 2002, 2004; Randall and Kulbicki, 2006). Two books on the shore fishes from New Caledonia have also been published (Fourmanoir and Laboute, 1976; Laboute and Grandperrin, 2000). French Polynesia has been sampled in a much less systematic way, with many small collections being made by visiting scientific teams. Several checklists have been produced for this territory, in particular Randall (Randall, 1985; Randall and Earl, 2000; Randall *et al.*, 2002) gave detailed lists for several areas of French Polynesia (Society Islands, Tuamotu Archipelago, Austral Islands, and Marquesas). Randall also produced a first checklist for the island of Rapa (Randall *et al.*, 1990) and more recently this island was sampled by a scientific expedition (Galzin *et al.*, 2006). Scientific teams are assisted in French Polynesia by several local underwater photographers whose pictures have enabled an appreciable increase in our knowledge of the distribution of many species. A field guide to reef fish was published by Bagnis *et al.* (1976) and another book is presently in press (Bacchet *et al.*, 2007). Wallis and Futuna is the least explored French territory in the Pacific regarding coastal fishes. A recent exploration of Wallis reefs enabled a first checklist (Williams *et al.*, 2006) but this fauna needs probably more work to be at a comparable level of knowledge with New Caledonia or French Polynesia. The island of Futuna still needs to be explored, only a few visual censuses of commercial fishes being available at present for this island (Wantiez, 2000).

Endemism of reef fishes is supposed to be low, but little has been published on this issue for the tropical Pacific (Randall, 1992; Robertson, 2001; Roberts *et al.*, 2002; De Martini and Friedlander, 2004). In particular the appreciation of endemism is linked to the level of our knowledge on the geographical distribution of species, but also to the improvement of taxonomy as many genera and families are in need of revision with a high number of synonyms still in use or species which status needs to be confirmed. The geographical distribution of the species which are easily collected or observed is rather well known at present for most of the Pacific, but on the opposite the geographical range of families such as Gobiidae, Blenniidae, Apogonidae, Trypterigiidae,… is far from satisfactory and it is likely that endemism rates within these families may drastically change as our knowledge improves.

The geographical distribution of species within the Pacific is known to be linked to many physical factors. Bellwood and Hughes (2001) showed that distance to the biodiversity centre, latitude and island size significantly affected the distribution of 13 families of reef fishes across the Indo-Pacific. These factors are probably not the only ones coming in play. In particular the degree of isolation could contribute to the explanation of the distribution of several families or genera.

The purpose of the present work is to give an overall picture of our knowledge of reef fishes from the French Territories in the Pacific. Special attention will be given to similarities and divergences within and between these territories. In particular endemism will be evaluated for each separate area within these French Territories. The affinities in the composition of the species lists from these territories with neighbouring areas will also be presented. At last, the influence of several large scale factors such as distance to the biodiversity centre, island size or degree of isolation will also be explored.

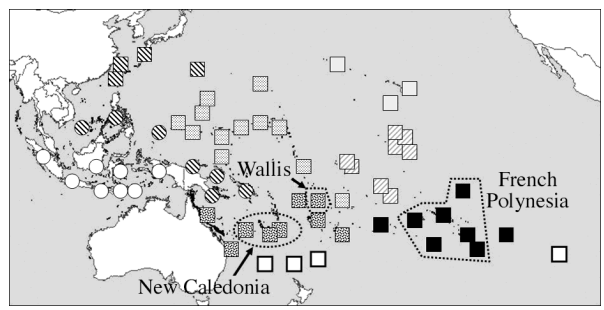

Figure 1. - Position of the 64 fish checklists available with geographical distribution of the groups issued from the clustering presented on figure 4. French Territories are surrounded by doted lines. *[Position des 64 listes faunistiques disponibles accompagnée de la répartition géographique des groupes issus de l'analyse hiérarchique présentée sur la figure 4. Les Territoires français sont entourés de pointillés.]*

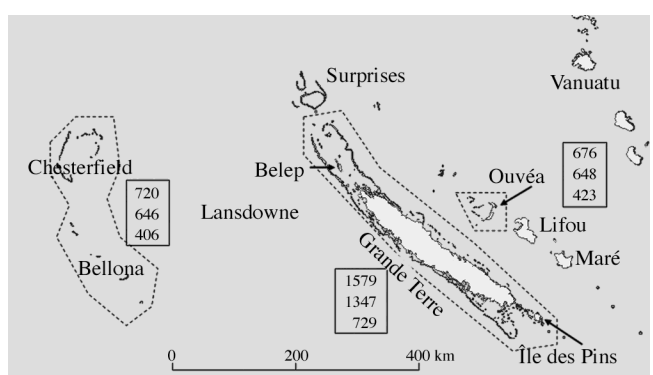

Figure 2. - Map of New Caledonia with location of the 3 major survey areas : Grande Terre, Chesterfield and Ouvéa (surrounded by doted lines). The numbers are from top to bottom: number of coastal species, number of reef species, number of reliable reef species. *[Carte de la Nouvelle-Calédonie avec l'emplacement des 3 principales zones étudiées : Grande Terre, Chesterfield et Ouvéa (entourés de pointillés). Les nombres sont, de haut en bas : le nombre d'espèces côtières, le nombre d'espèces récifales, le nombre d'espèces récifales "fiables".]*

MATERIAL AND METHODS

Study Zone

The study was conducted on the fish species of the three French Territories of the South Pacific (Fig. 1). These species lists were compared with lists from 55 other islands or regions across the Pacific. Within each French territory the following areas were considered: in New Caledonia, the main island (Grande Terre), Ouvea atoll and the Chesterfield Archipelago (Fig. 2); in French Polynesia, the Society Islands, Tuamotu Archipelago, Marquesas, Gambier Islands, Austral Islands and Rapa (Fig. 3); in Wallis and Futuna, there was data available only for Wallis Island.

Species lists

The level of knowledge of the geographical distribution of species in the Pacific varies between families. There are many gaps in our knowledge of most families composed of small species such as Gobiidae, Trypterigiidae, Apogonidae, Bleniidae, Syngnathidae,… as well as families with species that tend to hide such as Muraenidae, Ophichthidae, Holocentridae,… Finally, some families such as Clupeidae, Atherinidae, Mugilidae are either in profound need of revision or have species which are so difficult to differentiate that many published locality records may be questionable. Therefore if one wishes to make valid comparisons of diversity amongst islands and regions it is necessary to restrict the list of species used to those which geographical distribution is the most reliable. In the present study it was decided to restrict the range of the species used for regional comparisons to the families and genera considered reliable (Tab. I). The species lists for these families and genera for the 64 islands or regions considered in the present analysis were drawn from many different sources which are referenced in FAO (1998), Bellwood and Hughes (2001) and Randall (2005).

Endemism

A species is defined as endemic to an area if it is known only from that area. Within French Territories we considered endemism at the local level (areas defined in paragraph "Sites studied") as well as for the entire Territories. Only described species were considered in defining endemism rates. All undescribed species were excluded from estimates of endemism.

Factors

Four factors were used in analysing the distribution of species from the French Territories: 1. distance to the biodiversity centre; 2. island size; 3. latitude; 4. degree of isolation.

There is a general agreement on the existence of a centre of biodiversity for reef fishes in the Indo-Pacific (Bellwood and Hughes, 2001; Santini and Winterbottom, 2002; Briggs, 2003; Carpenter and Springer, 2005). However there is less agreement on where this centre is actually located (*ibid.*). For the purpose of our study, the precise location of this biodiversity centre is not really relevant, we essentially need to be able to grade the various islands and regions according to their distance to this centre. Therefore we chose arbitrarily to position this centre in Indonesia at: 0° x 117 W.

Island size is obtained either from national statistics, geographical atlases or from satellite image analyses. The major problem is to relate an island size with regions which can not really be considered as "islands". This in particular the case of the Great Barrier Reef, China sea, Papua or the largest islands of Indonesia. To try to take this problem into account, island size was considered on a log scale and for continental areas or the largest islands, land area was restricted to a 100 km wide costal strip.

The degree of isolation of an island or a region was estimated according to the following scale: 1. the island is more than 400 km from an island or archipelago which surface is over 100 km^2; 2. the island is between 200 and 400 km; 3: the island is between 100 and 200 km; 4: the island is less than 100 km.

