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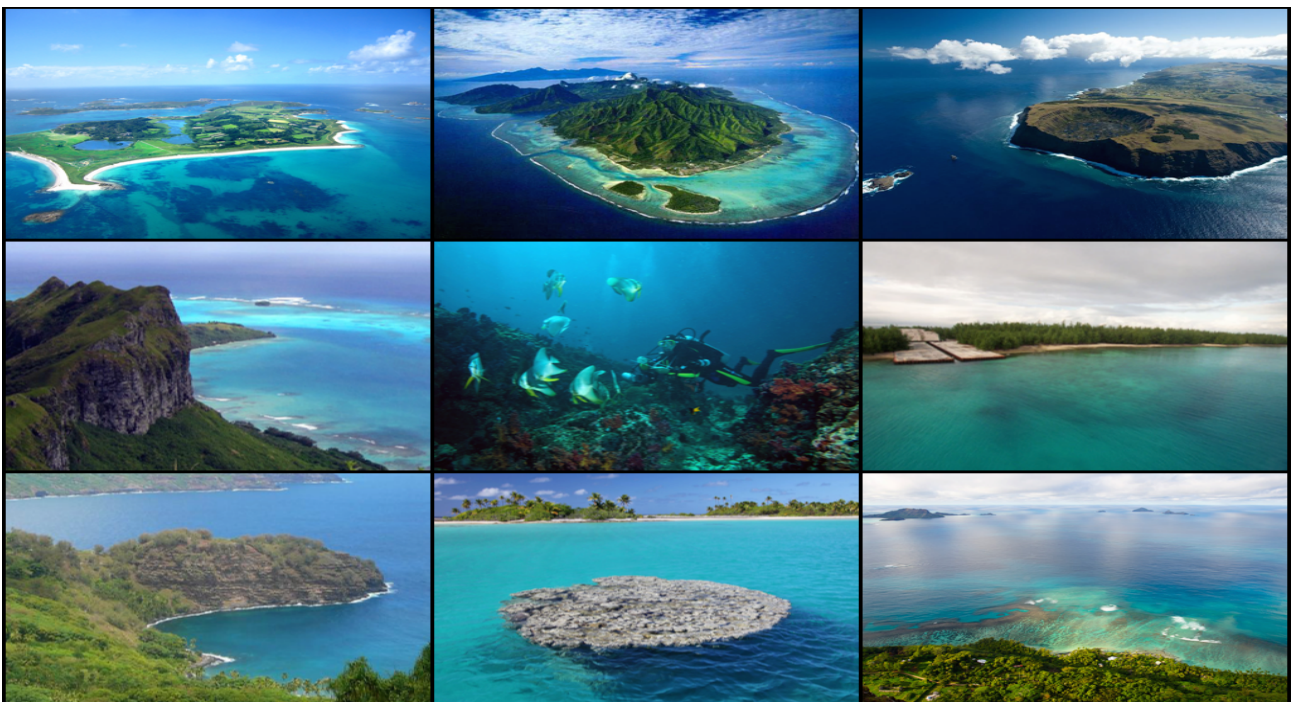
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d'un autre établissement (étudiant arrivé en M2)

# Study of the fish distribution in French Polynesia

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**Soutenu à Rennes le 14 Septembre 2016**

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" Because the most important is not what you are,  
but what you choose to be " - **Quentin Postel**

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## **Acknowledgements**

On the first hand I would like to thank my two tutors for everything they have done for me. I am extremely grateful to **René Galzin** for the meals he organized and the boat trips he took me on to discover Moorea island and understand its uniqueness. He truly made it a beautiful experience and his scientific advice, always given at the right time, was infinitely valuable. I am also indebted to my second tutor **Valeriano Parravicini** whose human support and constant good mood were precious to me throughout my internship. I thank him for the PhD opportunity he gave me and hope that we will be brought to work together again in December.

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**- Thank you everyone for everything you have done -**

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## Synthèse

La biogéographie est une branche entre les sciences naturelles, la géographie physique, l'écologie et aussi, la phylogénie. Il se base sur la compréhension de la distribution des espèces sur la planète en cherchant une explication sur les raisons de leur distribution. Parce que cette dernière est pluridisciplinaire, plusieurs sous-domaines ont pu voir naître le jour : 1) la paléobiogéographie (étude de la biogéographie passée et de la répartition géographique des êtres vivants à l'échelle des temps géologiques) ; 2) la biogéographie historique (étude de la répartition des taxons dans divers lieux du monde afin de découvrir quelles sont les relations mutuelles entre leurs distributions géographiques) ; 3) la phytogéographie (étude de la répartition et des causes de la répartition des plantes ou des associations végétales sur la terre) ; et 4) la zoogéographie (étude de la répartition et des causes de la répartition des animaux sur la terre). Dans cette étude, la zoogéographie a été favorisée pour expliquer la distribution de poisson en Polynésie française. La compréhension des facteurs qui mènent la richesse d'espèce est un processus clé pour définir une politique de conservation autour de l'écosystème étudié.

La région limitée par les Philippines, la péninsule Malaisienne, la Nouvelle-Guinée et l'Australie du nord a longtemps été reconnue comme un hotspot de biodiversité. Depuis les années 70', il est communément admis que cette région est l'épicentre de la biodiversité marine identifié sous le nom de hotspot de biodiversité de l'archipel indo-australien (AIA). De plus, la diversité taxonomique baisse avec la latitude et longitude: un modèle identifié chez les coraux, mais également depuis peu chez les poissons. Cependant, aux vues de la dernière mission effectuée par le Centre de Recherches Insulaires et Observatoire de l'Environnement (CRIOBE), il semblerait que la Polynésie ne réponde pas à ce schéma. En effet, les îles de Mopélia et de Scilly, îles les plus à l'ouest de la Polynésie, se voient appauvries en espèces. Le but de cette étude était donc de comprendre quels facteurs expliquaient la distribution des espèces ichthyques au sein de la Polynésie française. Cet objectif étant relativement vaste, **l'étude s'est divisée en deux parties**. Dans un premier temps, il a fallu créer la base de données en compilant l'ensemble des suivis effectués par le CRIOBE, tout en effectuant certaines missions de terrains pour enrichir notre jeu de données en espèces observées. Dans un second temps, nous avons cherché à définir le nombre d'espèces pour chaque île et à expliquer la distribution des espèces ichthyques en fonction de 2 études antérieures effectuées sur d'autres écosystèmes : 1) la relation Aire-Espèces, permettant d'établir le postulat que plus l'aire est grande et plus il y a d'espèces ; 2) Le Modèle Général Dynamique (MGD) permettant d'établir une relation entre la surface de l'île et son âge.

Ainsi, dans un premier temps, le travail a été de compiler les suivis effectués par le CRIOBE, le Museum National d'Histoire Naturelle (MNHN) et la campagne scientifique Reef Life Survey (RLS), et ce, depuis 1988 avec Fangataufa comme plus ancien suivi accompagné de l'île de Moorea. La difficulté de la compilation de données résidait dans l'hétérogénéité des données. En effet, certains transects étaient de largeurs fixes (5 ou 10 mètres) alors que d'autres étaient de largeur variable. Une transformation des données de comptage en densité a donc été nécessaire. De plus, dans le cadre de cette étude, certains comptages ont pu être effectués. C'est le cas du suivi des Aires Marines Protégées (AMP) de Moorea. Ainsi, nous avons pu effectuer des comptages supplémentaires durant l'année 2015. Une fois les données faunistiques compilées, il a fallu dans un second temps acquérir de la donnée fonctionnelle sur les poissons observés. Pour

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cela, nous avons pu définir 7 catégories de variables pour les 899 poissons observés : 1) leur régime alimentaire (planctonophage, herbivore détritique, herbivore de macroalgue, carnivore d'invertébrés sessiles, carnivore d'invertébrés mobiles, carnivore piscivore et omnivore) ; 2) leur taille moyenne (< 8 cm, entre 8,1 et 15 cm, entre 15,1 et 30 cm, entre 30,1 et 50 cm, entre 50,1 et 80 cm et > 80,1 cm) ; 3) leur mobilité (sédentaires, mobile dans le reef, mobile entre reefs) ; 4) leur rythme nyctéméral (diurne, nocturne ou les 2) ; 5) leur distribution verticale (pélagique, benthos pélagique ou benthique) ; 6) leur type d'agrégation (solitaire, paire, petit banc < 20 poissons, banc moyen < 50 poissons, banc important > 50 poissons) ; et 7) leur type de reproduction (pélagique, benthique, ovipare, ovovivipare, incubation buccale). Enfin, une fois la table fonctionnelle bâtie, et la table faunistique dressée, une table environnementale a pu voir naître le jour. Cette dernière se compose de plusieurs variables, dont les variables géomorphologiques indiquant le type d'environnement échantillonné. La couverture du sol a également été quantifiée en prenant en compte les débris, les coraux, les macroalgues, le turf, la dalle, le sable et la boue. L'exposition au vent dominant, et la puissance du courant ont également été renseignées de manière semi-quantitative. Une information sur les cyclones a également pu être prélevée pour expliquer la destruction ou non du récif et donc de sa biocénose. De plus, les concentrations en Phosphates, Nitrates et Chlorophylle a ont été renseignées pour juger de la qualité du milieu, ainsi que la Sea Surface Temperature (SST, température à la surface de l'eau). Pour finir, la connectivité inter-îles a été calculée en utilisant une matrice de distance. Puis la somme des 10 premières îles les plus proches a été sommée permettant de donner un indice de connectivité.

Une fois la base de données établie, nous nous sommes concentrés sur l'estimation du nombre d'espèces à estimer et sur la mise en forme des deux études à reproduire. Pour l'estimation du nombre d'espèces, nous avons donc effectué des courbes d'accumulation suivant 3 modèles (Michaelis-Menten, Exponentiel et Logarithmique). Puis, selon le meilleur ajustement, nous avons défini le nombre d'espèces pour chaque île. En suivant, 1) pour l'étude Aire-Espèces, 8 modèles issus de la littérature ont été repris afin d'effectuer un modèle moyen. Pour se faire, nous avons déterminé l'AIC (Akaike Information Criterion) de chaque modèle afin de pondérer le modèle moyen par ces AIC. 2) Pour l'étude du MGD, nous avons défini l'âge des îles via une publication de Clouard et Bonneville et nous avons estimé l'âge des îles des Tuamotus avec l'aide de Bernard Salvat et de la vitesse de convergence des plaques lithosphériques. Pour la superficie des îles, nous avons travaillé sous SIG afin d'extraire la superficie des lagons et des îles de Polynésie française.

Nous avons pu de ce fait observer qu'il n'y avait pas de différences significatives dans la composition fonctionnelle des espèces bien que la richesse spécifique variait de manière importante. Les seules différences fonctionnelles significatives à signaler sont celles de la distribution verticale et de l'activité nyctémérale des espèces observées. Aux vues des courbes d'accumulation, il a été admis que le nombre d'espèces ne suivait pas de gradient longitudinal ou latitudinal comme attendu. De plus, 4 îles se voient dotées d'une richesse spécifique importante : Mururoa, Moorea, Hao et Makemo. D'un point de vue statistique, c'est le modèle logarithmique qui s'ajuste le mieux quand celui-ci atteint une asymptote. Par la suite, pour l'étude de la relation entre la surface de l'île et le nombre d'espèces, une relation a pu voir le jour avec un  $R^2$  de l'ordre de 98%. Ainsi, plus la surface est grande, et plus il y'a d'espèces jusqu'à l'obtention d'une asymptote se traduisant par la capacité maximale du milieu. De plus, nous avons pu démontrer que la relation linéaire utilisée dans la plupart des études n'était pas la plus adéquate. En effet, chaque

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modèle utilisé contribue de façon non négligeable à la formation du modèle moyen. Pour finir, nous avons également mis en avant des différences entre les patterns d'écologie terrestre et d'écologie marine lors de la mise en oeuvre du MGD. En effet, les résultats attendus ne sont pas du tout conformes aux résultats observés : la relation entre l'âge de l'île et la richesse spécifique est linéaire décroissante. De ce fait, 2 espèces disparaissent tous les millions d'années. La relation avec la surface est similaire à celle obtenue précédemment.

De manière générale, les estimations issues des courbes d'accumulations ne sont pas totalement fiables. Elles ne donnent qu'une indication du nombre d'espèces pour chaque île. Ces indications permettent toutefois d'affirmer qu'aucun gradient longitudinal ou latitudinal n'existe à l'échelle de la Polynésie française. Ces estimations sont principalement biaisées par le manque d'échantillonnage et par la non-convergence assez répétée du modèle logarithmique nous forçant la sélection du modèle de Michaelis-Menten. De plus, les 4 valeurs extrêmes ressorties peuvent être principalement expliquées par d'autres facteurs telles que la surface pour Makemo et Hao, l'absence de pêche pour Mururoa, ou encore la sur-évaluation pour Moorea. Concernant les relations Aire-Espèces, il a été suggéré que le modèle le plus approprié peut dépendre de l'échelle et de la nature des organismes ou de l'environnement. De plus, aucun modèle universel ne peut être écrit. Enfin, concernant le MGD, les résultats attendant une relation quadratique sur le temps ne se sont pas observés. Ce résultat suggère une différence notable entre les patterns d'écologie terrestre et les patterns d'écologie marine. La colonisation dans les milieux marins se faisant nettement plus rapidement, atteignant de ce fait, quasi instantanément (à l'échelle des temps géologiques) la capacité maximale du milieu et ne laissant d'autre alternative qu'à une diminution du nombre d'espèces avec le temps.

Cette étude est loin d'être terminée. La distribution de la faune ichthyque a pu être expliquée en partie par la surface et l'âge de l'île, mais d'autres modèles prenant en compte l'hydrodynamisme pour le transfert des larves d'île en île peuvent être étudiés. Il semble évident d'inclure un aspect humain dans les modèles pour prendre en compte l'aspect halieutique. Le souci principal étant qu'aucune donnée de pêche n'est recensée dans ces îles et que des enquêtes sont à effectuer pour traiter de cet aspect. Outre l'halieutique et l'hydrodynamisme, nous pouvons prendre en compte les perturbations cycloniques, abîmant ainsi l'écosystème corallien et la faune qu'il abrite. Ces études sont à approfondir dans le futur et la création de la base de données donne une solide base pour continuer l'étude de la distribution des poissons au sein de la Polynésie française.