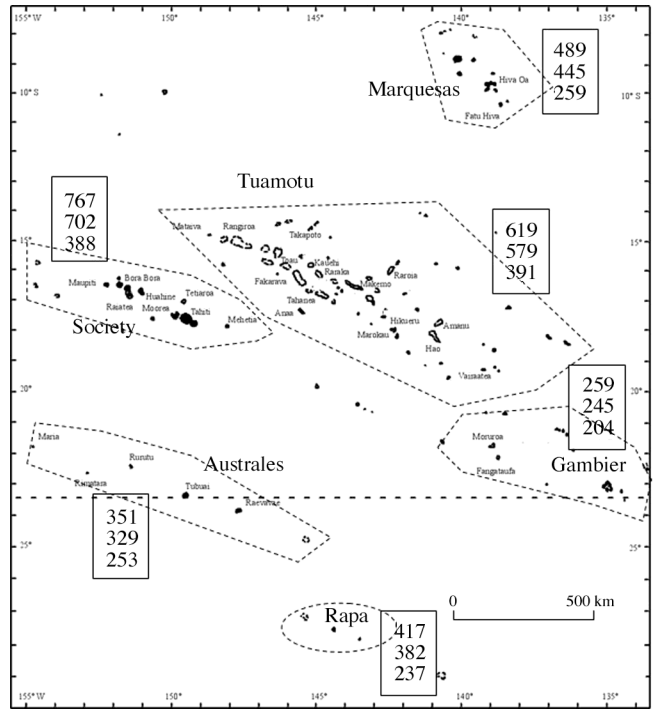

Figure 3. - French Polynesia and location of the six checklist areas and main islands. The numbers are from top to bottom: number of coastal species, number of reef species, number of reliable reef species. *[Polynésie française avec l'emplacement des six listes faunistiques et des îles principales. Les nombres sont, de haut en bas : le nombre d'espèces côtières, le nombre d'espèces récifales ; le nombre d'espèces récifales "fiables".]*

Table I. - Number of described species for the first 40 families in the three French Territories of the South Pacific. Families which name are followed by * are considered as "reliable" (see text). Families in bold are those for which the number of species decreases from New Caledonia to French Polynesia. Numbers in bold indicate families for which Polynesia has the highest diversity. Other reef fish families and genera considered as reliable in this work (alphabetical order): *Amblyeleotris* spp., *Amblygobius* spp., *Archamia* spp., *Aspidontus* spp., *Assessor* spp., *Bothus* spp., Centriscidae, Cheilodactylidae, *Cheilodipterus* spp., Dasyatidae, *Dendrochirus* spp., Diodontidae, Echeneidae, *Exallias* spp., *Fistularia* spp., Girellidae, Glaucosomatidae, *Gobiodon* spp., Hemiscyllidae, Heterodontidae, Kyphosidae, Labracoglossidae, *Meiacanthus* spp., Microcanthidae, Myliobathidae, *Neoniphon* spp., Oplegnathidae, Orectolobidae, Ostraciidae, *Pardachirus* spp., *Periophthalmus* spp., *Plagiotremus* spp., Plotosidae, *Pterois* spp., Rhinobathidae, Rhinopteridae, *Samaris* spp., *Sargocentron* spp., Scyliorhinidae, *Sphaeramia* spp., Sphyrnidae, *Stonogobiops* spp., Trichonotidae, Urolophidae, *Valenciennea* spp., Zanclidae. *[Nombre d'espèces décrites pour les 40 familles les plus importantes des trois territoires français du Pacifique sud. Les familles dont le nom est suivi par * sont considérées comme "fiables" (voir texte). Les familles en gras sont celles pour lesquelles le nombre d'espèces décroît de la Nouvelle Calédonie vers la Polynésie. Les nombres en gras indiquent les familles pour lesquelles la Polynésie comporte la diversité la plus élevée. Les autres familles et genres considérés comme "fiables" dans cet article sont par ordre alphabétique.]*

Family	NC-Total	Wallis	PF-Total	Family	NC-Total	Wallis	PF-Total
Gobiidae	162	59	82	Ophichtidae	16	12	**34**
Labridae*	110	56	83	Microdesmidae	14	8	12
Pomacentridae*	95	56	52	Mullidae*	14	7	14
Apogonidae	76	41	43	Monacanthidae*	14	5	10
Serranidae*	72	20	48	**Pseudochromidae**	13	7	2
Muraenidae	61	30	**62**	Synodontidae	12	2	6
Blenniidae	53	21	45	**Siganidae***	11	4	2
Scorpaenidae	48	16	31	Sphyraenidae*	11	1	4
Syngnathidae	43	8	20	Carcharhinidae*	11	1	10
Acanthuridae*	35	24	**36**	**Caesionidae***	11	6	2
Chaetodontidae*	32	30	**33**	Antennariidae	10	3	**11**
Tripterygiidae	28	5	10	Haemulidae*	10	1	2
Scaridae*	27	22	25	**Pinguipedidae***	9	4	2
Holocentridae	26	20	**30**	**Nemipteridae***	9	2	0
Carangidae*	25	6	16	Cirrhitidae*	8	4	**15**
Lutjanidae*	24	13	12	Malacanthidae*	7	2	3
Pomacanthidae*	19	8	14	**Plesiopidae**	6	2	1
Tetraodontidae*	19	8	15	Callionymidae	6	1	3
Lethrinidae*	18	6	10	Platycephalidae	6	1	3
Balistidae*	17	11	17	Carapidae	5	1	**7**

RESULTS

General description of the fish faunas

Within French Territories of the South Pacific, New Caledonia has the highest number of coastal fish species with 1,715 taxa known at present (Fig. 2). The number of reef affiliated species is 1,453 which represents 85% of the coastal species. Three areas in New Caledonia have received specific attention (Fig. 2): the Grande Terre (main island) with 1,579 coastal fish taxa of which 1,347 are reef affiliated (85%); Ouvea atoll with 676 coastal species, 648 of which are reef affiliated (96%) and the Chesterfield archipelago with 720 species of which 646 are reef affiliated (90%). These three areas have received very unequal sampling efforts, the Grande Terre being far more extensively sampled than the two others. It is difficult to assess the quality of the sampling but one way to evaluate this quality is to consider the ratio of the reliable reef species recorded for an area with the total number of reef fish species known in that area. The higher this ratio and probably the worst is the sampling in the area. For New Caledonia, the ratios are 54 % for the Grande Terre, 56% for the Chesterfield and 63% for Ouvea (Tab. II). The higher diversity of the Grande Terre is easy to explain by the great variety of habitat found around this island. The Chesterfield has also a very large area but a low number of habitats as there is almost no emerged land. Ouvea is intermediate with the presence of extensive mangroves and the proximity of the Grande Terre (60 km).

French Polynesia has a total of 1,024 taxa of coastal fishes of which 966 are reef affiliated (94%). The distribution of these species amongst the 6 areas of this region is indicated on figure 3. The highest number of reef fish species is known from the Society Islands (702) followed by the Tuamotu (579). The higher diversity of the Society Islands may be explained by: 1. the level of sampling being, much higher there than for the rest of French Polynesia; 2. the higher number of habitats in the Society Islands, in particular mangroves and important terrestrial inputs due to the presence of high islands and rivers in comparison to the Tuamotu, which are comprised only of atolls. The Marquesas have only 445 species. This low number is probably due to the isolation of this archipelago, the absence of lagoons and the relatively young geological age. Further south, Rapa has 382 species. This low number is explained by its isolation and high latitude. The Austral (329) and the Gambier Islands (245) have not been well explored, as indicated by the high values of

Table II. - Relative importance of the major "reliable" (see text) families for all the areas defined within the French Territories of the south Pacific. The last line indicates the ratio (%) of reliable reef species / all recorded reef species. *[Importance relative des principales familles "fiables" (cf texte) pour toutes les zones définies à l'intérieur des Territoires français du Pacifique sud. La dernière ligne indique le ratio (%) : espèces "fiables" / toutes les espèces répertoriées.]*