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## **List of the abbreviations**

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Abbreviation	
AIC	Akaike Information Criterion
AICc	Akaike Information Criterion corrected
ATTP	Agencement Temporel des Populations et des Peuplements
CRIOBE	Centre de Recherches Insulaires et OBservatoire de l'Environnement
df	Degree of Freedom
GDM	General Dynamic Model
GIS	Geographic Information System
GRS	Global Reference System
IAA	Indo-Australian-Archipelago
LMM	Linear Mixt Model
MNHN	Museum National d'Histoire Naturelle
MPA	Marine Protected Area
PhD	Doctor of Philosophy
REML	Restricted Maximum Likelihood estimates
RLS	Reef Life Survey
SAC	Species Accumulation Curve
SAR	Species-Area Relationship
SST	Sea Surface Temperature
UTM	Universal Transverse Mercator
UVC	Underwater Visual Census

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# 1. Introduction

## **Personal goal:**

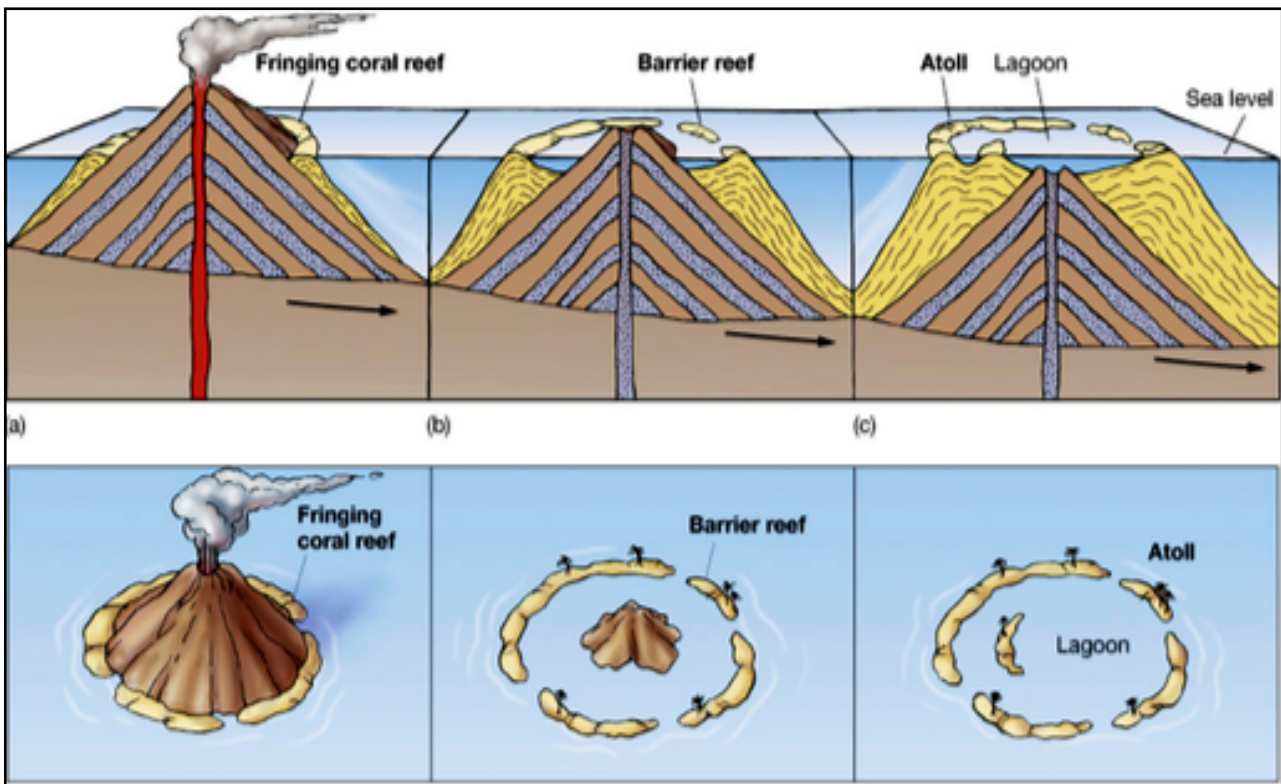
During this internship, I have been involved in the study of the biogeography of French Polynesia. More precisely, I studied the role of habitat area and island age in explaining evolutionary and ecological mechanisms related to present-day biodiversity patterns in reef fish species richness across French Polynesia. Despite the large efforts of the CRIOBE in sampling biodiversity across Polynesian archipelagoes, so far a coherent dataset allowing to test biogeographical and evolutionary hypotheses was still lacking. During my internship I collected all the available information to build a large scale database on the presence/absence and abundance of reef fish in French Polynesia. My main interest during the internship was to apply methods and theoretical frameworks used in terrestrial ecology to explain present-day biodiversity patterns on coral reefs.

The biogeography is a branch between the natural sciences, the physical geography the ecology (Hedgpeth, 1957) and also, nowadays, phylogeny (Harbaugh & Baldwin, 2007). It focuses on the understanding of the distribution of species on the Earth and try to explain the reasons of their geographical distribution. Because the biogeography is multidisciplinary, several sub-domains exist: 1) paleobiogeography (study of the past biogeography and the geographical distribution on the scale of geological time) (Bellwood & Wainwright, 2002; Bianchi *et al.*, 2012), 2) historic biogeography (study of the taxa distribution in diverse places of the world to discover what are the mutual relations between their geographical distributions) (Briggs, 1974; Kulbicki *et al.*, 2000; Briggs & Bowen, 2012; Ricklefs & Renner, 2012), 3) phytogeography (study of the distribution and the causes of the distribution of plants or plant associations on the earth) (Kingston *et al.*, 2003) and 4) zoogeography (study of the distribution and the causes of the distribution of animals on the earth) (Ekman, 1953; Longhurst, 1998; Adey & Steneck, 2001; Veron *et al.*, 2009). In our case, the zoogeography was favored to explain the fish distribution in French Polynesia. Understanding the factors who leads the species richness is a key process to define a conservation policy around the studied ecosystem (Rondinini *et al.*, 2011).

The interest in conducting biogeographical studies on coral reef ecosystems is twofold. On the one hand, despite living in oligotrophic waters, coral reefs are the most diverse and productive marine ecosystem on Earth (Odum & Odum, 1955; Hatcher, 1990; Steven & Atkinson, 2003; Mellin *et al.*, 2007). On the other hand, reef fish represent one of the best model to conduct large scale quantitative assessment because of their crucial role in the system, their high diversity and their relatively well-known taxonomy compared to other taxa (Robertson & Allen, 2002; Allen, 2009; Floeter *et al.*, 2008). Indeed, the region bounded by the Philippines, the Malaysian peninsula, New Guinea and northern Australia has long been recognized as a biodiversity hotspot (Stehli & Wells, 1971; Veron, 1993; Randall, 1998; Bellwood *et al.*, 2012; Briggs & Bowen, 2013). There is a wide agreement that this region is the epicenter of marine biodiversity (Cowman & Bellwood, 2013), and herein we refer to the biodiversity hotspot of the Indo-Australian-Archipelago (IAA). Taxonomic diversity declines with distance from this area, both latitudinally and longitudinally: a pattern identified in corals by Stehli & Wells (1971) and since then recognized across a broad array of fish taxa (Briggs, 1974; Paulay, 1991; Veron, 1995; Parravicini *et al.*, 2013).

The general pattern in species richness described above does not seem to apply at smaller scale in French Polynesia. During the last mission of the CRIOBE (Centre de Recherches Insulaires et Observatoire de l'Environnement), Galzin *et al.* (2015) sampled the westernmost islands of French Polynesia, namely Mopelia and Scilly. Contrary to the expectation of a higher biodiversity while getting closer to the biodiversity hotspot of the IAA, Galzin *et al.* (2015) documented relatively poor fish assemblages compared to other islands of French Polynesia. More precisely, the faunistic composition was more similar to the Fidji islands than the Society islands. This first result is clearly not enough to understand why the species richness gradients in

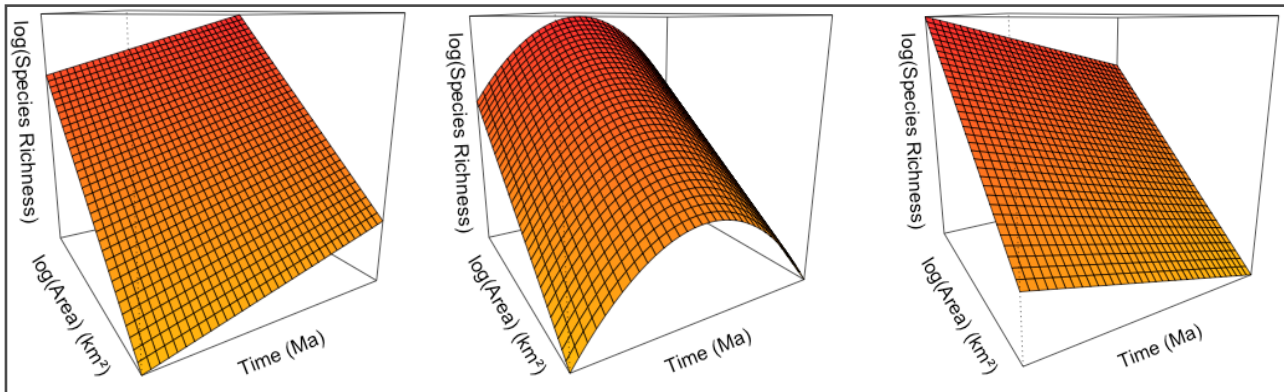
French Polynesia deviates from that described at the scale of the Indo-Pacific, i.e. a regularly decreasing gradient from the IAA to peripheral islands of the Est Pacific. The French Polynesia includes 118 volcanic islands and atolls with huge diversity in geologic patterns. Indeed, some islands are very young like Tahiti in the Society (1 Ma) against older like Fakarava in the Tuamotu (60 Ma) as well as differences in lagoon and land areas (3 km<sup>2</sup> for the smallest and 1 280 for the biggest). This allow to hypothesize that the observed deviation from larger scale patterns may be explained by the biogeographical theory of island biogeography. An interesting way to explore the ability of this theory to explain the species richness patterns for volcanic islands is the general dynamic model of oceanic island biogeography (GDM; Whittaker *et al.*, 2008) that so far has been tested only for terrestrial systems. Building on the dynamic equilibrium theory of MacArthur & Wilson (1967), the GDM explicitly places the outcome of the processes of immigration, speciation and extinction in a temporal context dictated by the geological development of the islands.



**Figure 1:** Formation of the island in 3 steps : a) the fringing reef (the emergence of the island), b) the barrier reef (the collapse of the island. A lagoon could exist and c) the atoll (the final step of the island, when lands disappear due to the collapse of the island) (Encyclopedia Britannica, <http://stjoeh2o.ning.com/forum/topics/how-are-they-constructed-two>)

The GDM is based on 3 premises: (1) that emergent properties of island biotas are a function of predictable trends in rates of immigration, speciation and extinction; (2) that evolutionary dynamics predominate in large, remote islands/archipelagos; and (3) that oceanic islands are relatively short-lived. Thereby, in terrestrial ecology, the species colonize the island while the island is growing and reach the carrying capacity several million years later. Crossed an optimum, the area of the island decreases as the ontogeny of the island continues. Thus, a reduction of habitat complexity and area as well as terrestrial resources decrease and landmasses showing a characteristic humped trend in carrying capacity over their life span. The model predictions for fish assemblages may be, with due exceptions, quite similar. Indeed, Darwin (1842) reasoned that a fringing coral reef surrounding a volcanic island in the tropical sea will grow upwards as the island subsides (sinks), becoming an "almost atoll", or barrier reef island. The fringing reef becomes a barrier reef for the reason that the outer part of the reef maintains itself near sea level through biotic growth, while the inner part of the reef falls behind, becoming a lagoon because conditions are less favorable for the coral and calcareous algae responsible for

most reef growth. In time, subsidence carries the old volcano below the ocean surface and the barrier reef remains. At this point, the island has become an atoll (Fig. 1). In terrestrial ecology, Whittaker *et al.* (2008) suggest that the role of island evolution in explaining the observed patterns in species richness could be tested by examining contemporary data across the differently aged islands of an oceanic archipelago. This generates an expectation of a positive relationship between species richness and island area combined with a parabolic relationship with time, provided that the archipelagos concerned display a full range of island developmental stages. As this is not always the case, the relationship with time could vary according to the extent of the geological ages involved, from positive, to hump-shaped, or negative (Fig. 2). Unfortunately, in the marine domain, nobody studied this relation and so, knows if the relations are the same or not.



**Figure 2:** The 3 different forms of the species–area–time relationship for oceanic island groups predicted within the context of the general dynamic model of oceanic island biogeography (Whittaker *et al.*, 2008, 2010; Triantis *et al.*, 2010, 2012)

The objectives of the study are (1) to make a complete database for reef fish of French Polynesia. This database has to include four parts: (a) a presence/absence table, (b) an abundance table with all transect detail, (c) an environment table in order to explain the distribution and (d) a functional table describing the life history traits of each species present in the database. Furthermore, (2) the second objective is to check if the richness gradient exists and if not as predicted, to explain why it does not exist at this scale.

## 2. Material and Methods

### **Main study:**

This internship has two aims. The first one is to establish a complete database around the islands of French Polynesia with several variables (physical, chemical, demographical, geological and biological) to explain the fish distribution. To complete this study, we defined 3 main tables: a) an environmental table R b) a functional table Q and c) a species table L. The idea behind this was to establish multivariate analysis (like RLQ analysis) to cross two tables at a time. Then, modeling could be done by using variables stemming from the multivariate analysis. The database making is time-consuming. Thereby, the aim of such process is to develop the database for the internship and for the future resulting PhD. This part will only be treated in the paragraph 2.7.

The second aim is to take back some studies like Guilhaumon *et al.*, 2008 and Whittaker *et al.*, 2008 to explain the fish distribution around the islands of French Polynesia. Obviously, a lot of studies could be selected, but we chose the first study (Guilhaumon *et al.*, 2008) to improve the mathematical algorithm and the second (Whittaker *et al.*, 2008) to compare the results between terrestrial ecology and marine ecology. A fishery study could not be done in only 6 months at the French Polynesia scale because there is no data about fisheries in the majority of the islands.

## 2.1 Location study

The French Polynesia is composed of 118 geographically dispersed islands and atolls stretching in the South Pacific Ocean, between 155°W (Manunae) and 134°W (Bench Portland) for longitudinal scale and between 8°S (Motu One) and 28°S (Marotiri) for latitudinal scale. The total land area is 4 167 km<sup>2</sup> (Fig. 3). The largest and most populated island is Tahiti in the Society Islands with 183 420 out of total of 268 207 citizens in 2012 (Institut de la statistique de Polynésie française, <http://www.ispf.pf>). French Polynesia is divided into 5 archipelagos: The Society Islands archipelago composed of the Windward Islands and the Leeward Islands, the Tuamotu Archipelago, the Gambier Islands, the Marquesas Islands and the Austral Islands. Among its 118 islands and atolls, 67 are inhabited. For the study, 48 islands and atolls were sampled: 8 for the Society Islands, 12 for the Marquesas Islands, 6 for the Australs Islands, 20 for the Tuamotu Islands and finally, only one for the Gambier. Because the communities are really different, the observer wrote when they sampled a lagoon or an outer slope transect and described if possible the nature of the marine landscape (current, wind exposition, slope...).

The campaigns were done at different periods between 1988 for Fangataufa (in the Tuamotu archipelago), and 2015 for Moorea (in the Society archipelago). Some islands were sampled several times while some islands, only one as it is the case for some islands of the Marquesas archipelago (for example the Clark bench at the west of the archipelago).

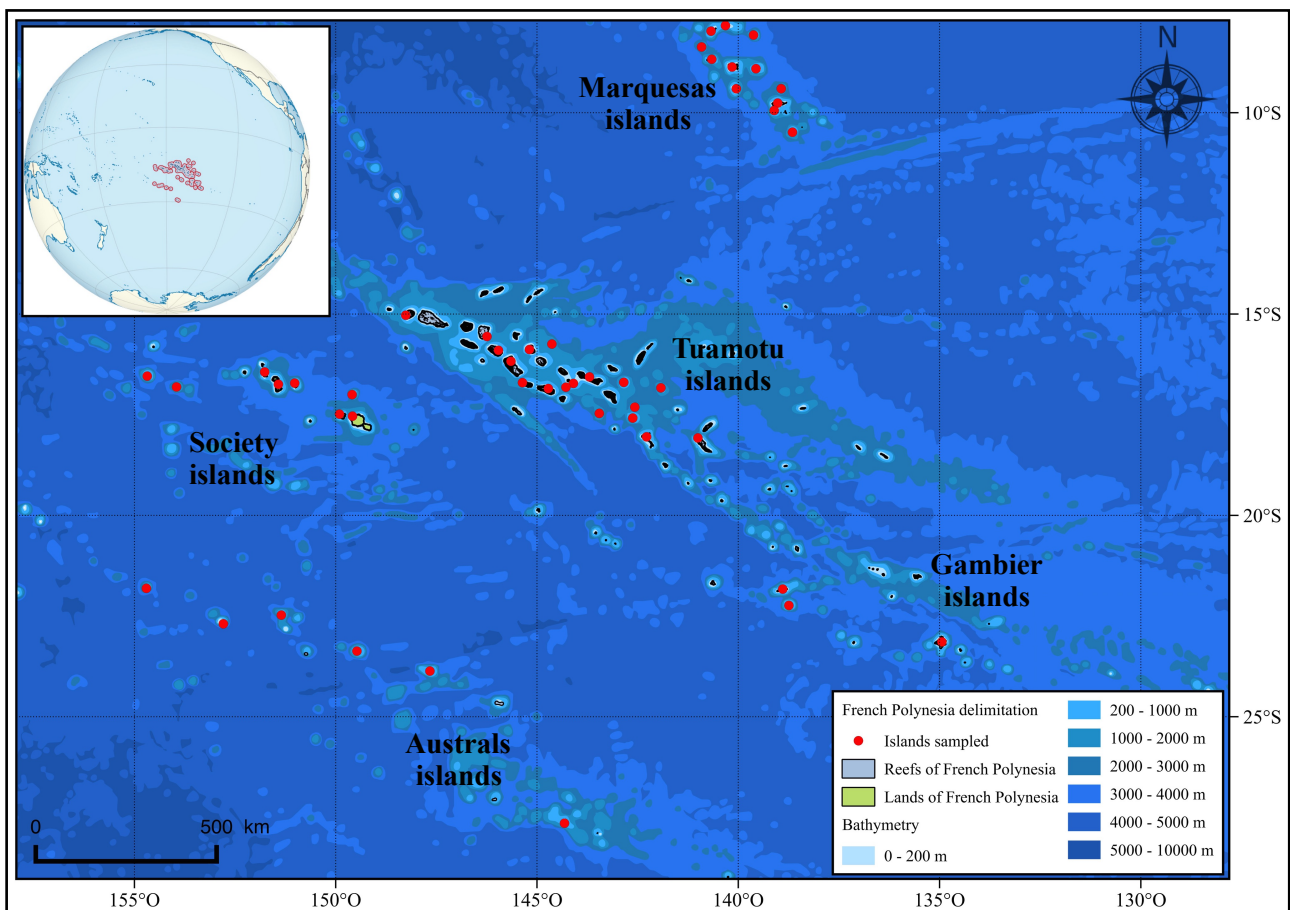


Figure 3: Representation of the 48 islands sampled (red points) of the 118 islands of French Polynesia between 1988 and 2015 (Service of the town planning, topography department; Personal conception and realization, 2016)

## 2.2 Sampling methods

### 2.2.1 Campaigns

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The study is built thanks to 3 different sources: CRIOBE, Reef Life Survey (RLS) (Edgar and Stuart-Smith, 2014) and National Museum of Natural History (MNH) campaigns.

#### CRIOBE samplings:

**Society:** The oldest campaign used is for Moorea island. This last one is also the most studied island of French Polynesia with the implantation of the CRIOBE in 1971 under the will of Bernard Salvat to build the station distant from the population. Afterward, René Galzin begins a fish monitoring just in front of the station (the Tiahura radial) since 1983 for 3 biotopes (fringing reef, barrier reef and the outer slope). Thereby, 4 monitorings were set up in Moorea: (1) Polynesia Mana (2004-2015), (2) the MPA monitoring (2004-2015), (3) the ATPP monitoring (Agencement Temporel des Populations et des Peuplements - 1990-2015) and (4) the Tiahura radial (1983-2015). Subsequently, more westerly than Moorea and at a larger scale, the most westerly islands of French Polynesia, in 2015, the Islands of Mopelia and Scilly could be sampled during 1 month.

**Marquesas:** For this archipelago, 2 monitoring were used. The first was the same as Moorea, namely to the ATPP monitoring. In this archipelagos, this sample mission targets 2 islands: Nuku Hiva and Ua Huka. Moreover, a special campaign was made by the CRIOBE in 2011 where the scientists of the CRIOBE sampled the 12 stations of the final database.

**Tuamotu:** For this archipelago 2 islands were sampled: Mururoa (Moruroa) and Fangataufa islands. The 2 islands were old nuclear location for french atomic bomb test. Consequently, the data was difficult to obtain except for military and searchers who worked for monitoring at these places. Galzin was in charged to observe the diversity in these islands.

**Australs:** For this archipelago only one mission was used for the 6 islands of the Australs

**Gambier:** For this archipelago, only Mangareva has been sampled.

#### Another campaigns:

To increase the sampling effort of Polynesian islands, the Reef Life Survey (RLS) database has also been integrated. In the RLS data for the the 5 archipelagos are available. Afterward, the Tuamotu were better studied and 7 islands could be added to the database. It was the same case for Society islands which 5 islands were also added. For the others, the data was counted up.

#### Anesthetic monitorings:

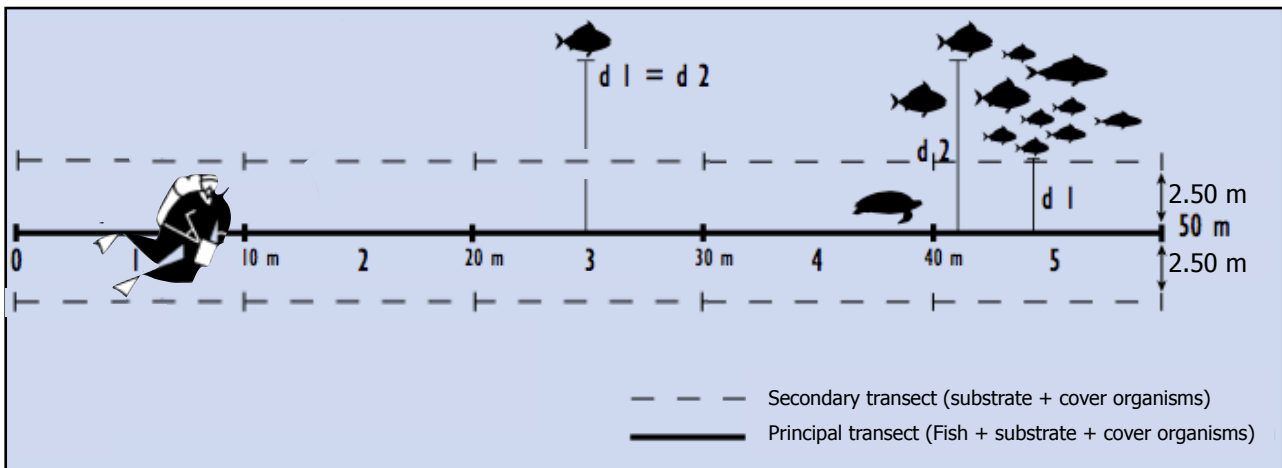
Finally, 8 biodiversity assessments using anesthetic (presence/absence data) has been made by the Smithsonian National Museum of Natural History (NMNH). These had the goal to quantify the total diversity of the Archipelagos of French Polynesia. These data were added to the presence/absence database and allowed to add information for some islands of the 5 archipelagos (Scilly, Mopelia, Moorea, Nuku Hiva, Mururoa, Maria, Motu One etc.).

These 22 campaigns were the baseline to built a presence absence database. This last one permitted to undertake a descriptive analysis of the species richness gradient for the 5 archipelagos. Afterward, the 14 first campaigns were used to built the quantitative database.

## **2.2.2 Methods of sampling**

### Underwater visual censues (UVC)

UVC is a technique commonly used to measure the abundance of fish on coral reefs and has been used extensively in reef fish studies of population dynamics, ecology and management (Barans & Bortone 1983; Harmelin-Vivien *et al.*, 1985; Thresher & Gunn 1986; Cappo & Brown 1996). To count fish 3 steps are necessary: (1) count the larger mobile species: like roving serranids such as *Plectropomus spp.*; lethrinids, larger lutjanids such as job fish (*Aprion viriscens*) and bass (*Lutjanus bohar*), large scarids, the mobile acanthurids (*Naso spp.*), etc. This ensures these types of fish are counted before they leave the census area. (2) Second, concentrate on the smaller more sedentary fish such as the smaller lutjanids, other scarids and acanthurids. These types of fish are less likely to leave the census area because they are less mobile. (3) Don't count any fish that enter the census area after the stop watch has started (incoming fish - Fig. 4).



**Figure 4:** Underwater visual censuses (UVC) representation with the 2 secondary transects at 2.50 m for a transect 50 x 5 m. The variable distance transect is also possible by written the distance between the fish and the diver (Labrosse et al., 2001)

For the study, 2 methods of counting were selected: (1) the fixed-width strip transects and (2) the variable distance transects. The only difference between the 2 methods is the width. Concerning the first method, this last one is generally fixed at 2 x 2 or 2.50 m. It depends on the campaign. For the second method, the counting only depends on the visibility. For example, if a fish is located above 5 meters, it is counted and its distance is listed. For the school of fish, a distance  $d_1$  is written for the fish closest to the diver and a distance  $d_2$  for the most distant.

#### Sampling using anesthetic

The employment of anesthetic allow to sample cryptic and small species which are generally not observed using UVC and are therefore an essential complement for biodiversity assessments. The technique allows to identify fish species while keeping them alive the majority of the catch. Sampling implies measure and weigh living fish and return them to the water alive. Currently, one of the only anesthetic licensed in France to fish for a surgical grade of anesthesia is the benzocaine. This anesthetic must be ordered by a veterinarian. It may be administered by injection or by dipping. A sufficiently large and airy wide tray must be in place before returning the fish to the water alive (Lepage et al., 2008).

Thus, the campaigns could be summarized in this table (Table 1).

**Table 1:** Summary for each campaigns used in the quantitative database

<b>Archipelagos</b>	<b>Campaign</b>	<b>Fish monitoring</b>
Society	Tiahura radial	50 x 2 m
Society	ATPP	50 x 2 m
Society	Polynesia Mana	50 x 5 m
Society	MPA monitoring	25 x 2 m
Society	Scilly and Mopelia	50 x variable distance
Marquesas	Polynesia Mana	50 x 5 m
Marquesas	Special Campaign	50 x variable distance
Tuamotu	Mururoa	50 x 2 m
Tuamotu	Fangataufa	50 x 2 m
Australs	Special Campaign	50 x 5 m
Australs	Rapa iti	50 x 5 m
Gambier	Special Campaign	50 x variable distance



Archipelagos	Campaign	Fish monitoring
All	Reef Life Survey	50 x 10 m

## 2.3 Data homogenization

### 2.3.1 Database homogenization

Because data provides of some campaigns, the data is really heterogenous (Table 1). Homogenization is crucial to pursue analyses.

#### Fish database

For variable distance transects or stationary points, the density and biomass estimates presented below are based on the calculation of a mean weighted distance ( $dm$ ) of the individuals in the transect or at the stationary point. Either side of the transect is divided into one-meter-wide corridors, the closest from 0 to 1 meter, the second from 1 to 2 meters and so on. Depending on the fish's distance at the time of observation, it will then be associated to one of these corridors and given its median value (Labrosse *et al.*, 2001). For that reason, the mean weighted distance of a species is given by (equation 1):

$$dm_j = \frac{\sum_{i=1}^p n_{ij}(d_{ij}+0.5)}{\sum n_{ij}} \quad (1)$$

where  $p$  is the total number of observations of species  $j$   
 $n_{ij}$ : number of fish in observation  $i$   
 $d_{ij}$ : perpendicular distance of fish  $i$  to the transect.

The estimated density can then be obtained by (equation 2):

$$D_j = \frac{\sum_{i=1}^p n_{ij}}{dm_j \cdot L} \quad (2)$$

Calculations were made by considering all the species taken as a whole and not by calculating the estimated sum per species. Differences between these 2 types of estimates can be huge, especially when the number of species is high (Labrosse *et al.*, 2001).

### 2.3.2 Sampling effort homogenization

In order to visualize the gradient of diversity in French Polynesia, the most important part was to homogenize the sampling effort. Indeed, for example, 86 500 km<sup>2</sup> of the transect area were sampled in Moorea while only 500 m<sup>2</sup> in Tahiti. To overcome this problem, one solution was to make a Species Accumulation Curve (SAC) for each islands with the aim to obtain the capacity of the biotope. All islands with 2 transects or less were deleted. Afterward, 3 models were fitted to the residues: (1) The most known is Michaelis-Menten (Clench, 1979). In function of the sampling effort  $n$ , estimated in time, the bare number of species increases up to an asymptote corresponding to the total number of species.  $K$  is a constant connected to the collection difficulty (equation 3):

$$S^n = S \frac{n}{K+n} \quad (3)$$

(2) Soberón & Llorente (1993) develop a broader theoretical frame which allows to fit the SAC to several models. These models are effective empirically but are lacking theoretical support to justify their shape. The simplest model is exponential negative. If the probability to find a new species is proportional to undiscovered species (equation 4) then:

$$S^n = S(1 - e^{-Kn}) \quad (4)$$

(3) A more realistic model defines that the probability of discovering a new species decreases faster than the number of species remaining to discover. This probability is as a decreasing function of the number of missing species (Holdridge & Grenke, 1971). The simplest function is exponential negative but it never nullifies and the number of species has no asymptote. An additional parameter to obtain the asymptote is necessary (equation 5):

$$S^n = \frac{1}{z} \log\left(\frac{a}{c} - \frac{a-c}{c} e^{-cn}\right) \quad (5)$$

These 3 models were fitted by non-linear squared for 34 islands. Then, the model which obtained the minimal residual sum of square was selected to define the species richness of the island (see Results 3.2).