	Chesterfield	Grande Terre	Ouvéa	Society	Tuamotu	Marquesas	Australes	Gambier	Rapa	Wallis
Labridae	18.0	15.0	17.0	16.0	16.0	15.0	18.0	16.0	15.0	16.0
Pomacentridae	13.0	13.0	15.0	9.7	10.0	9.7	9.2	6.9	9.4	16.0
Acanthuridae	6.6	5.0	6.0	8.1	8.1	9.3	8.8	11.0	7.3	6.9
Chaetodontidae	6.1	4.6	7.4	7.3	7.3	6.1	8.8	6.9	9.4	8.6
Serranidae	5.6	7.3	7.4	6.8	7.0	6.1	6.8	5.4	6.4	4.6
Scaridae	5.4	3.9	4.8	5.2	5.5	2.4	4.8	6.4	7.7	6.3
Carangidae	2.6	3.6	2.6	3.7	3.6	4.5	4.8	3.9	5.1	1.7
Lutjanidae	2.8	3.5	3.3	2.9	2.3	3.2	3.6	3.4	2.1	3.7
Balistidae	2.3	2.4	2.4	3.9	3.6	4.5	2.4	3.9	3.4	3.1
Mullidae	2.6	2.0	3.1	2.6	3.1	4.0	3.6	3.9	3.4	2.0
Pomacanthidae	2.8	2.6	3.1	3.4	2.9	1.2	2.4	2.9	3.0	2.3
Lethrinidae	3.3	2.4	3.8	2.6	2.3	2.4	1.2	2.5	1.7	1.7
Tetraodontidae	2.0	2.6	1.4	2.9	2.6	2.4	2.0	3.4	2.1	2.3
Cirrhitidae	1.0	1.2	1.4	2.3	3.6	2.8	2.4	2.9	2.6	1.1
Carcharhinidae	1.8	1.6	1.4	2.3	2.6	3.2	2.8	3.4	0.9	0.3
Monacanthidae	2.3	1.9	1.4	1.8	2.3	1.6	0.8	1.0	1.7	1.4
Caesionidae	1.5	1.3	2.4	0.5	0.5	0.8	0.4	0.5	0.4	1.7
Kyphosidae	0.5	0.4	0.2	0.8	0.8	2.0	2.4	1.0	1.3	0.3
Siganidae	0.5	1.6	0.7	0.5	0.5	0.4	0.8	0.5	0.4	1.1
Ratio reliable/all (%)	56.0	54.0	63.0	55.0	63.0	57.0	77.0	83.0	62.0	56.0

their "reliable/all" species ratio (77% and 83% respectively) and therefore their present diversity is probably a considerable underestimate of their true diversity.

Wallis is the only island for which coastal fish diversity has been assessed in the Wallis-Futuna group. The present figure is of 636 coastal species of which 611 (96%) are reef affiliated. This island has been probably relatively well explored as indicated by the low "reliable/all" species ratio (56.0%).

Major families

The major families are essentially the same for all three territories (Tab. I). For most families New Caledonia has the highest diversity followed by French Polynesia, then Wallis. This order is due to a combination of factors, which will be analysed further, in particular New Caledonia being closer to the biodiversity centre, Wallis is a small and isolated island, French Polynesia is far from the diversity centre and constituted of small islands. For several families there is a drastic decrease from New Caledonia to French Polynesia, this in particular the case for the Siganidae, Plesiopidae, Caesionidae, Haemulidae and Pseudochromidae. These families are associated to either strong terrestrial influence or to the distance to the biodiversity centre.

However there are a number of families for which there is a higher diversity in French Polynesia. This is the case in particular for anguilliform fishes (Muraenidae and Ophichthidae) which have leptocephalae larvaes and for the Cirrhithidae.

Within New Caledonia there is surprisingly little difference amongst the three sampling areas for the relative importance of the major reliable families (Tab. II). The exceptions are the Chaetodontidae which are relatively less diverse on the Grande Terre, the Carangidae and the Siganidae which are relatively more diverse on the Grande Terre. In French Polynesia the major differences are for Scaridae which are less important in the Marquesas than elsewhere and the Carangidae which tend to be relatively more diverse on the isolated archipelagos (Marquesas, Australes, Gambier, Rapa). One may also notice the low importance of Carcharhinidae on Rapa, an isolated island, the same observation being true for Wallis.

Similarity

One characteristic of reef fishes in the Indo-Pacific is the large geographical range of many species. This results in a very high similarity between islands in the tropical Pacific. The similarity of the French Territories will be analysed at several levels: 1. with the other islands of the Pacific; 2. amongst territories; 3. within each territory.

With other islands of the Pacific

This analysis is based only on the reliable reef species. The species composition is available for 64 islands or regions in the tropical Pacific. A cluster analysis using Pearson "r" distance and Ward's aggregation procedure (Legendre and Legendre, 1998) on this species composition allowed to classify these islands or regions into 9 groups that

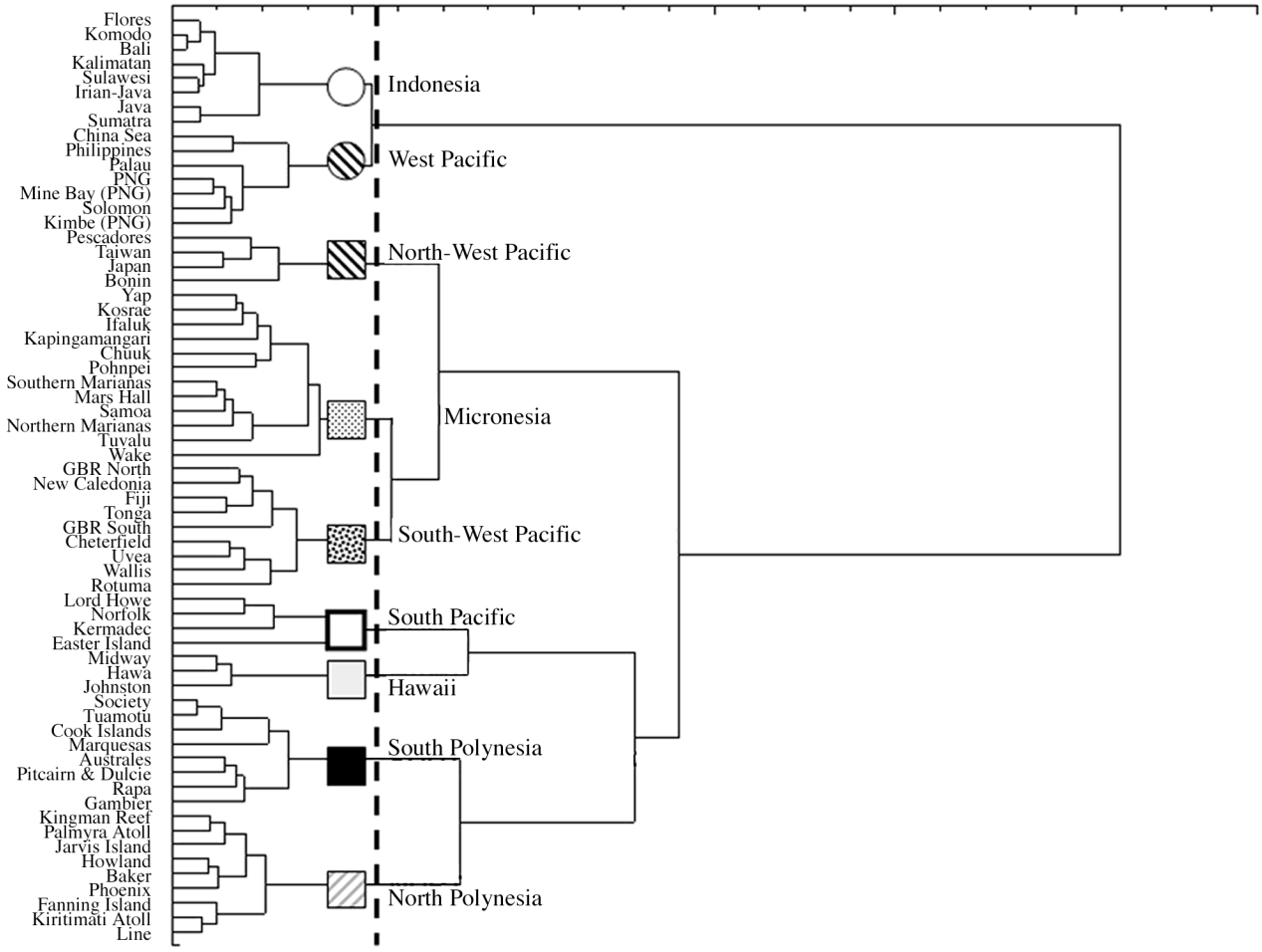

Figure 4. - Cluster analysis (Ward's aggregating method; Pearson's r) of 64 islands and regions of the tropical Pacific according to the composition of their reef reliable fish fauna. *[Analyse hiérarchique (méthode d'agrégation de Ward ; distance : r de Pearson) de 64 îles et régions du Pacifique tropical en fonction de la composition de leur faune en espèces "fiables" de poissons de récif.]*