## **2.4 Definition of the Area and the Age of the island**

### Age of the island

There are several ways in which the age of an island can be measured such as the birth of the volcanic base (buried from now on) or the emergence of the reef. To be homogeneous, and to facilitate the data collection, the emergence of each island (in million years ago) was selected. For Australs, Gambier, Society and Marquesas archipelagos, the age was determined by Clouard & Bonneville (2005). Concerning the Tuamotu it is more difficult. The islands must be separated in two sets from which the origin is very different (Salvat *et al.*, 2012). The islands of the archipelago in northern position on one hand, and those of an alignment going Gambier to Hereheretue, on the other hand. The age of Mururoa and Fangataufa could be also estimated by Clouard & Bonneville (2005), concerning the others, the age of the islands was estimated between 40 and 60 million years ago (Salvat *et al.*, 2012). Thus, the age was defined most exactly possible by Salvat for the most westerly island of the Tuamotu in our possession (Fakarava) and the most easterly (Hao). A virtual line was drawn between these 2 islands and the age was approximated for the islands of the Tuamotu when they are perpendicular to this virtual line.

### Area of the island

Thanks to the service of the town planning (topography department), a vector of French Polynesia could be recovered. This data contain polygons about reefs and lands locations and the Coordinate Reference Systems was generated with a conform UTM projection, in the zone 6 (South). The Global Reference Systems (GRS) was the GRS80 and the units are defined in meters. The first step was to re-project the data with Behrmann Cylindrical Equal-Area Projection (equivalent projection) because the UTM used by default could not give a correct estimation of the area. Finally, the area was defined for each polygon of the dataset by area function in QGIS ®. Then, each polygon listed for one island are summed and the area for the island and for the lagoon were determined. Because Marquesas islands do not possess lagoon, the total area used for the island was the sum of the land area and the lagoon area. The ideal would have been to define a living space in the marine domain for Marquesas but this is really difficult to obtain this kind of data.

## **2.5 Determination of Species Area Relationship (SAR)**

In order to test for the relationship between habitat area and species richness, linear regression models were used:  $\log(\text{Area}) = f(\log(\text{Index}))$  where the index was the ranking of the islands areas (rank 1 corresponds to the smallest area and rank 34 to the biggest). Thanks to this relation, a proportional number of transects was randomly sampled for each islands in relation to their area. Thus, for Fakarava (high disponible area), 5 transects were randomly selected and only one for the Clark Bench. This subset was done 3 times: One for lagoon transects, another for outer slope transects and the last one for all transects sampled.

**Table 2:** Forms of Species Area Relationship (SAR) used in the study (Guilhaumon *et al.*, 2008) Taxonomic and regional uncertainty in species-area relationships and the identification of richness hotspots)

Name	Formula	Parameters	Shape	Asymptotic nature
Power	$S = cA^z$	2	Convex	No
Exponential	$S = c + z \log(A)$	2	Convex	No
Negative exponential	$S = c(1 - e^{-zA})$	2	Convex	Yes
Monod	$S = (cA) / (z + A)$	2	Convex	Yes
Rational function	$S = (c + zA) / (1 + fA)$	3	Sigmoid	Yes
Logistic	$S = c / (1 + e^{-(zA + f)})$	3	Sigmoid	Yes
Lomolino	$S = c / 1 + (z \log(f/A))$	3	Sigmoid	Yes
Cumulative Weibull	$S = c(1 - e^{-(zA^f)})$	3	Sigmoid	Yes

Then, for the 3 conditions a Species-Area-Relationship (SAR) was established. In the main studies, these relationships take the classical form of a log-linearizable power function. However, the log-linear power law is incorrect when the error term in the power law,  $S = cA^z$ , is additive (Wright, 1981; Patten & van Huelst, 1998; Fattorini, 2006). To overcome this problem, Guilhaumon *et al.* (2008) fitted a suite of curvilinear SAR models to species–area data. Afterward, 8 SAR models were fitted to the aim to obtain an average model (Table 2).

Information-theoretic Criteria (IC such as AIC and AICc) are built in a way to the first term, representing the lack of fit of the model to the observed data, is penalized by the second term which captures model complexity. The lower the IC associated to the model is, the better this model will be considered to explain the data. In the present study, we used AIC. Because this last one produces relative measures, absolute values are not relevant to compare models and the selection is usually based on Akaike weights. For a fitted model  $i$ , the weight  $\omega_i$  is given by (equation 6):

$$\omega_i = \frac{e^{-1/2\Delta_i}}{\sum_{r=1}^M e^{-1/2\Delta_r}} \quad (6)$$

where  $M$  is the number of models in the set and  $\Delta_i$  is defined as  $\Delta_i = IC_i - IC_{\min}$  with  $IC_{\min}$  the IC value for the best model. Akaike's weights are interpreted in terms of probabilities of a given model being the best in explaining the data within a predefined set of alternative models. As advocated for non-nested models, we obtained multimodel SARs by averaging the model predictions with respect of their weight (equation 7):

$$\bar{S} = \sum_{i=1}^M S_i \omega_i \quad (7)$$

where  $S$  is the multimodel averaged species richness and  $S_i$  is the vector of species richness inferred from model  $i$ .

## 2.6 General Dynamic Model (GDM)

In studies such as the present one, the small number of islands per archipelago can lead to low power in detecting trends, instability in parameter estimation and model over-fitting (Burnham & Anderson, 2002). Bunnefeld & Phillimore (2012) recently suggested the use of linear mixed effect models (LMMs) to overcome such limitations. In the models I developed fixed effects were island area (in  $\text{km}^2$  and log-transformed), time elapsed since island formation (date of emergence

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of each island, in million years ago), and a quadratic term for the time elapsed ( $\text{Time}^2$ ). The grouping factor considered as a random effect was the archipelago that each island belongs to, as the values of the intercept and the slopes of the relationships between the diversity metrics, area and time could vary across archipelagos. Once the employment of the random effect was validated evaluating the AICc of the model with Restricted Maximum Likelihood estimates (REML), the model was fitted by using maximum likelihood (ML) allowing the selection of the fixed terms. The model with the lowest AICc value is considered to fit the data best (Burnham & Anderson, 2002). To facilitate comparison with the LMM applications (Bunnefeld & Phillimore, 2012), we log-transformed values of the diversity metrics considered and also for the untransformed values. As log-area was used in the analysis, this particular implementation assumed a power law species-area relationship, the most general and widely applied species-area relationship model (Rosenzweig, 1995; Triantis *et al.*, 2010 - see Results 3.3). However, the employment of a power curve was chosen to allow for the comparison with other terrestrial models testing for the GDM.

## **2.7 On way to complete the database**

### **2.7.1 The environmental data**

This part mainly concerns the PhD that could stem from this internship. However, the database making is the cornerstone to continue the study. Thus, the first table to build is the environmental data with 33 variables. Indeed, each transect was included with an ID (3 first letter of the archipelago and the number of the transect. For example, Apataki island, in the Tuamotus (TUA41) and the campaign was recorded in another column. Then, locality was added consisting of island identification, archipelago identification, and coordinates (latitude and longitude) in decimal degrees for homogenization. Finally, as explained previously, there are 5 categories of variables: physical, biological, chemical, demographical and geological.

#### The geomorphology, the current and the wind:

The detail of the geomorphology was recorded by the diver in 3 levels. The first level, slightly rough, refers if the transect is located between the coast and the fringing reef, the fringing reef, or the barrier reef. It is the first indicator for the species richness. The closer we are to the island, the more species there are in the lagoon (fringing reef). The second level is more detailed and relies on the first level of geomorphology: 1) For the closer part to the island, we could obtain different locations like the back of the bay, the coast linear (< 50 m of the coastline), the lagoon floor, the channel, or also the motu. 2) For the fringing reef, we could obtain location with pinacles (rocks emerging of the water), islets, channel, or also submerged reef. 3) Finally, for the barrier reef, the choice is more restrained. We could obtain the back reef (lagoon side) or, inversely, the outer slope. It is also possible to observe Hoa (it is a channel allowing the interaction between the lagoon and the ocean). To finish, the topography was recorded in a third level, flat (slope < 1°), gentle slope (slope < 2°), slope (slope < 3°), steep slope (slope < 4°), and the talus (slope > 4°).

The current and the exposition to the dominant wind was also recorded in semiquantitative way: none, medium or strong. Divers assessed the current and the wind (trade winds with a direction West-East) when they are ready to dive.

#### The storms and the chemical components:

Because the storms destroyed the reef ecosystem, it seems obvious to integrate this information. Thereby all storms were recorded and thanks to buffers on GIS, we could cross locate the transect with the storms trajectories. Then, the distance between the transect and the trajectory was computed, together with the intensity of the storm (speed in km/h) and whether the storm destroyed the ecosystem.

In the same way, we defined the concentration of Phosphate, Nitrate and Chlorophyll a for the nutrients thanks to a raster used in GIS. There is a confidence interval (5%) for the estimation of these measures. We also determined the Sea Surface Temperature (SST) with the same confidence interval.

#### The substrate cover:

The data about the substrate cover was available for each campaign. The obtention of the data depends on 2 kinds of monitoring: (1) the transects and (2) the quadrats. For the transects

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monitoring there are two ways to determine the substrate cover : a) the Point Intercept Transect (PIT) and b) the Line Intercept Transect (LIT). In the first case, each category of substrate (Algae, Coral, Rubble, Pavestone, Sand, Mud, Other) is listed each 5 meters along the 50m transect. For the second case, the category of substrate is listed in distance along the transect. For example, the transect begins with coral from 0 to 2.15 meters and continues from 2.16 to 7.70 meters with macro- algae and so on until the end of the transect. Then, there is the second kind of monitoring divided in two sub-monitoring: a) the point intersect and b) the individual counting and cover estimate. For the point intersect, it is the same principle as the PIT. There is a grid of one hundred cells (10 x 10) in the quadrat and for each intersection, the category of substrate is listed. Finally, the last monitoring determines for each cell of the quadrat a category of substrate. Each cell represents one percent and the cover could be represented by a percentage for the seven categories.

#### Connectivity:

We took the coordination of the center of the island and built a matrix of distance between each island. For that, we defined the distance by using both longitudes and latitudes. If we consider 2 points A and B, on the sphere, with latitudes  $\varphi_A$  and  $\varphi_B$  and with longitudes  $\lambda_A$  et  $\lambda_B$ . Then the angular distance in radians  $S_{A-B}$  between A and B is given by the fundamental relation of spherical, using trigonometry  $d\lambda = \lambda_B - \lambda_A$ :

$$S_{A-B} = \arccos (\sin \varphi_A \sin \varphi_B + \cos \varphi_A \cos \varphi_B \cos d\lambda) \quad (8)$$

The distance S in kilometer, obtains by multiplying  $S_{A-B}$  by the radius of the ( $\approx 6\,378$  km). Then, distances were ranged and summed for the 10 first. The final value gives an indicator of connectivity inter-island in kilometre.

## **2.7.2 The functional data**

Finally, a functional table was built (the table Q). In the same way that last one includes an ID for each species. The ID used stemmed from FishBase. For each species, the class, the family, the genus and the species was recorded. The work was carried out before the major taxonomic change that affected the labridae.

#### Reproduction:

The mode of reproduction was also determined by using the study of Rong-Quen, 2000. This last one allowed us to define 6 categories of reproduction for fish observed among the islands of French Polynesia: 1) Brooded, The parents incubate eggs in their mouth. 2) Pelagic, parents spawn and the eggs travel with the current. 3) Demersal, the eggs were fixed on substrate until hatching. 4) Viviparous, the embryo is inside the body of the parent, eventually leading to live birth, as opposed to reproduction by laying eggs that complete their incubation outside the parental body. 5) Ovoviviparous, embryos that develop inside eggs remain in the mother's body until they are ready to hatch. 6) Unknown, when the reproduction of the species selected is not recorded.

#### Diet, Schooling, Size, Vertical distribution, Mobility and Activity:

For these 6 variables, we could define a gradient. For the Diet, 7 classes could be selected: 1) Planktivorous, 2) Herbivorous Detritic, 3) Herbivorous Macroalgae, 4) Sessiles invertebrates, 5) Mobile invertebrates, 6) Carnivorous and 7) Omnivorous.

For Schooling, 5 class: 1) Solitary, 2) Couple or three, 3) Small group (< 20 individuals), 4) Medium group (< 50 individuals) and 5) Large group (> 50 individuals).

For Size, 6 class: 1) < 8 cm, 2) < 15 cm, 3) < 30 cm, 4) < 50 cm, 5) < 80 cm and 6) > 80 cm. For the vertical distribution: 1) Pelagic, 2) Demersal and 3) Benthic.

For the mobility: 1) Sedentary, 2) Mobile within the reef and 3) Mobile among reefs. And finally, for the activity: 1) Diurnal, 2) Nocturnal and 3) Both.

### 3. Results

#### 3.1 General informations

A total of 896 fish species was identified during these last 30 years by the CRIOBE. There are 348 species (with 94 250 km<sup>2</sup> sampled) on the west, 399 in the Tuamotu archipelagos (160 000 km<sup>2</sup> sampled) and 231 on the east (14 000 km<sup>2</sup> sampled). On the North, only 193 were listed (14 500 km<sup>2</sup> sampled) and on the south 219 (9 250 km<sup>2</sup> sampled). The species richness was lower in the Marquesas and more important in the Tuamotu islands. It is important to note that sampling was not homogeneous between the archipelagos (see Results 3.2). Then, the number of species present in one, 2, 3, 4 or each archipelagos was analyzed. As expected, most of the species (35 %) are only present for one. A second interesting observation is 16,5 % (75 species) were present everywhere. Thus the fish communities are relatively heterogeneous.