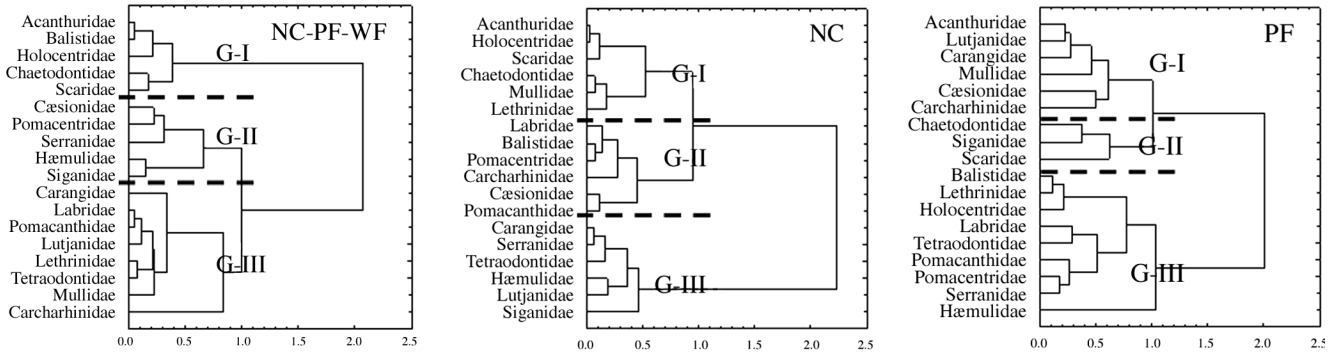

Figure 5. - Grouping of the major reliable reef fish families according to their similarity. NC: New Caledonia; PF: French Polynesia; WF: Wallis and Futuna. The clusterings were performed using the Ward's aggregation and Euclidian distances based on data from table 3. G-I, G-II, G-III indicate the group number. *[Groupement des principales familles de poissons de récif fiables en fonction de leur similarité. NC : Nouvelle-Calédonie ; PF : Polynésie française ; WF : Wallis et Futuna. Les analyses hiérarchiques ont été réalisées avec la méthode d'a - grégation de Ward et des distances euclidiennes et sur les données du tableau 3. G-I, G-II, G-II indique le numéro de chaque groupe.]*

Table III. - Similarity between regions and areas for the major reliable families. Similarity S between 2 areas was estimated by S = C / (A + B - C) where A: species of area A; B: species of area B; C: species in common between the two areas. *[Similarité entre régions et zones pour les principales familles "fiables". La similarité S entre deux zones est estimée par S= C/ (A + B - C) où A : espèces de la zone A ; B : espèces de la zone B ; C : espèces communes aux deux zones.]*

	NC-PF	NC-Wallis	PF-Wallis	Grande Terre-Uvea	Grande Terre-Chesterfield	Ouvea-Chesterfield	Society-Tuamotu	Society-Marquesas	Society-Australes	Society-Rapa	Society-Gambier
Acanthuridae	0.65	0.64	0.58	0.71	0.74	0.70	0.82	0.69	0.66	0.45	0.66
Balistidae	0.70	0.65	0.56	0.59	0.53	0.73	0.93	0.63	0.40	0.44	0.53
Caesionidae	0.18	0.55	0.14	0.73	0.67	0.45	1.00	1.00	0.50	0.50	0.50
Carangidae	0.58	0.24	0.38	0.44	0.40	0.40	0.87	0.79	0.73	0.63	0.57
Carcharhinidae	0.75	0.09	0.10	0.55	0.64	0.86	0.90	0.89	0.78	0.22	0.78
Chaetodontidae	0.63	0.88	0.70	0.97	0.75	0.72	0.93	0.48	0.67	0.67	0.50
Haemulidae	0.20	0.10	0.50	0.50	0.30	0.60	0.50	0.00	0.50	0.50	0.00
Holocentridae	0.51	0.59	0.61	0.73	0.77	0.70	0.87	0.58	0.48	0.46	0.41
Labridae	0.43	0.47	0.48	0.62	0.63	0.62	0.67	0.47	0.64	0.37	0.43
Lethrinidae	0.47	0.33	0.45	0.94	0.67	0.61	0.90	0.60	0.30	0.40	0.50
Lutjanidae	0.44	0.48	0.56	0.58	0.46	0.56	0.67	0.73	0.82	0.45	0.64
Mullidae	0.56	0.50	0.40	0.93	0.71	0.77	0.69	0.82	0.73	0.80	0.80
Pomacanthidae	0.43	0.42	0.47	0.63	0.61	0.50	0.85	0.23	0.36	0.43	0.46
Pomacentridae	0.29	0.51	0.33	0.62	0.56	0.63	0.85	0.36	0.50	0.40	0.31
Scaridae	0.73	0.75	0.68	0.74	0.78	0.78	0.71	0.24	0.52	0.81	0.65
Serranidae	0.29	0.26	0.24	0.49	0.37	0.42	0.70	0.29	0.44	0.37	0.31
Siganidae	0.18	0.25	0.50	0.27	0.18	0.67	1.00	0.50	1.00	0.05	0.50
Tetraodontidae	0.48	0.35	0.53	0.33	0.37	0.40	0.62	0.42	0.45	0.33	0.64

	New Caledonia 70 endemics			Wallis 0	French Polynesia 60 endemics					
	Grande Terre	Ouvea	Chesterfield	Wallis	Society	Tuamotu	Marquesas	Australes	Rapa	Gambier
Endemic	40	8	9	0	6	2	37	2	9	0
	53	12	17	0	10	5	39	4	10	0
Undescribed	73	5	17	5	9	3	17	2	7	1
	93	3	36	5	14	7	21	4	9	1

Table IV. - Number of endemic and undescribed coastal fish species for the French Territories of the south Pacific. For each category (endemic ; undescribed) the first line corresponds to the area level and the second line to the region level. *[Nombre d'espèces endémiques et non décrites de poissons côtiers dans les Territoires français du Paci - fique sud. Pour chaque catégorie (endémique, non décrite) la première ligne correspond au niveau local et la seconde ligne au niveau régional.]*

we will name "biogeographical regions" for reef fishes (Figs 1, 4). New Caledonia and Wallis are part of the "south-west Pacific" biogeographical region which groups in particular the Great Barrier Reef, Fiji and Tonga. French Polynesia is part of the "south Polynesia" biogeographical region, which also includes Pitcairn and Dulcie as well as the Cook Islands.

Amongst territories

The similarities for the global fish species composition is given by the clustering (Fig. 4). Chesterfield, Ouvea and Wallis are very similar in the composition of their reliable reef fishes and close to Grande Terre ("New Caledonia" on figure 4). French Polynesian territories are well separated from both New Caledonia and Wallis.

The similarities for the major families (Fig. 5A) show that one may cluster families into three groups. The first group comprises families with very high similarities between the various territories (Tab. III). The similarities amongst territories are homogeneous within these families. The second group is made of families with the lowest similarities, each of these families, except the Serranidae, having however a higher similarity for one of the three comparisons, e.g. there was a much higher similarity between Wallis and Polynesia than between Wallis and New Caledonia for Haemulidae and Siganidae (Tab. III), whereas the Pomacentridae and Caesionidae were more similar between New Caledonia and Wallis. The third group is made of families with intermediate similarities, homogeneously distributed across territories, except for Carangidae which display a higher similarity between New Caledonia and French Polynesia.

Within territories

The three areas of New Caledonia display the same overall similarity level between one another (0.45 for Grande Terre-Ouvea and Grande Terre-Chesterfield; 0.51 for Ouvea-Chesterfield). When comparing these three areas the major reliable reef fish families may be clustered into three groups

(Tab. III; Fig. 5B). The first group has the highest similarity. Chaetodontidae, Lethrinidae and Mullidae have a higher similarity between Grande Terre and Ouvea, the Chesterfield Islands having less species for these three families. The similarities of the other families within this group are very close. The second group of families is characterised by lower similarity values than group I. Balistidae and Carcharhinidae display the highest similarity between Ouvea and the Chesterfield, these two areas having slightly more than half the species for these families than in Grande Terre. The difference is due to species linked to terrestrial inputs or/and large islands. The other families in this group display very close similarities amongst areas, except Caesionidae which have a higher similarity between Ouvea and Grande Terre, the diversity of these fishes being associated to large land masses. The last group has the lowest similarities. Siganidae and Haemulidae, two families associated with large islands have low similarities between either Ouvea or Chesterfield with Grande Terre, Ouvea and Chesterfield having a low number of species within these two families. The other families within group III have comparable similarities amongst areas.

In French Polynesia the Society Islands and Tuamotu have the closest overall species composition (Fig. 4), the Marquesas being the next closest area, Rapa, the Austral Islands and Gambier Islands making a group of southern islands. The comparisons amongst families were performed with the Society Islands as the pivot point (Tab. III; Fig. 5C).