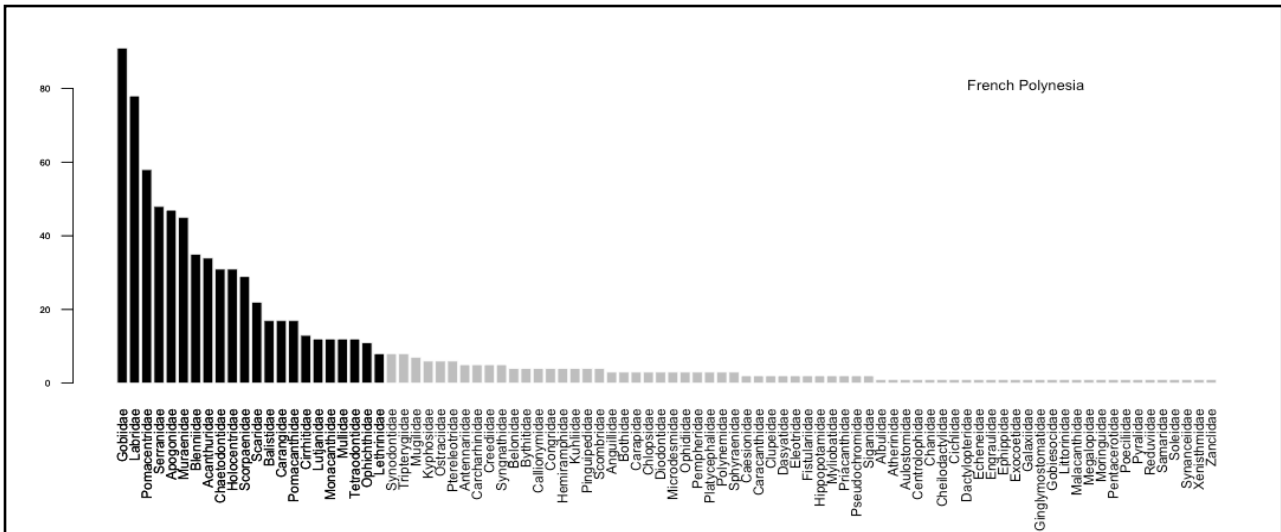


Figure 5: Distribution of families sampled (highlighted the 22 most abundant families to make an analogy with the past studies of Kulbicki, 2007)

To study the fish distribution, a complement analysis about taxonomic distribution was carried out (Fig. 5). The results are similar to Kulbicki (2007): the species are distributed very unevenly among the different families. Indeed, 88 families of coastal fish in the Pacific Islands which include 50 species reef-associated were determined. Moreover, 22 of these have more than 30 genus each. By themselves they include 80 % of species, the Gobiidae representing more than 10 % (with 91 species) of the total. It is important to note these main families consist mainly of small species (Gobiidae, Apogonidae, Pomacentridae, Blenniidae, Syngnathidae, Trypterigiidae) or cryptic (Muraenidae, Ophichthidae, Scorpaenidae) which pose problems of sampling or identification. This means that our level of knowledge is still very imperfect. In the world, 1 142 genus of coastal fish are listed and 735 can be associated with reefs. It is important to note that severals genus (290) are monospecific (Kulbicki, 2007).

Since the GDM does not account for the potential role of functional traits in the assembly of fish communities of the island, the first step was to evaluate test for the existence of a potential role of traits in explaining the observed pattern. (Fig. 6). Differences in the functional structure of fish assemblages among islands were tested with a Kruskal–Wallis one-way analysis of variance. The distribution of fish size among the islands of French Polynesia were similar (p-value = 0.28). Likewise the diet (p-value = 0.41), the mobility (p-value = 0.46), and the schooling behavior (p-value = 0.13). Among the 6 functional traits explored here only the activity (p-value = 0.04) and the vertical position in the water columns were slightly significant (p-value = 0.03). Considering that when significant p-values were always close to 0.05, the role of functional traits was considered as minor and not considered in further analyses.

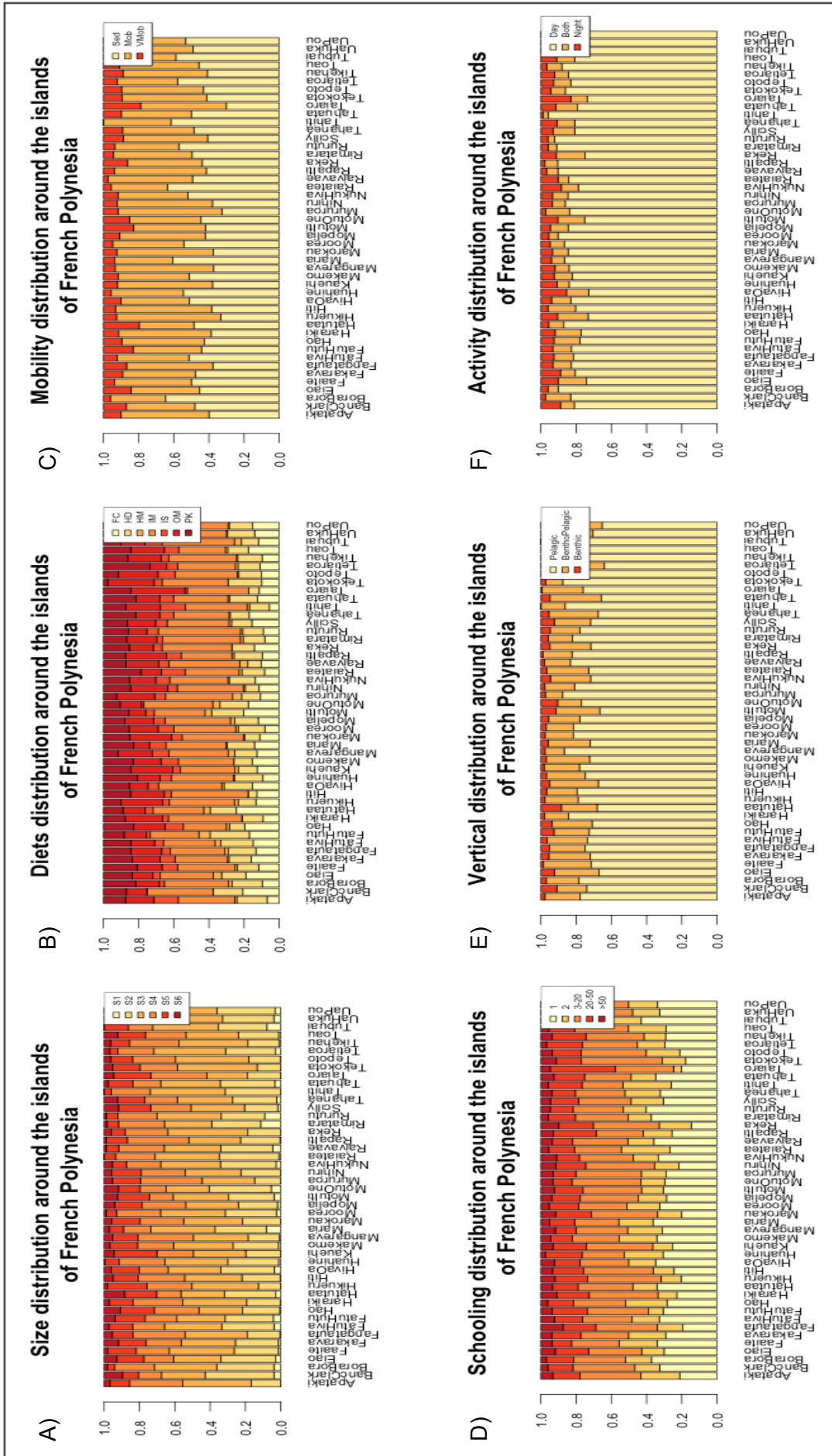
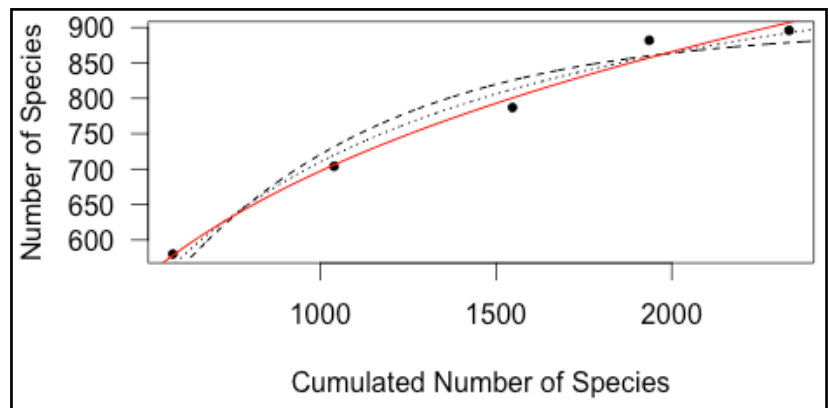


Figure 6: Coral fish distribution in French Polynesia for 6 functional variables. A) Size distribution (S1 < 8 cm, S2 < 15 cm, S3 < 30 cm, S4 < 50 cm, S5 < 80 cm and S6 > 80 cm), B) Diet distribution (FC: Fish Carnivorous, HD: Herbivorous detritic, HM: Herbivorous macroalgae, IM: Mobile invertebrates, IS: Sessiles invertebrates, OM: Omnivorous and PK: Planktivorous), C) Mobility distribution (Sed: sedentary, Mob: mobile within the reef, VMob: mobile among reefs), D) Schooling distribution, E) Vertical distribution and F) Activity distribution

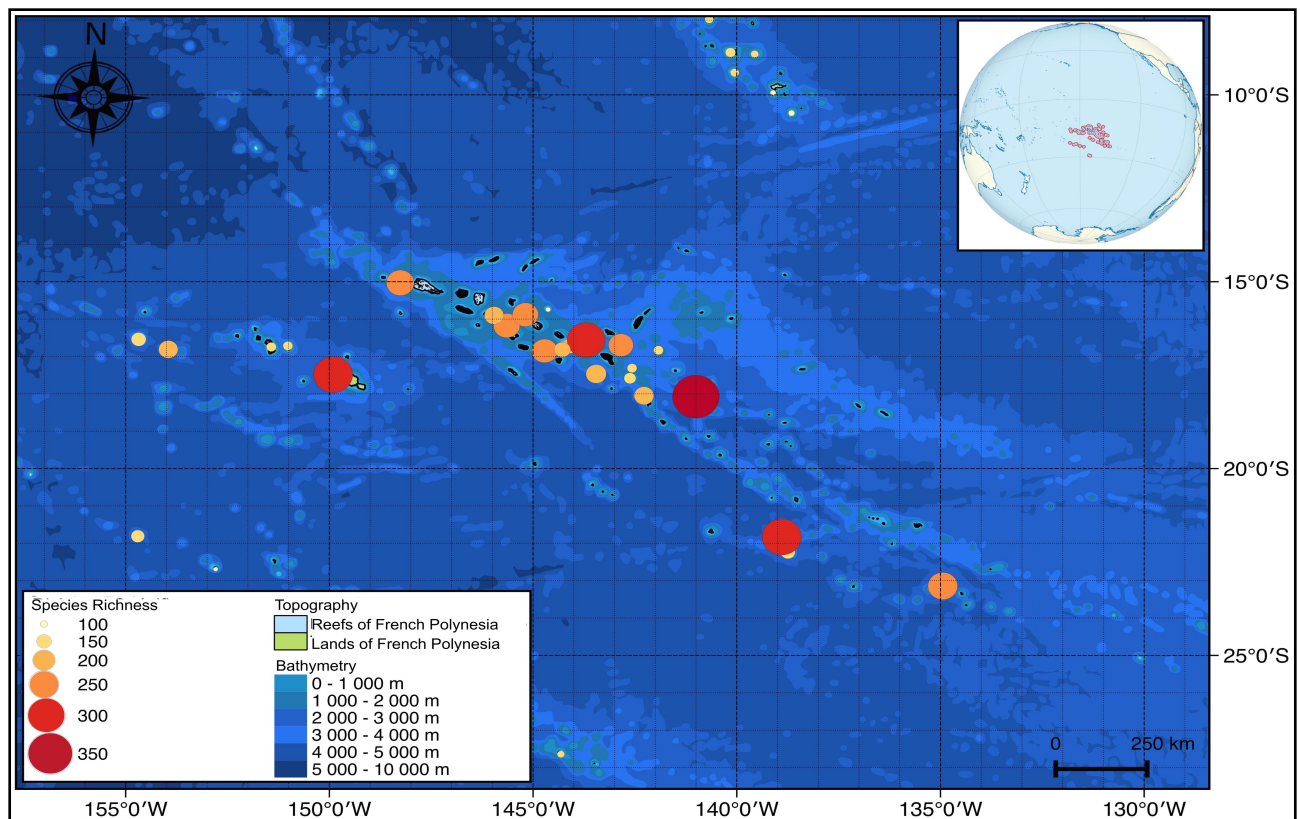
## 3.2 Species Accumulation Curve and fish distribution

In this paragraph, the species richness was estimated with the aim to homogenize the data set. Thereby, the species richness of French Polynesia was determined by using the 3 models described in the paragraph 2.3. The best expected model (Fig. 7, in red) does not attend the asymptote, the Michaelis-Menten model is thus favored with a species richness equal to 1105 species ( $AIC_1 = 49.43$  against  $AIC_2 = 53.75$  and  $AIC_3 = 48.28$ ). It is important to note that result is certainly underestimate. On the same way, the analysis was done at the scale of the



**Figure 7:** Species Accumulation Curve in French Polynesia. dashed lines for the Michaelis-Menten model, black solid for exponential model and red solid for logarithmic model

archipelagos and at the scale of the islands. The results were similar to the observed richness species (see Results 3.1). Indeed, the species richness in the Society archipelago was established at  $328 \pm 27$  species, in the Marquesas islands at  $195 \pm 8$  species, in the Gambier islands at  $246 \pm 15$  species, in the Australs islands at  $235 \pm 8$  species and to finish, in the Tuamotu at  $340 \pm 21$  species. The same conclusion concerning the underestimation could be done here for the archipelagos, except the Australs (see Table 3).



**Figure 8:** Representation of the species richness in the 34 islands sampled more than 2 transects of French Polynesia (Service of the town planning, topography department; Personal conception and realization, 2016)



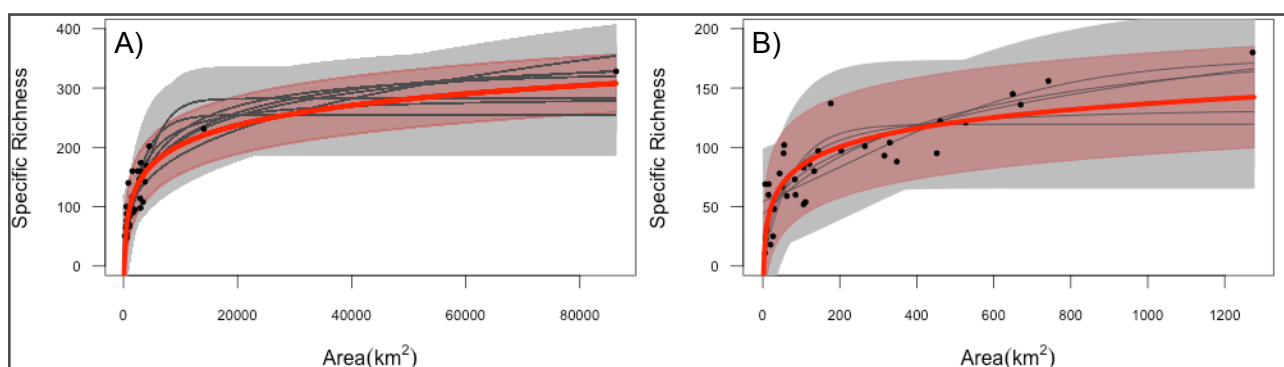
**Table 3:** Species richness prediction for archipelagos according to 3 Species Accumulation Curve models (the model favored is following by a star). The models were referred in Material and Methods 2.3.2

Archipelagos	Observed species	Predict Model 1	Predict Model 2	Predict Model 3
Australs	219	212 ± 11.3	196 ± 16.7	235 ± 8.1 (*)
Gambier	231	246 ± 15.1 (*)	213 ± 20.0	NaN
Marquesas	193	195 ± 8.0 (*)	172 ± 12.4	NaN
Society	348	328 ± 26.8 (*)	308 ± 34.1	NaN
Tuamotu	399	340 ± 21.0 (*)	312 ± 30.0	NaN

The same analysis was conducted separately for each island (Fig. 8). Overall, we did not detected any longitudinal gradient of species richness in French Polynesia at the scale of the island. Indeed, the maximum number of species was determined for Hao ( $359 \pm 7.8$ ), Mururoa ( $310 \pm 6.2$ ), Moorea ( $309 \pm 8.2$ ) and Makemo ( $301 \pm 8.2$ ). Moreover, the most of the highest species richness are placed in the Tuamotu. However, some islands of the Tuamotu like Taiaro, Reka Reka and Tekokota, with respecting richness of  $86 \pm 4.1$ ,  $117 \pm 1.6$  and  $117 \pm 7.2$  species are also present. These results suggest a factor lead this distribution. Mainly, the most of the highest species richness are placed in islands with a huge area like Fakarava, Makemo, Hao, etc.

### 3.3 Species Area Relationship

In order to check the relationship between the island area and species richness, a first Species-Area Relationship was done by testing the number of species with the area transect for each island. This relation fits well with a  $R^2$  equals to 0.98 (Fig. 9A). It is important to note that models are mainly pulled by Moorea, unique observation with an area upper 20 000  $\text{km}^2$ . Because the relation is strongly robust, the islands are sampled in function of their area (see Material and Methods 2.4). Thus, a main relation between the number of species with the area of the island and its lagoon could be fitted with a  $R^2$  equals to 0.72 (Fig. 9B). In this case, the best fitting model was the rational function (sigmoid relation) with an Akaike weight of 49 %, following by Weibull, (sigmoid relation and 24 %) and power (convex relation and 16 %). This result suggests that islands above the curve are up-sampled (12 islands) and the ones under the curve, under-sampled (22 islands). Thereby, the area of the island seems to explain almost three-quarters of the model variation (MacArthur and Wilson theory).



**Figure 9:** Species-Area Relationship. The black solid lines represent the 8 models fitted and the red solid represents the multi-model Species Area Relationship. A) Species richness observed in function of the transect area sampled. B) Relation between the species richness and the island when species richness sampled proportionally than the island area

### 3.4 General Dynamic Model

The last and main goal of the study was to explore the relationship between species richness, habitat area and island age. The best model selected was the model including age and area (log-transformed) suggested by Whittaker, 2008. The model expected with a quadratic term for the time elapsed was refuted because the  $\Delta AICc$  is superior than 2 (Table 4). A positive relationship between the area and the species could be determined as studied in the Results 3.3. The relation with the age of the island is negative: older is the island and poorer its species richness is (Fig. 10). Despite the small coefficient for the time (-0.008) this variable considerably improve the model performance. Thus, according to the best model, for each 2 millions of years, 1 species disappears and almost 2 species appears for each square kilometer.

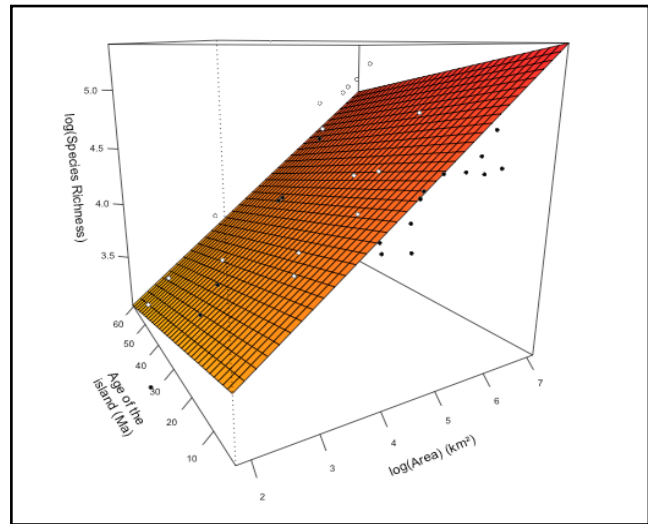


Figure 10: GLM representation according to the best model fitted (black points for islands under the model and white for them upper)

Table 4: Parameter estimates for the fixed effects of the most parsimonious linear mixed effect models based on AICc

Intercept	Age	Age <sup>2</sup>	log(Area)	df	LogLik	AICc	$\Delta AICc$	weight
2.879	-0.0080		0.3507	5	-8.673	29.4	0.00	0.737
2.872	-0.0068	-2.2e <sup>-05</sup>	0.3513	6	-8.671	32.3	2.93	0.170
2.771			0.3468	4	-12.113	33.6	4.15	0.093
4.283				3	-32.688	72.2	42.74	0.000
4.431	-0.0064			4	-31.553	72.4	43.02	0.000
4.661	-0.0678	1.1e <sup>-03</sup>		5	-30.492	73.1	43.64	0.000

## 4. Discussion

### 4.1 Limits to determinate the species richness in French Polynesia

The best model explaining the species richness is the logarithmic model (model 3). However, the shape of the model is convex and potentially influenced by outlier (particularly data using several monitoring like Moorea), it is difficult to predict a correct number of species. The exponential model (model 2) always gave an under-estimate and never be selected except for Hao island. The linear model (model 1) instead generally approaches the best model. In several cases, the data is not sufficient to estimate the total species richness. On the other hand, the species richness estimation for French Polynesia only depends on 5 measures (according to qualitative and quantitative observations). The results is obviously under-estimated also in this case (for example, in the Tuamotu islands, the specific richness estimated by SAC equals 348 while observations tend to 399 species). The SAC do not fit at the archipelagos scale (because the islands are different), it was just used as proxy (by using the same method for each point). Indeed in French Polynesia, 1 193 fish species, among which 7 species of rays and 21 of sharks were inventoried to this day. Nearly sixty are endemic (<http://www.environnement.pf>). Several news species are discovered according to recreation scuba-diving or also during special missions

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which do not include fish monitoring. It is undeniable to better fit species accumulation curves, a larger sampling has to be effected in almost each islands studied (for example, the Hiti island fit well and a negative exponential prediction is disponible). If possible, the estimation could be ameliorated by using the same methods of sampling (transect 2 x 50 m). Finally, The estimation of the species by extrapolation is more uncertain than by the non-parametric methods like Chao or Jackknife estimators, although it is less used (Marcon, 2015). The point is that species richness is not the topic of this study and using SAC is just a proxy, permitting to produce the same method of prediction with the aim to visualize if a species gradient exists or not. Thus, results are underestimated but conserve the same « coefficients ».

Concerning the high species richness islands, some results were not expected like Hao. This high value is the result of poor sampling with a large difference species composition with different proportions. Nearly to 120 species were observed in only 1 500 m<sup>2</sup> of sampling. the species richness is certainly bigger than observations but this island is certainly the only one overestimated. Make is the second one unexpected but the large area of this atoll (third bigger of the French Polynesia) could explain this high value. Concerning Mururoa, this high value could be certainly explained by the quasi-pristine condition of the atoll. Indeed, this atoll covered nuclear bomb test and was closed for everyone since the eighties (see Conclusion). Finally, the island of Moorea is the most sampled in area and time and partially explain the high diversity in this place. About Australs islands and Marquesas islands, the species richness is poorer than the center of the French Polynesia and could be discussed later.

## **4.2 Multi-model SAR, limits and Interests**

Some studies have been done in marine domain concerning the SAR (McLachlan & Dorvlo, 2007; Foster *et al.*, 2013) but no-one used a multi-model. In some cases, it is still used to estimate local species richness and to predict the effects of habitat loss and fragmentation on biodiversity. These applications of the SAR may be especially useful in the design of marine reserves, which often differ in purpose from conventional terrestrial reserves and may require fundamentally different approaches (Neigel, 2003). Nevertheless, some limits have to be noticed. Firstly, it has been suggested that the most appropriate model may depend on scale and the nature of the organisms or of the environment (Connor & McCoy, 1979; Tittensor *et al.*, 2007, Guilhaumon *et al.*, 2008). Indeed, all of the different shapes of SARs represented by the set of models used were selected. This suggests that none of a wide range of potential SAR models can a priori be ignored, and that a universal model does not emerge. The applied implications of this observation could be further complicated. Therefore, this highlights the importance of considering multiple models when making inferences about SARs. Then, it also draws attention to the need to remember there is commonly substantial spatial variation in species richness not attributable to variation in area. Finally, assuming that a power model is the most appropriate description of SARs can make a substantial difference to the outcome of analyses and the conservation recommendations that may follow (Connor & McCoy, 1979).

## **4.3 Discussion around the GDM**

All studies using the GDM have been done in the terrestrial domain (Whittaker *et al.*, 2010, 2010; Triantis *et al.*, 2010; Borregaard *et al.*, 2015) but never in the marine domain. The results concerning this analysis are innovative and predict a new scenario: Older is the island, and poorer the species richness is. This result suggests than species colonized rapidly the island at the beginning and then, decrease as the ontogeny of the island continues. In terrestrial ecology, 3 stages are explained by the model: 1) a rise of the species richness due to the terrestrial species colonization, 2) the optimum, translate by the system capacity to finally, 3) decrease for several reasons including the decrease in terrestrial resources, biotic process (predation, competition...) and a reduction of habitat complexity and area. However, the colonization of coral fish is easier and faster than for the terrestrial faunas. Reef fishes have pelagic larvae that can be transported beyond 500 km (Lo-Yat *et al.*, 2006). It is likely that the system capacity is very quickly reached

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compared to the terrestrial environment. We therefore hypothesize that the decreasing relationship found between species richness and island age may be the result of a different balance between immigration and extinction processes compared to the terrestrial environment (Whittaker *et al.*, 2008). While the carrying capacity is probably achieved early for the marine realm, older island has higher chances of being involved in unfavorable climatic conditions and events determining extinction. Although further studies accounting for the phylogenetic relationship among species and focused on endemics are certainly needed to clarify mechanisms, the observed patterns allow at least to hypothesize that the differential balance between immigration and extinction between terrestrial and marine system may be a major determinant of the observed patterns.

## **5. Conclusion**

Among these last 6 months, the goal of my research was to understand the mechanisms explaining the atypical gradient of species richness in French Polynesia thanks to the scientific observations available. A key problem to analyse the number of species was to merge and homogenize sparse datasets. However, to overcome this problem, we created Species-Accumulation-Relationship. By using the advancement in terrestrial ecology research, a theory concerning the ontogeny of the islands and areas could be put in place: the General Dynamic Model. According to my results it seems that predictions are different between terrestrial and marine ecology. Indeed, while the carrying capacity is probably achieved early for the marine realm, older island has higher chances of being involved in unfavorable climatic conditions and events determining extinction. These results are the first in marine domain and need to be confronted in others regions but are innovative and open doors to a better understanding of fish distribution.

However, several limits could be advanced. Firstly, one of the biggest regrets of this study is to not success to couple the mmSAR and the GDM. Indeed, the best model to fit the SAR is the rational function (see Results 3.3), nevertheless the GDM is in favour of the power relation. The power relation is selected to facilitate the run of the model by using linear mix model (log-transformation). But it is obvious that coupling of two models give a better explication of fish distribution. Secondly, 2 other analyses could be made within the framework of other internships. 1) First, the connectivity. The most of the high species richness is located along the Tuamotu archipelago following by the Gambier islands. The Society, Marquesas and Australs are poorer and are located among each cardinal points. The most easterly islands (Gambier archipelago) could received coral fish larvae thanks to several French Polynesia storm trajectories (north west in south east) (Larrue & Chiron, 2010). A model considering larvae dispersion properties (Lagrangian model) like number of storms in the last decade (including intensity), type of atoll (open, closed, semi-closed) the average current (Andrefouet *et al.*, 2012) and the distance between each islands (Lo-Yat *et al.*, 2006) could be improve the understanding of the fish distribution. These variables are in our possession and we did not have the necessary time to analyze them in this study. 2) And second, the human factor. Indeed, Mururoa is one of the richest islands but not one of the biggest. One of the process which could explain this is the absence of fisheries. Because Mururoa and Fangataufa were nuclear bomb test islands, nobody could move into these areas and consequently could not fish since the nineties. A model considering social factors like human presence or fisheries pressures (Schaefer, Fox-Garrod and Pella-Tomlinson models) could also help for a better understanding of the distribution. In this case, in French Polynesia, it is extremely difficult to estimate the fisheries parameters because there is no monitoring about fish landings. To obtain informations about that, it would be necessary to lead investigations on the 48 islands sampled and it is not possible within the framework of a Master's degree.