Table V. - Regression model for the total number of reef fish species according to distance to the biodiversity centre, island size, degree of isolation and latitude; p = probability of rejecting H0 of no effect of the factor; C.I.: confidence interval; *: observed value not within CI. Number of reef species = 1619.3 - 0.0452 DCB + 0.00051 IS - 837 DI1 - 528 DI2 -461 DI3. Where DCB = distance to the biodiversity centre (km); p = 0.0233; IS: island size (km^2); p = 0.0299; DI1 = degree of isolation 1 (see methods); p = 0.000009; DI2 = degree of isolation 2; p = 0.00341; DI3 = degree of isolation 3; p = 0.0169. *[Régression du nombre total d'espèces de poissons de récif en fonction de la distance au centre de biodiversité, de la taille de l'île, du degré d'isolement et de la latitude ; p = probabilité de rejeter H0 de l'absence d'effet d'un facteur ; C.I. : intervalle de confiance ; * : valeur observée hors de l'intervalle de confiance. Nombre d'espèces récifales = 1619,3 - 0.0452 DCB + 0,00051 IS - 837 DI1 - 528 DI2 -461 DI3. Où DCB : distance au centre de biodiversité (en km) ; p = 0,0233 ; IS : taille de l'île (km^2) ; p = 0,0299 ; DI1 : degré d'isolement 1 (voir méthodes) ; p= 0,000009 ; DI2 : degré d'isolement 2 ; p = 0,00341 ; DI3 : degré d'isolement 3 ; p = 0,0169.]*

	Observed	Predicted	95% C.I.
Grande Terre	1581	1333	1059-1607
Chesterfield *	720	521	366-676
Ouvea	676	791	526-1056
Wallis	636	816	622-1009
Society	767	682	470-893
Tuamotu	619	657	436-879
Marquesas *	489	263	82-445
Australes	351	299	138-459
Rapa	417	267	89-446
Gambier *	259	603	355-851

The first group has the highest similarities. In this group Carcharinidae, Lutjanidae and Acanthuridae have the lowest similarity between Society and Rapa, probably showing an effect of latitude on the distribution of these species. The second group has intermediate similarity values, the Marquesas having consistently the lowest values, in particular Chaetodontidae and Scaridae are less diverse in this area than elsewhere in French Polynesia. The third group has the lowest values of similarity. The Tuamotus have consistently the highest similarity with the Society Islands for all families within this group. The Marquesas display the lowest values for Serranidae and Pomacanthidae, the first family having a combination of low diversity and strong endemism and the second family having a particularly low diversity (3 species out of 14 known from French Polynesia).

Endemism

There are a total of 70 described coastal fish species which are found only in New Caledonia. This represents 4.37% of the described species for New Caledonia (Tab. IV). The Grande Terre has a much larger number of endemic species, with 53 species New Caledonian endemics (3.3% of described species from Grande Terre) and 40 species restricted to Grande Terre (2.5%), whilst Ouvea and the Chesterfields have only 12 (1.8%) and 17 (2.5%) New Caledonian endemics respectively with 8 species restricted to Ouvea (1.2%) and 9 species restricted to the Chesterfield (1.3%). The main families of endemics in New Caledonia are Gobiidae (13 species), Syngnathidae (7 species), Apogonidae (5 species) and Blenniidae (5 species).

There is are no endemic species known to date from Wallis and Futuna (Tab. IV).

There are at present 60 described coastal species known only from French Polynesia (Tab. IV), which represents 6.1% of described coastal species. The Marquesas Islands have a much higher rate of endemism (8.3% of species restricted to French Polynesia; 7.9% of species restricted to the Marquesas) than the other areas of French Polynesia. Rapa follows with an endemism from 2.5% (species restricted to Polynesia) to 2.2% (species restricted to Rapa) followed by the Society (1.9%; 1.2%), the Tuamotu (1.1%; 0.5%), the Australes (1.1%; 0.6%) and Gambier (0.4%). The major families of endemics are Pomacentridae (9 species), Gobiidae (7 species), Apogonidae (5 species), Blenniidae (5 species), Ophichtidae (5 species) and Labridae (5 species).

Besides described endemic species there are many undescribed species in museum collections known from the French Territories in the south Pacific. These species, as long as they are not described can not be considered as endemic, but in general the rate of endemism in such species is high. An account of the number of these species is given in table IV. This account is certainly far from complete as we did not check for all known collections from these regions, but it

Table VI. - Correlation coefficient r between total diversity and the relative importance of the 17 major reliable reef fish families in the tropical Pacific. Families are ordered according to the level of the correlation. NS: not significant; ** p < 0.01; *** p < 0.001. *[Coefficient de corrélation r entre la diversité totale et l'importance relative de 17 familles de poissons "fiables" dans le Pacifique tropical. Les familles sont rangées par niveau de corrélation. NS : non significatif ; ** : p < 0,01 ; *** p < 0,001.]*

Family	r	Family	Family	Family	Family
Mullidae	-0.77***	Pomacanthidae	-0.40***	Lethrinidae	0.05 NS
Chaetodontidae	-0.73***	Serranidae	-0.36**	Caesionidae	0.15 NS
Labridae	-0.70***	Tetraodontidae	-0.23 NS	Siganidae	0.31**
Acanthuridae	-0.67***	Pomacentridae	-0.17 NS	Haemulidae	0.67***
Balistidae	-0.62***	Monacanthidae	-0.14 NS	Nemipteridae	0.79***
Scaridae	-0.53***	Lutjanidae	0.03 NS		

gives a first proxy of what needs to be described. The number of undescribed species is much higher in New Caledonia (113 taxa) than in French Polynesia (44) or Wallis (5). The numbers within each area are in general proportional to the level of endemism, with for instance the highest numbers for Grande Terre and the Chesterfield in New Caledonia, or the Marquesas followed by the Society and Rapa in French Polynesia (Tab. IV). The families with the highest numbers of undescribed species are the Gobiidae (37 species for New Caledonia; 13 for French Polynesia; 2 for Wallis), the Muraenidae (11 for New Caledonia, 1 for French Polynesia), the Plesiopidae (7 in New Caledonia), the Apogonidae (5 for French Polynesia) and Pomacentridae (4 for French Polynesia; 2 for New Caledonia).

Table VII. - Effects of four factors on the family structure (major reliable reef fish families) of 64 islands or regions of the tropical Pacific. The number in each cell indicates the rank of the factor in the analysis. (-) indicates that the factor is negatively correlated. (+) indicates that the factor is positively correlated. NS: not significant; * p < 0.05; ** p < 0.01; *** p < 0.001. *[Effets de quatre facteurs sur la structure des peuplements (principales familles "fiables" de poissons de récif) de 64 îles ou régions du Pacifique tropical. Le nombre dans chaque cellule indique le rang du facteur dans l'analyse. (-) indique que le facteur est corrélé négativement. (+) indique que le facteur est corrélé positivement. NS : pas d'effet significatif ; * p < 0,05 ; ** p < 0,01 ; *** p < 0,001.]*

Family	Distance to B.C.	Island size	Isolation	Latitude	R^2
Haemulidae	1*** (-)	NS	NS	2*** (+)	0.72
Nemipteridae	1*** (-)	2*** (+)	NS (-)	NS	0.80
Siganidae	1*** (-)	NS	2**	NS	0.40
Lethrinidae	1* (-)	NS	NS	NS	0.07
Labridae	NS	1*** (-)	NS	NS	0.51
Scaridae	NS	1*** (-)	3* (-)	2** (-)	0.44
Acanthuridae	3** (+)	1*** (-)	NS	2*** (-)	0.62
Chaetodontidae	NS	1*** (-)	NS	NS	0.43
Mullidae	NS	1*** (-)	2* (+)	NS	0.56
Serranidae	NS	1*** (-)	NS	2** (-)	0.27
Pomacanthidae	NS	1*** (-)	NS	NS	0.23
Balistidae	3** (+)	1*** (-)	NS	2*** (-)	0.61
Monacanthidae	NS	NS	1** (+)	NS	0.15
Pomacentridae	NS	2** (-)	NS	1*** (-)	0.35
Lutjanidae	NS	NS	NS	1*** (-)	0.19
Tetraodontidae	NS	NS	NS	1** (+)	0.10
Caesionidae	2*** (-)	NS	3* (-)	1*** (-)	0.43

Factors affecting diversity

Total diversity

The four selected factors were tested on the diversity of the 64 checklists from the tropical Pacific we have available in order to identify which factors may be the most influent to explain the diversities observed within the French Territories. The relationship between the total number of reliable reef fish species and these four factors was evaluated using a forward stepwise multiple regression (Statistica VI software) with three factors taken as continuous variables (distance to the biodiversity centre, island size, latitude) and one factor taken as categorical (degree of isolation). The model is given in table V. The degree of correlation is significant ($r^2 = 0.74$; $N = 64$; $p < 10^{-6}$), the most significant variable being the degree of isolation followed by the distance to the biodiversity centre and by island size, latitude not being significant. The number of reef species decreases with the distance to the biodiversity centre and degree of isolation and increases with island size. The previsions of the model for the French Territories are given in table V. As only 74% of the variance is explained by the factors available, the differences between observed and expected values are at times important. The largest variations occur for the Chesterfield, Marquesas, Rapa and Gambier, with only the latter having a higher predicted value than the one observed.