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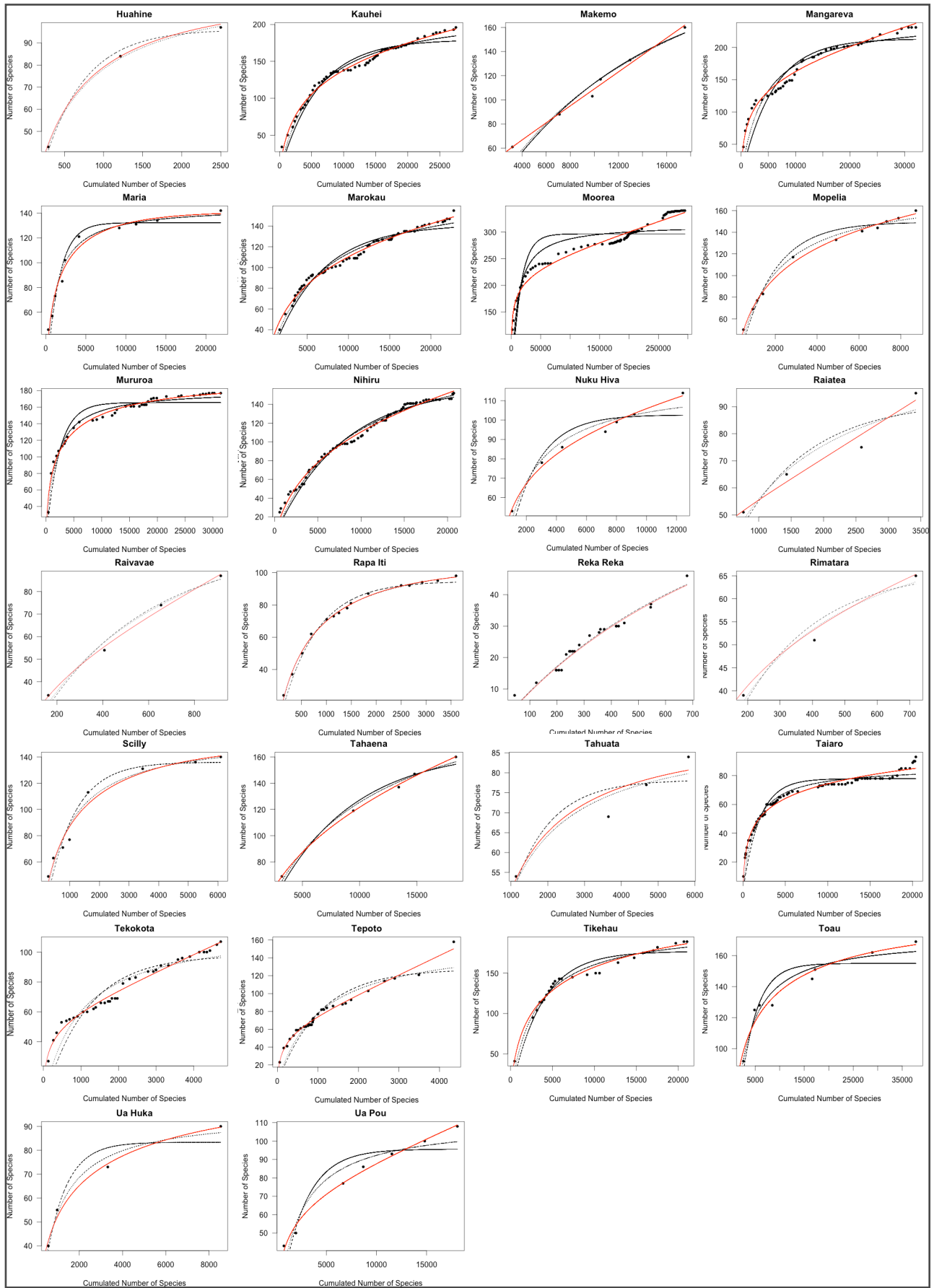


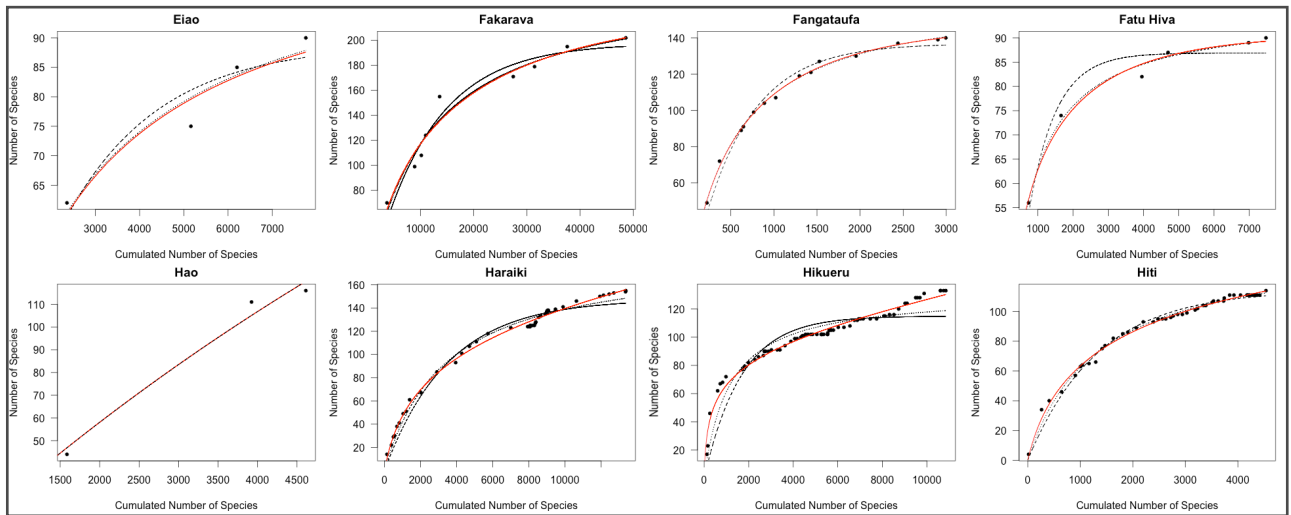
## 7. Appendices

**Appendix I:** Species richness prediction for the 34 islands sampled in French Polynesia according to 3 Species Accumulation Curve models (the model favored is following by a star)

Archipelagos	Island	Obs	Pred linear	Pred exp	Pred log	Nb Transect
Australs	Maria	142	145 ± 6.7	132 ± 9.7	141 ± 6.3 (*)	10
Australs	Raivavae	87	141 ± 3.7 (*)	100 ± 4.6	NaN	4
Australs	Rapa Iti	98	114 ± 1.3	95 ± 3.0	102 ± 1.3 (*)	15
Australs	Rimatara	65	84 ± 3.2 (*)	66 ± 4.7	NaN	3
Gambier	Mangareva	231	246 ± 15.1 (*)	213 ± 20.0	NaN	43
Society	Huahine	97	117 ± 1.2	96 ± 3.6	NaN	3
Marquesas	Eiao	90	110 ± 4.0 (*)	89 ± 5.2	NaN	4
Marquesas	Fatu Hiva	90	95 ± 1.5 (*)	87 ± 3.4	91 ± 2.0	6
Marquesas	Nuku Hiva	114	120 ± 4.7 (*)	103 ± 8.1	NaN	7
Marquesas	Tahuata	84	91 ± 4.9 (*)	78 ± 6.6	NaN	4
Marquesas	Ua Huka	90	134 ± 3.8	83 ± 7.5	104 ± 4.0 (*)	4
Marquesas	Ua Pou	108	110 ± 8.1 (*)	96 ± 11.7	NaN	7
Society	Moorea	328	309 ± 22.8 (*)	291 ± 30.6	NaN	64
Society	Mopelia	160	179 ± 4.2 (*)	149 ± 7.5	NaN	11
Society	Raiatea	95	118 ± 7.1 (*)	92 ± 8.5	NaN	4
Society	Scilly	140	157 ± 7.3	136 ± 9.4	150 ± 7.3 (*)	8
Tuamotu	Fakarava	202	247 ± 10.0	198 ± 11.0	225 ± 7.3 (*)	9
Tuamotu	Fangataufa	146	164 ± 1.8	137 ± 4.1	147 ± 1.7 (*)	14
Tuamotu	Haraiki	155	186 ± 4.8 (*)	147 ± 7.1	NaN	45
Tuamotu	Hikueru	133	131 ± 7.4 (*)	114 ± 10.5	NaN	69
Tuamotu	Hiti	114	145 ± 2.3	114 ± 3.3	158 ± 2.0 (*)	47
Tuamotu	Hao	116	676 ± 7.8	359 ± 7.7 (*)	NaN	3
Tuamotu	Kauehi	196	222 ± 6.1 (*)	179 ± 9.1	NaN	59
Tuamotu	Makemo	160	301 ± 8.2 (*)	205 ± 8.9	NaN	6
Tuamotu	Marokau	155	181 ± 4.0 (*)	141 ± 6.0	NaN	65
Tuamotu	Mururoa	174	310 ± 5.5 (*)	214 ± 10.7	NaN	12
Tuamotu	Nihiru	152	215 ± 4.5 (*)	159 ± 5.5	NaN	72
Tuamotu	Reka Reka	46	117 ± 1.6 (*)	71 ± 1.6	NaN	23
Tuamotu	Taiaro	93	86 ± 4.1 (*)	78 ± 6.3	NaN	72
Tuamotu	Tahanea	160	221 ± 4.2 (*)	166 ± 6.6	NaN	5
Tuamotu	Tekokota	107	117 ± 7.2 (*)	98 ± 9.1	NaN	36
Tuamotu	Tepoto	158	160 ± 8.6 (*)	27 ± 10.4	NaN	34
Tuamotu	Tikehau	189	208 ± 6.1	177 ± 9.0	234 ± 5.4 (*)	25
Tuamotu	Toau	169	172 ± 6.1	155 ± 10.4	179 ± 6.2 (*)	8

**Appendix II:** Species richness prediction for the 34 islands sampled in French Polynesia according to 3 Species Accumulation Curve models (dashed lines for the Michaelis-Menten model, black solid for exponential model and red solid for logarithmic model)





### Appendix III: Presence/Absence for the fish in French Polynesia within the 5 archipelagos

Species	ID FishBase	Australis	Society	Tuamotus	Marquesas	Gambier
Ablennes hians	972		1			
Abudefduf conformis	55476				1	
Abudefduf septemfasciatus	5687		1	1		
Abudefduf sexfasciatus	5688	1	1	1		1
Abudefduf sordidus	5689	1	1	1	1	1
Acanthocybium solandri	89				1	
Acanthurus achilles	4306	1	1	1	1	1
Acanthurus blochii	4750		1	1	1	
Acanthurus guttatus	4736	1	1	1	1	1
Acanthurus leucopareius	4737	1	1	1	1	1
Acanthurus lineatus	1258		1	1	1	
Acanthurus mata	1255		1	1	1	
Acanthurus nigricans	6011	1	1	1	1	1
Acanthurus nigricauda	4747	1	1	1	1	1
Acanthurus nigrofuscus	4739	1	1	1		1
Acanthurus nigroris	4738	1	1	1		1
Acanthurus nubilus	4733	1	1	1	1	1
Acanthurus olivaceus	4744	1	1	1		1
Acanthurus pyroferus	4742	1	1	1	1	
Acanthurus reversus	58792				1	
Acanthurus thompsoni	4734	1	1	1		1
Acanthurus triostegus	1260	1	1	1	1	1
Acanthurus xanthopterus	1261		1	1	1	
Aetobatus ocellatus	12600		1	1	1	
Albula glossodonta	11512		1			
Alionemachthys piger	64965		1	1		1
Alticus simplicirrus	61229				1	
Aluterus scriptus	4275		1	1		
Amanses scopas	6672	1	1	1		
Amblycirrhitus bimacula	5829	1	1	1		1
Amblycirrhitus unimacula	23501	1				
Amblyeleotris fasciata	7229		1			
Amblyeleotris marquesas	61005				1	
Amblyeleotris periophthalma	7231	1				
Amblyglyphidodon leucogaster	5691			1		
Amblygobius decussatus	7197		1			
Amblygobius nocturnus	7243	1				1
Amblygobius phalaena	7198	1	1	1		1
Amphiprion chrysopterus	4551		1	1		1
Amphiprion clarkii	5448			1		
Anampses caeruleopunctatus	4888	1	1	1	1	1
Anampses femininus	4892	1	1	1		1
Anampses melanurus	5622	1	1	1	1	1
Anampses meleagrides	4889		1	1	1	
Anampses neoguinaicus	4890			1		
Anampses twistii	4893	1	1	1		1
Anarchias exulatus	65812	1				
Anarchias seychellensis	6485	1	1	1	1	1
Anguilla marmorata	1275		1			
Anguilla megastoma	12408		1			
Anguilla obscura	7511	1				
Antennarius randalli	7295		1			
Antennarius striatus	5474				1	
Antennatus coccineus	5402		1	1	1	1
Antennatus nummifer	5403	1			1	
Antennatus tuberosus	11150	1	1	1	1	1
Aphareus furca	81	1	1	1	1	1
Aplochiton taeniatus	12870		1			
Apogon brevispinis	61523	1				
Apogon caudicinctus	58152	1			1	
Apogon coccineus	5752		1			
Apogon crassiceps	12992	1	1	1		1
Apogon deetsie	51830		1	1		
Apogon doryssa	5753	1	1	1		
Apogon indicus	60052	1				
Apogon lativittatus	59452			1	1	
Apogon marquesensis	60054				1	
Apogon susanae	60053	1				1
Apogonichthys ocellatus	5740		1	1	1	
Apogonichthys perdix	5741	1			1	1
Aporops bilinearis	14996	1	1	1	1	1
Aprion virescens	84	1	1	1	1	1
Apterichtus klazingai	12884				1	
Ariosoma scheelei	7672	1	1			
Arothron hispidus	5425	1	1		1	1