Major families

Bellwood and Hughes (2001) tested the relationship between total diversity and the relative importance of various major reef fish families for 60 islands or regions distributed across the entire Indo-Pacific. They did so because, as we just did, they found that several factors affected total diversity and therefore they thought that this variable could be a good proxy of the influence of these factors on the composition of checklists across the zone studied. These authors found that at the level of the entire Indo-Pacific the relationship between total diversity and the relative diversity of the major reef fish families was constant when total diversity was over 200 species. Our results do not suggest such constancy when the relationship is restricted to the tropical Pacific and therefore we tested the significance of this relationship for the most important reliable reef fish families (Tab. VI).

One way to consider the structure of species composition is to analyse the relative importance of the major families (Tab. II). The same factors play a significant role as for total diversity (Tab. VII), however the role of each factor changes with families.

Haemulidae, Nemipteridae, Siganidae and Lethrinidae are first influenced by the distance to the biodiversity centre. This relation is negative for these families, thus indicating that their relative importance in meta-populations decreases as the distance to the biodiversity centre increases. These families will therefore be more important in New Caledonia than in Wallis or French Polynesia. A majority of families (Labridae, Scaridae, Acanthuridae, Chaetodontidae, Mullidae, Serranidae, Pomacanthidae, Balistidae) are first influenced by island size, their relative importance decreasing as island size increases. These families will therefore tend to be more important on the small islands of Polynesia than on the larger islands of Grande Terre, of the Society or Marquesas. For several of these families (Acanthuridae, Balistidae, Scaridae, Serranidae), latitude is also a significant negative factors, which means that their relative importance is highest near the equator. The degree of isolation is the main factor only for Monacanthidae, this family having an increasing importance on isolated islands. This factor is otherwise not often significant. Latitude is the major factor for Pomacentridae, Lutjanidae, Tetraodontidae and Caesionidae, the importance of these families decreasing as distance from the equator increases, except for the Tetraodontidae for which the opposite trend is observed. These families will therefore have a larger contribution to the meta-populations in Polynesia and Wallis than in New Caledonia, and more in the Marquesas, Society Islands and Tuamotu than in Rapa and the Austral or Gambier Islands.

DISCUSSION

Knowledge level

The level of knowledge in the South Pacific is far from homogeneous and in particular, sampling in the French Territories is very unevenly distributed.

In New Caledonia most of the sampling has taken place around the main city, Noumea, and its surrounding lagoon. In particular there have been numerous expeditions to collect fishes on reefs, mangroves and, shore line, sea-grass and, algae beds and soft bottoms. Elsewhere collections are scattered, with fish caught by trawling and line fishing in the North part of the main island, some reef sampling by rotenone along the East coast and the Isle of Pine and underwater observations and pictures from most reefs around Grande Terre. Recently Conservation International conducted a fish diversity survey in the northeast part of the main island, reporting more than 600 reef species in two weeks sampling (unpublished). Therefore very large expenses of the main island of New Caledonia remain unexplored. A recent workshop held by WWF pointed to the absence of collection on the outer slopes of most of the barrier reef, the very poor knowledge of remote areas such as Surprise and Huon atolls or the North of the main island (e.g. Balabio Island or the Diahot estuary) as well as the Isle of Pines. It is therefore likely that the number of species for Grande Terre is well underestimated. Recent surveys by underwater visual censuses on the East coast of the Grande Terre have indicated nearly 30 species of reef species which were not known to occur elsewhere in New Caledonia, but are recorded from nearby Vanuatu. At present it is difficult to say if such observations are the result of the real absence of these species on the West coast or if these species have not been recorded on the West coast due to insufficient sampling. Ouvea atoll has been the object of one major sampling campaign (Kulbicki and Williams, 1997). However, this campaign did not explore the outer slopes of this island, nor its mangroves. It is likely that the major species from Ouvea are known, but there could remain a large proportion of small species to record, probably several hundred species. The Chesterfields have been little explored with the exception of one major cruise in 1988 (Kulbicki *et al.*, 1994). During that cruise only a small proportion of that archipelago was explored, representing probably less than 5% of the reef areas. The Chesterfields present some remarkable but still unexplored features, such as pinnacles rising from more than 50 m to near the surface. The southern part of this archipelago (Bellona) is subject to colder waters and could have a very different fish fauna, being at the convergence of the tropical and subtropical faunas. It is therefore likely that the checklist for the Chesterfield area is the least complete for the three available for New Caledonia.

Wallis has been only very recently explored. A major expedition was conducted there in 2000 (Williams *et al.*, 2006) Since then several underwater visual surveys (Wantiez, unpublished) and larval collecting (Juncker, 2005) have been performed but the new species found during these works are not yet available. The island of Wallis is fairly isolated and its reef system is not very complex, therefore the checklist available is probably a fairly good picture of the species easily collectable. Around Wallis there are a number of sea mounts which reach almost the surface. They are at present unexplored and the same is true for Futuna and Alofi, two isolated islands surrounded by a narrow fringing reef.

In French Polynesia the situation is complex as the number of islands is very large and scattered over a huge EEZ of 5,030,000 km^2. The Society have received the most attention (Randall, 1985; Randall *et al.*, 2002). A recent survey (April 2006) collected nearly 500 species on the island of Moorea, but the list of these species is not yet available. Most other sites in French Polynesia have not been the object of specific collecting with the exception of Rapa (Galzin *et al.*, 2006). Compared to New Caledonia, which has a wide variety of coastal habitats, French Polynesia has a rather low number of habitats and therefore a lower sampling effort should be sufficient to reach a similar level of information than would

be required for New Caledonia. Outer barrier reefs, as in most islands of the Pacific, are probably the least explored habitats in French Polynesia. Lagoon habitats (fringing reefs, pinnacles, lagoon bottoms, and mangroves,…) are probably rather well explored as they are known to show little variability amongst islands in their species composition according to visual censuses (Kulbicki *et al.*, 2000). Two regions, the Austral and Gambier Islands are much less explored than the other areas of French Polynesia as indicated by their high ratio of "reliable/all" species (Tab. II). The Gambier Islands (Andrefouet *et al.* 2005) combine both high islands and atolls and therefore have a larger range of habitats than the Tuamotu and hence could harbour species absent from the latter. The Austral have no atolls but a larger number of habitats than Rapa (*ibid.*) and therefore could host at least as many species since they are at a higher latitude and are less isolated. The Marquesas have very little coral reefs as they are rather young from a geological point of view and few other habitats are found around these islands which may explain a rather low number of species compared to the nearby Tuamotu. The Marquesas are also difficult to explore due to their isolation and to the lack of good anchorage.

The number of undescribed species is rather important in all French Territories of the Pacific (Tab. IV) the proportion being 7.8% for New Caledonia and 4.4% for French Polynesia. However this is comparable to most of the tropical Pacific with the exception of Japan (1.4%) and Hawaii (1.1%). The families with the highest proportion of undescribed species are the Gobiidae, Trypterigiidae, Apogonidae, Labridae, and anguilliform fishes. All these species tend to be cryptic, except the Labridae, and most are small, except the anguilliform fishes. It is likely that most species left to be described in the French Territories of the Pacific are small or live hidden in the reef matrix.

Factors influencing species distribution in the French Territories

Overall diversity

The distribution of reef fishes in the Pacific has been the object of much research (e.g. Springer and Williams, 1990; Randall, 1998; Bellwood and Hughes, 2001; Connolly *et al.*, 2003; Carpenter and Springer, 2005). These studies indicate that there is an area called a biodiversity centre, located depending authors between Indonesia, the South China Sea and the Philippines, which harbours the highest number of species in the Pacific. The number of species in an island tends to decrease as the distance to this biodiversity increases (Bellwood and Hughes, 2001). The same authors have indicated that the number of species tends to increase as island size increases as suggested also by theory (McArthur and Wilson, 1967; Hubbell, 2001) and as one gets closer to the equator. The present study, based only on the reef fish species for which the geographical distribution is the most reliable, shows that: 1. in addition to the factors already analyzed in the literature, island isolation is also a significant factor, which can be related to the theory of island biogeography (McArthur and Wilson, 1967) or the "unified neutral theory" of Hubbell (2001); 2. the importance of these factors could be ranked, the order of significance in our model being island isolation, distance to the biodiversity centre and island size. Latitude, when the three previous factors are taken into account is not significant, but taken alone would be significant. The purpose of our article is restricted to the species of the French Territories and therefore only the implications of these findings to the diversity of reef fishes on these territories will be discussed. The much larger number of species found in New Caledonia can be related to the closer distance of this archipelago to the biodiversity centre compared to Polynesia. Within New Caledonia the much lower diversity found on Ouvea, despite its proximity of Grande Terre, is certainly due in part to its much smaller size (130 km^2 *vs* 12,000 km^2) and the lower number of habitats (no river on Ouvea and therefore very little terrigenous inputs). The Chesterfields have little land area. Their low number of species compared to Grande Terre is probably due to a combination of isolation and low number of habitats, in particular the absence of mangroves. Our model (Tab. V) does not account well for the number of species found in the Chesterfield, the confidence interval of the model not including the observed number of species of this archipelago. The larger number of observed species could be due to the presence of a very large underwater plateau which constituted a very large island (approximately 5,000 km^2) during the last glaciations and could have been a merging point of fish fauna coming from both the Great Barrier Reef and New Caledonia. Wallis, compared to nearby Fiji (1,455 species) or Samoa (975 species) has a low number of species probably because of its small size and its isolation. French Polynesia has a lower number of species compared to New Caledonia due to its greater distance to the centre of biodiversity (1,000 km on average compared to 6,500 km) and also the smaller size of its islands. Within French Polynesia the number of species for each area is a combination of island size, isolation and latitude. Thus, the Tuamotu have fewer species than the Society Islands since they are made of atolls which have less land area than the high islands of the Society Islands and mostly fewer types of habitats. The Marquesas have fewer species because of their isolation and the low development of reefs as these islands are geologically young. However the observed number of species is significantly higher than what is predicted by our model (Tab. V). The reasons for these differences are unknown, but maybe the Marquesas are a zone of species accumulation as attested in part by its high degree of endemism. Rapa, and the Austral and Gambier Islands are at a higher latitude (700 to

1,200 km further south than the Society) and are more isolated, especially Rapa. The Gambier Islands have significantly fewer species than predicted by our model (Tab. V). The low level of exploration of this archipelago is one reason for such differences but considering the magnitude of this difference it is likely than other reasons come into play. If one attributes the largest degree of isolation to the Gambier, then the observed values fit with the prediction of the model (227 species predicted). This could suggest that some physical feature (e.g. oceanic current patterns) tends to create a greater isolation for these islands than what is directly observable.

Major families

Bellwood and Hughes (2001) predicted that the relative importance of the major reef fish families should be constant or nearly so for all islands in the Indo-Pacific where total diversity exceeds 200 species. Our data (Tabs VI, VII) as well as a previous study on the species from New Caledonia (Kulbicki and Rivaton, 1997) clearly indicate that this finding does not apply when the study is restricted to the tropical Pacific. The reasons for this difference are beyond the scope of the present article, but it has major implications in explaining the distribution of the major families amongst the French Territories in the Pacific. Thus our model (Tab. VII) indicates that the importance of Haemulidae, Nemipteridae and Siganidae in New Caledonia is easily explained by the proximity of this region to the biodiversity centre. For Nemipteridae and Siganidae differences within New Caledonia (Grande Terre has higher proportions of these families) are explained by the influence of island size (Nemipteridae) and isolation (Siganidae). A large number of families are influenced primarily by island size (Tab. VII). This explains in part the differences observed in table II for the relative importance of these families amongst the regions studied. In particular families such as Acanthuridae, Scaridae and Chaetodontidae tend to make a larger contribution to diversity in the smallest islands.

Similarities

Most reef associated species have a wide geographical distribution in the Indo-Pacific (Randall, 1998), which is reflected in a high similarity in the species composition of reef fish assemblages from islands wide apart (Letourneur *et al.*, 1997; Harmelin-Vivien, 1989). The present study confirms this trend with high similarities being observed between the French Territories of the Pacific (Tab. II). Our definition of biogeographical regions (Figs 1, 4) allows us to better understand the distribution of these similarities. Thus New Caledonia and Wallis are part of the same biogeographical region. This region extends from the Great Barrier Reef to the limit of the West Pacific tectonic plate. The similarity within this region is probably linked to its geological history. One notices in particular that islands close to New Caledonia, such as Lord Howe or Norfolk in the south or the Solomon Islands in the north show less similarity with New Caledonia than with Wallis despite the latter being more distant.

Similarly that all French Polynesian islands belong to a single biogeographical region is probably related to the nature of these islands (most of them are atolls) and their similar geological genesis (all islands in South Polynesia are of volcanic origin). However geologic age and origin are not sufficient to define a region, as the north Polynesian region (Line Islands, Phoenix, Tuvalu,…) have a great similarity in their geological age and origin with South Polynesia.

Within each region, the similarities between areas (Tab. III) can in great part be explained by the effects of large scale factors on family distribution (Tab. VII). However these factors alone are not sufficient to explain some values, such as for instance the low similarities observed between the Society and the Marquesas for several families (e.g. Pomacentridae, Pomacanthidae, Scaridae, Serranidae). The factors behind the distribution of reef fish species across the Pacific are still little understood. The duration of larval life is one of the potential factors (Mora *et al.*, 2003), but this duration is at present known for only a limited number of species and in a limited number of areas. The large scale factors we studied (distance to the biodiversity centre, island size and isolation, latitude) have all an influence on larval dispersion and colonisation. Therefore if one wishes to better understand the similarities between islands it is likely that much more work is required on the larval characteristics of reef fishes.

Endemism

Endemism is difficult to define as it depends on the level of knowledge and the area considered. With the increase in fish sampling in the Pacific, our level of knowledge has dramatically increased in the last 30 years. This is attested by the decrease over time in the number of endemic species recognised for Hawaii (Randall, 1992; Kulbicki and Rivaton, 1997). This means that the level of endemism described in this article for the French Territories is likely to evolve, with probably lower rates as our knowledge level progresses. In the French Territories, the Marquesas are an exception, with a much higher proportion of endemic species than elsewhere. This makes this archipelago the third in endemism rate in the Pacific after Easter Island (20.3%) and Hawaii (17.5%). The reasons for this high rate of endemism are not well-known. Of course the Marquesas are isolated and are the last islands of a chain of islands, but other islands in the same situation such as the Line Islands have a very low level of endemism. The Marquesas, as Hawaii and Easter Island are geologically very young, which could be a factor which

interacts with isolation. The Grande Terre is second in endemism rate with 2.5%. This is not a high rate, but it represents more endemic species (40) than for the Marquesas (37). Grande Terre occupies a special place in the South Pacific, being at the convergence of two potential colonisation routes: 1. PNG-Solomon-Vanuatu-Grande Terre; 2. PNG-GBR-Chesterfield-Grande Terre. It should be reminded that during the last glaciations the sea level was much lower than at present and that several reefs, which are today submerged, were land areas at that time. This is in particular the case of reefs between the GBR and Grande Terre, with the Chesterfield representing a land area which exceeded 5,000 km^2 and Landsdown reefs an intermediate reef between Grande Terre and the Chesterfield, which probably covered several hundreds of km^2. In addition Grande Terre is also in the line of Norfolk Island (3.9 % endemism) and may constitute a cul de sac for subtropical species. Rapa has a rate of endemism very close to the Grande Terre (2.2%), this rate could be explained by the high isolation of Rapa and its position at the southern end of Polynesia. All the other islands have a rate between 1.2% (Society) and 0% (Wallis) with no particular trend linked to the type of island (atolls and high islands have similar rates) or the degree of isolation (Society are less isolated than the Tuamotu but have a larger rate, 1.2% *versus* 0.5%).

The low endemism level for Pacific reef fishes is probably linked to the long larval pelagic stage of most species. Endemic species are usually small and cryptic, at least in the South Pacific. The data on French Territories confirm this trend with very few large endemic species. This is somewhat opposite to what is observed in Hawaii where a large proportion of the endemic species are of large size (De Martini and Friedlander, 2004). In addition, most endemic species in the South Pacific are not abundant and are often rare (Kulbicki, 2005). The French Territories are no exception to this trend, since no endemic species are abundant.

REFERENCES

ANDREFOUET S., CHAUVIN C., SPRAGGINS S., TORRES-PULIZA D. & C. KRANENBURG, 2005. - Atlas des Récifs coralliens de Polynésie française. Centre IRD de Nouméa. février 2005, 38 p.

BACCHET P., LEFÈVRE Y. & T. ZYSMAN, 2007. - Guide des Poissons de Tahiti et ses Îles. 610 p. Papeete: Éditions Au Vent des Îles.

BAGNIS R., MAZELLIER P., BENNETT J. & E. CHRISTIAN, 1976. - Poissons de Polynésie. 368 p. Tahiti, Polynésie Française: Les Éditions du Pacifique.

BELLWOOD D.R. & T.P. HUGHES, 2001. - Regional-scale assembly rules and biodiversity of coral reefs. *Science*, 292: 1532-1534.

BRIGGS J.C., 2003. - Marine centres of origin as evolutionary engines. *J. Biogeogr*., 30 :1-18.

CARPENTER K.E. & V.G. SPRINGER, 2005. - The center of the center of marine shore fish biodiversity: The Philippines Islands. *Environ. Biol. Fish.*, 72 : 467-480.

CONNOLLY S.R., BELLWOOD D.R. & T.P. HUGHES, 2003. - Indo-Pacific biodiversity of coral reefs: Deviation from a mid-domain model. *Ecology*, 84: 2178-2190.

DEMARTINI E.E. & A.M. FRIEDLANDER, 2004. - Spatial patterns of endemism in shallow water reef fish populations of the Northwestern Hawaiian Islands. *Mar. Ecol. Prog. Ser*., 271: 281-296

FAO, 1998. - FAO Species Identification Guide for Fishery Purposes. The Living Resources of the Western Central Pacific (Carpenter K.E. & V.H. Niem, eds). Vol. I-VI. Rome: FAO.

FOURMANOIR P. & P. LABOUTE, 1976. - Poissons de Nouvelle-Calédonie et des Nouvelles-Hébrides. 376 p. Tahiti, Polynésie Française: Les Éditions du Pacifique.

FRICKE R., 2000. - Callionymidae of New Caledonia, with remarks on related species and descriptions of 10 new species from New Caledonia, Australia, New Guinea and Hawaii (Teleostei). *Stuttg. Beitr. Naturk.*, Stuttgart, (A) 617: 1-81.

FRICKE R., 2002. - Tripterygiid fishes of New Caledonia, with zoogeographical remarks. *Envir. Biol. Fish*., 65(2): 175-198.

FRICKE R., 2004. - Review of the pipefishes and seahorses (Teleostei: Syngnathidae) of New Caledonia, with descriptions of five new species. *Stuttg. Beitr. Naturk*., Stuttgart, (A) 668: 1-66.

FROESE R. & D. PAULY, 2004. - FishBase 2004: Concepts, design and data sources. ICLARM, Manila, Philippines.

GALZIN R., LECCHINI D., WILLIAMS J.T., PLANES S. & J.L. MENOU, 2006. - Diversité de l'ichtyofaune corallienne à Rapa (Polynésie Française). *Cybium*, 30(3): 221-234.

HARMELIN-VIVIEN M., 1989. - Reef fish community structure: An Indo Pacific comparison. *In:* Ecological Studies (Harmelin-Vivien M. & F. Bourlière, eds), pp. 21-60. New York: Springer Verlag.

HUBBELL S.P., 2001. - The unified neutral theory of biodiversity and biogeography. 375 p. Princeton Univ. Press.

JUNCKER M., 2005. - Approvisionnement en larves de poissons du lagon de Wallis (Pacifique Sud). Thèse de doctorat, 277 p. Université de Nouvelle-Calédonie.

KULBICKI M., 2005 Endemism of reef fish across the tropical Pacific. *In*: 7th Indo-Pacific Fish Conference. Taipe, Taiwan, May 2005. Abst., p. 49.

KULBICKI M., GALZIN R., HARMELIN-VIVIEN M.L., MOU THAM G. & S. ANDRÉFOUËT, 2000. - Les communautés de poissons lagonaires dans les atolls des Tuamotu, principaux résultats du programme TYPATOLL (1995-1996). Nouméa, IRD, *Doc. Sci. Tech*., II3: 26-125.

KULBICKI M., RANDALL J.E. & J. RIVATON, 1994. - Checklist of the fishes from the Chesterfield islands. *Micronesica*, 27(1/2): 1-43.

KULBICKI M. & J. RIVATON, 1997. - Inventaire des poissons lagonaires et récifaux de Nouvelle-Calédonie. *Cybium*, 21(1) suppl.: 81-98.

KULBICKI M. & J.T. WILLIAMS, 1997. - Preliminary checklist of the reef fishes from the Ouvea Atoll, New Caledonia. *Atoll Res. Bull.*, 444, 26 p.

LABOUTE P. & R. GRANDPERRIN, 2000. - Poissons de Nouvelle-Calédonie. 520 p. Éditions Catherine Ledru.

LEGENDRE P. & L. LEGENDRE, 1998. - Numerical Ecology. Developments in Environmental Modeling 20. 853 p. Elsevier.

LETOURNEUR Y., KULBICKI M., GALZIN R. & M. HARMELIN-VIVIEN, 1997. - Comparaison des poissons marins de trois îles océaniques tropicales de l'Indo-Pacifique (Réunion, Nouvelle Calédonie, Mooréa). *Cybium*, 21(1) suppl.: 129-145.

McARTHUR R.H. & E.O. WILSON, 1967. - The Theory of Island Biogeography. Princeton Univ. Press.

MORA C., CHITTARO P.M., SALE P.F., KRITZER J.P. & S.A. LUDSIN, 2003. - Patterns and processes in reef fish diversity. *Nature*, 421: 933-936.

RANDALL J.E., 1985. - Fishes of French Polynesia. *In*: Proceedings 5th International Coral Reef Congress, 1: 462-481.

RANDALL J.E., 1992. - Endemism of fishes in Oceania. *In*: Coastal Resources and Systems of the Pacific Basin: Investigation and Steps toward Protective Management. *UNEP Region. Seas Rep. Stud.*, 147: 55-67.

RANDALL J.E., 1998. - Zoogeography of shore fishes of the Indo-pacific region. *Zool. Stud*., 37: 227-268.

RANDALL J.E., 2005. - Reef and Shore Fishes of the South Pacific. 720 p. Honolulu: Univ. of Hawai'i Press.

RANDALL J.E., BACCHET P., WINTERBOTTOM R. & L. WROBEL, 2002. - Fifty new records of shore fishes from the Society Islands and Tuamotu Archipelago. *Aqua*, 5(4): 153-156.

RANDALL J.E. & J.L. EARLE, 2000. - Annoted checklist of the shore fishes of the Marquesas islands. *Occas. Pap. Bishop Mus*., 66: 1-39.

RANDALL J.E. & M. KULBICKI, 2006. - A review of the goatfishes of the genus *Upeneus* (Perciformes: Mullidae) from New Caledonia and the Chesterfield Bank, with a new species, and four new records. *Zool. Stud*., 45(3): 298-307.

RANDALL J.E., SMITH C.L. & M.N. FEINBERG, 1990. - Report on fish collections from Rapa, French Polynesia. *Am. Mus. Novit*., 1966: 1-42.

RIVATON J., FOURMANOIR P., BOURRET P. & M. KULBICKI, 1989. - Catalogue des Poissons de Nouvelle-Calédonie. Catalogues Sciences de la Mer, ORSTOM, Nouméa 2: 170 p.

ROBERTS C.M., MCCLEAN C.J., VERON J.E., HAWKINS J.P., ALLEN G.R., MCALLISTER D.E., MITTERMEIER C.G., SCHUELER F.W., SPALDING M., WELLS F., VYNNE C. & T.B. WERNER, 2002. - Marine biodiversity hotspots and conservation priorities for tropical reefs. *Science*, 295: 1280-1284.

ROBERTSON D.R., 2001. - Population maintenance among tropical reef fishes: inferences from small-island endemics *Proc. Natl. Acad. Sci.*, 98(10): 5667-5670.

SANTINI F. & R. WINTERBOTTOM, 2002. - Historical biogeography of Indo-Western Pacific coral reef biota: Is the Indonesian region a centre of origin? *J. Biogeogr*., 29: 189-205.

SPRINGER V.G. & J.T. WILLIAMS, 1990. - Widely distributed Pacific plate endemics and lowered sea-level. *Bull. Mar. Sci.*, 47: 631-640.

WANTIEZ L., 2000. - Expertise biologique de Futuna et Alofi (Wallis et Futuna). Rapport final. Le Substrat et les Poissons coralliens. Rapport de l'Université de Nouvelle-Calédonie, Nouméa, 42 p.

WILLIAMS J.T., WANTIEZ L., CHAUVET C., GALZIN R., HARMELIN-VIVIEN M., JOBET E., JUNCKER M., MOU THAM G., PLANES S. & P. SASAL, 2006. - Checklist of the shorefishes of Wallis islands (Wallis and Futuna FrenchTerritories, South Pacific). *Cybium*, 30(3): 247-260.