Arothron meleagris	6401	1	1	1	1	1
Arothron stellatus	6526		1	1	1	
Aseraggodes melanostictus	22522		1			
Aspidontus dussumieri	6065			1		
Aspidontus taeniatus	6066		1	1	1	
Asterorhombus filifer	63068		1			1
Asterropteryx ensifera	7247		1			1
Asterropteryx semipunctata	7200	1	1	1		1
Atherinomorus lacunosus	1303	1				
Atrosalarias fuscus	17462		1			
Aulostomus chinensis	1309	1	1	1	1	1
Balistapus undulatus	6025		1	1	1	
Balistoides viridescens	6026		1	1	1	
Bathygobius coalitus	25423		1			1
Bathygobius cocosensis	7202	1		1		1
Bathygobius cotticeps	7249	1	1			
Bathygobius cyclopterus	11801				1	
Bathystethus orientale	55307	1				
Blenniella caudolineata	27178			1		
Blenniella chrysospilos	6047			1		
Blenniella gibbifrons	7871	1	1	1	1	1
Blenniella paula	27183			1		1
Bodianus anthioides	5497	1		1		
Bodianus axillaris	5498	1	1	1	1	1
Bodianus bilunulatus	6580			1	1	
Bodianus loxozonus	12744	1		1	1	
Bodianus mesothorax	5501			1		
Bodianus oxycephalus	6925	1				
Bodianus perditio	7734	1				1
Bothus mancus	7641	1	1	1		1
Bothus pantherinus	1321	1	1	1	1	1
Brosmophyciops pautzkei	7299					1
Brotula multibarata	7297		1		1	1
Brotula townsendi	17414			1		
Bryaninops ridens	7250				1	
Bryaninops yongei	7251		1		1	
Cabillus tongarevae	7252		1			1
Callechelys marmorata	12889		1		1	
Callechelys randalli	53955				1	
Callionymus marquesensis	60077				1	
Callionymus simplicicornis	17470	1	1	1		1
Callogobius maculipinnis	7206	1	1	1		1
Callogobius sclateri	7257	1	1	1		1
Calotomus carolinus	4355	1	1	1	1	
Calumia godeffroyi	13765		1			
Cantherhines dumerilii	5836	1	1	1	1	1
Cantherhines longicaudus	54607	1		1		1
Cantherhines nukuhiva	66329				1	
Cantherhines pardalis	6635	1	1	1	1	1
Cantherhines sandwichiensis	7835	1	1	1		1
Canthigaster amboinensis	7840	1	1		1	1
Canthigaster axiologus	65366	1				1
Canthigaster bennetti	6541		1	1		
Canthigaster criobe	67437				1	1
Canthigaster janthinoptera	6543	1	1	1	1	1
Canthigaster marquesensis	55005				1	
Canthigaster papua	55072	1	1	1		
Canthigaster punctatissima	14159			1		
Canthigaster rapaensis	55008	1				
Canthigaster solandri	6578	1	1	1	1	1
Canthigaster valentini	6544		1	1		
Caracanthus maculatus	7873	1	1	1	1	1
Caracanthus unipinna	12899	1	1	1		1
Carangoides ferdau	1921		1	1		1
Carangoides orthogrammus	1909	1	1	1	1	1
Caranx ignobilis	1895	1	1	1	1	1
Caranx lugubris	1936	1	1	1	1	1
Caranx melampygus	1906	1	1	1	1	1
Caranx papuensis	6360				1	1
Caranx sexfasciatus	1917		1	1		
Carapus mourlani	16791		1			
Carcharhinus amblyrhynchos	861	1	1	1		
Carcharhinus galapagensis	870	1				
Carcharhinus melanopterus	877	1	1	1	1	1
Carcharias taurus	747			1		
Centropyge bicolor	5454			1		
Centropyge bispinosa	5458	1	1	1		
Centropyge fisheri	7813			1		
Centropyge flavicauda	5664	1	1			1
Centropyge flavissima	5457	1	1	1	1	1

Centropyge heraldi	5665	1	1	1		1
Centropyge hotumatua	10982	1				
Centropyge loriculus	7814	1	1	1	1	1
Centropyge multicolor	11000		1			
Centropyge nigriocella	11100	1	1		1	
Cephalopholis argus	6396	1	1	1	1	1
Cephalopholis aurantia	6443		1			
Cephalopholis leopardus	6448		1	1		
Cephalopholis microprion	6449			1		
Cephalopholis sexmaculata	6453		1	1	1	
Cephalopholis spiloparaea	6455	1	1	1	1	1
Cephalopholis urodeta	6456	1	1	1	1	1
Cercamia cladara	58339	1				1
Cetoscarus ocellatus	66097		1	1		
Chaetodon auriga	5557	1	1	1	1	1
Chaetodon bennetti	5559	1	1	1		1
Chaetodon citrinellus	5561	1	1	1	1	1
Chaetodon declivis	12259				1	
Chaetodon ephippium	5562	1	1	1	1	1
Chaetodon flavirostris	6527	1		1		1
Chaetodon kleinii	5446	1				
Chaetodon lineolatus	5564		1	1		
Chaetodon lunula	5565	1	1	1	1	1
Chaetodon lunulatus	14300	1	1	1		1
Chaetodon melannotus	5566		1			
Chaetodon mertensii	5567	1	1	1	1	1
Chaetodon meyeri	5568			1		
Chaetodon ocellicaudus	5569			1		
Chaetodon ornatissimus	6550	1	1	1	1	1
Chaetodon pelewensis	6606	1	1	1	1	1
Chaetodon quadrimaculatus	5572	1	1	1	1	1
Chaetodon reticulatus	5574	1	1	1	1	1
Chaetodon semeion	5575		1	1		
Chaetodon smithi	12648	1				
Chaetodon trichrous	12537	1	1	1	1	
Chaetodon trifascialis	5578	1	1	1		1
Chaetodon trifasciatus	5579		1		1	
Chaetodon ulietensis	5580	1	1	1	1	1
Chaetodon unimaculatus	5581	1	1	1	1	1
Chaetodon vagabundus	5582	1	1	1		1
Chaetodontoplus duboulayi	10823			1		
Chalixodytes chameleontoculis	16930	1	1		1	1
Chalixodytes tauensis	17454	1			1	1
Chanos chanos	80		1	1	1	
Cheilinus chlorourus	5598	1	1	1		1
Cheilinus oxycephalus	5602	1	1	1		1
Cheilinus trilobatus	5603	1	1	1		1
Cheilinus undulatus	5604		1	1		
Cheilio inermis	5623	1	1			1
Cheilodactylus plessisi	24447	1				
Cheilodipterus artus	5780		1	1		1
Cheilodipterus macrodon	5781	1	1	1	1	1
Cheilodipterus quinquelineatus	5482	1	1	1		1
Cheilopogon pitcairnensis	15351		1			
Chilorhinus platyrhynchus	7446		1			
Chlorurus frontalis	5547		1	1		
Chlorurus microrhinos	60479	1	1	1		
Chlorurus sordidus	5556	1	1	1		1
Choeroichthys brachysoma	5958		1	1		
Chromis abrupta	58941				1	
Chromis acares	5668	1	1	1		1
Chromis agilis	5669	1	1	1		1
Chromis alpha	5670		1	1	1	
Chromis atripectoralis	5450	1	1	1		1
Chromis bami	26704	1		1		1
Chromis dimidiata	11861		1			
Chromis fatuhivae	58943				1	
Chromis flavapicis	58948				1	
Chromis iomelas	8126		1	1		
Chromis leucura	6599				1	
Chromis margaritifer	5675	1	1	1	1	1
Chromis nitida	9225			1		
Chromis opercularis	12427		1			
Chromis pamae	26693	1				1
Chromis planesi	62017	1				
Chromis vanderbilti	5678	1	1	1		1
Chromis viridis	5679	1	1	1		1
Chromis xanthura	5682	1	1	1	1	1
Chrysiptera brownriggii	5697	1	1			1
Chrysiptera galba	12439	1		1		1

Chrysiptera glauca	5696		1	1		1
Chrysiptera rollandi	5486		1			
Chrysiptera talboti	5700			1		
Chrysiptera traceyi	5701				1	
Cirrhilabrus exquisitus	5614	1	1	1		1
Cirrhilabrus punctatus	13028			1		
Cirrhilabrus scottorum	12728	1	1	1		1
Cirrhichthys falco	5445				1	
Cirrhichthys oxycephalus	5830	1	1	1	1	1
Cirrhitops hubbardi	12693					1
Cirrhites pinnulatus	5831	1	1	1	1	1
Cirripectes alboapicalis	4385	1				1
Cirripectes fuscoguttatus	4390	1	1			
Cirripectes jenningsi	4394	1				
Cirripectes quagga	4399	1	1		1	1
Cirripectes springeri	4401				1	
Cirripectes variolosus	4404	1	1	1	1	1
Conger cinereus	6654	1	1	1	1	
Coris aygula	5624	1	1	1	1	1
Coris bulbifrons	12729			1		
Coris gaimard	5625	1	1	1	1	1
Coris hewetti	55344				1	
Coris marquesensis	55347				1	
Coris roseoviridis	55349	1		1		1
Coryphopterus humeralis	59445		1			
Corythoichthys conspicillatus	66915		1	1		
Corythoichthys flavofasciatus	5959		1	1		
Crenimugil crenilabis	5653	1	1	1		1
Cryptocentrus caeruleomaculatus	25798			1		
Crystalloides cookei	58169				1	
Ctenochaetus binotatus	6012	1	1	1		
Ctenochaetus cyanocheilus	59486			1		
Ctenochaetus flavicauda	59589	1	1	1	1	1
Ctenochaetus hawaiiensis	6013	1	1		1	1
Ctenochaetus marginatus	6014				1	
Ctenochaetus striatus	1262	1	1	1		1
Ctenochaetus strigosus	6015	1	1	1		
Ctenogobiops feroculus	7238		1			
Cymolutes praetextatus	5607				1	
Dactyloptena orientalis	4485		1			
Dascyllus aruanus	5110	1	1	1		1
Dascyllus flavicaudus	11972	1	1	1		1
Dascyllus reticulatus	5113		1	1		
Dascyllus strasburgi	9254		1		1	
Dascyllus trimaculatus	5112	1	1	1		1
Decapterus macarellus	993	1	1			1
Dendrochirus biocellatus	5827		1	1		
Diagramma labiosum	56923			1		
Diancistrus katrineae	63208		1	1		
Diodon holocanthus	4659	1		1		
Diodon hystrix	1022	1	1	1	1	
Diodon lituosus	6552	1	1	1		1
Diplogrammus goramensis	13764	1		1		1
Discordipinna griessingeri	7212					1
Doryrhamphus excisus excisus	5969	1	1	1	1	1
Dunckerocampus dactyliophorus	5972			1		
Echeneis naucrates	2467		1	1		
Echidna leucotaenia	6486		1			1
Echidna nebulosa	5388		1			
Echidna polyzona	5389		1			
Echidna unicolor	6487	1		1		1
Ecsenius midas	7561				1	
Elagatis bipinnulata	412	1	1	1	1	
Eleotris fusca	8034	1	1			
Ellochelone vaigiensis	5656	1	1	1		1
Encheliophis boraborensis	16829			1		
Enchelycore bayeri	6488		1			
Enchelycore pardalis	7451				1	
Enchelynassa canina	6491				1	
Enchelyurus ater	13753	1	1	1	1	1
Enneapterygius hemimelas	14196		1			
Enneapterygius nigricauda	51547		1			1
Enneapterygius pyramis	46984		1	1		1
Enneapterygius randalli	51551	1				
Enneapterygius rhabdotus	46987				1	
Enneapterygius williamsi	51561	1				
Entomacrodus caudofasciatus	6037	1				1
Entomacrodus corneliae	58172				1	
Entomacrodus cymatobotus	6038	1	1			1
Entomacrodus macropsilus	60082				1	

<i>Entomacrodus niuafoouensis</i>	6040	1				1
<i>Entomacrodus randalli</i>	60081				1	
<i>Entomacrodus sealei</i>	6041	1		1		1
<i>Entomacrodus striatus</i>	6043	1		1		
<i>Entomacrodus thalassinus</i>	6044	1	1			1
<i>Epibulus insidiator</i>	5606		1	1		1
<i>Epinephelus fasciatus</i>	5348	1	1	1	1	1
<i>Epinephelus hexagonatus</i>	6660	1	1	1		1
<i>Epinephelus irroratus</i>	7393				1	
<i>Epinephelus macrospilos</i>	6661		1	1	1	
<i>Epinephelus melanostigma</i>	6471			1		
<i>Epinephelus merra</i>	4923	1	1	1		1
<i>Epinephelus polyphkadion</i>	6473	1		1		1
<i>Epinephelus sexfasciatus</i>	4825			1		
<i>Epinephelus socialis</i>	7362	1	1	1		
<i>Epinephelus spilotoceps</i>	5837			1		
<i>Epinephelus tauvina</i>	4461	1	1	1		1
<i>Euthynnus affinis</i>	96				1	
<i>Eviota afelei</i>	7258		1	1	1	1
<i>Eviota albolineata</i>	7259		1	1		1
<i>Eviota deminuta</i>	67174				1	
<i>Eviota disrupta</i>	61063	1	1			1
<i>Eviota distigma</i>	7261	1	1	1		
<i>Eviota dorsimaculata</i>	67173				1	
<i>Eviota epiphanes</i>	23544	1				
<i>Eviota herrei</i>	7263	1				
<i>Eviota hinanoae</i>	67167	1	1			1
<i>Eviota infulata</i>	7264		1	1	1	1
<i>Eviota lacrimosa</i>	67171				1	
<i>Eviota latifasciata</i>	7266	1	1			
<i>Eviota melasma</i>	7267	1				1
<i>Eviota nebulosa</i>	7268			1		
<i>Eviota pellucida</i>	7269	1				
<i>Eviota prasites</i>	7271		1			1
<i>Eviota randalli</i>	65416	1				
<i>Eviota zonura</i>	22459		1			
<i>Evistias acutirostris</i>	12350	1				
<i>Exallias brevis</i>	6032	1	1	1		1
<i>Feia nympha</i>	52936	1				
<i>Fistularia commersonii</i>	5444	1	1	1	1	1
<i>Fistularia petimba</i>	3276				1	
<i>Foa leisi</i>	67006	1				
<i>Forcipiger flavissimus</i>	5584	1	1	1	1	1
<i>Forcipiger longirostris</i>	5585	1	1	1	1	1
<i>Fowleria aurita</i>	8010		1			
<i>Fowleria isostigma</i>	59779		1	1		
<i>Fowleria marmorata</i>	5744		1		1	
<i>Fowleria punctulata</i>	5743	1				
<i>Fowleria vaiulae</i>	8592		1	1		1
<i>Fowleria variegata</i>	5745					1
<i>Fusigobius duospilus</i>	17056		1	1	1	
<i>Fusigobius inframesulatus</i>	26684				1	
<i>Fusigobius neophytus</i>	7215	1	1	1		1
<i>Genicanthus bellus</i>	5667		1			
<i>Genicanthus spinus</i>	11158	1				
<i>Genicanthus watanabei</i>	8711	1	1			1
<i>Glyptoparus delicatulus</i>	6045		1			
<i>Gnathanodon speciosus</i>	4464		1	1	1	
<i>Gnathodentex aureolineatus</i>	1832	1	1	1	1	1
<i>Gnatholepis anjerensis</i>	23595	1	1	1	1	1
<i>Gnatholepis cauerensis</i>	9950	1	1		1	1
<i>Gnatholepis knighti</i>	66652		1			
<i>Gobiodon ceramensis</i>	61404	1				
<i>Gobiodon citrinus</i>	7789	1		1		
<i>Gobiodon oculolineatus</i>	23659	1	1			1
<i>Gobiodon prolixus</i>	62645			1		1
<i>Gobiodon quinquestrigatus</i>	22462	1	1			
<i>Gobiodon rivulatus</i>	9952	1	1	1		
<i>Gobiodon unicolor</i>	59869					1
<i>Gobiopsis exigua</i>	61025		1			
<i>Gomphosus varius</i>	5626	1	1	1	1	1
<i>Gorgasia galzini</i>	55050				1	
<i>Gracila albomarginata</i>	6477		1	1		
<i>Grammatorcynus bilineatus</i>	104		1	1		
<i>Grammistes sexlineatus</i>	4925	1	1	1		1
<i>Grammistops ocellatus</i>	7315		1			
<i>Gunnellichthys monostigma</i>	12678		1		1	
<i>Gymnapogon urosilotus</i>	5787		1		1	
<i>Gymnapogon vanderbilti</i>	59175	1			1	
<i>Gymnocranius grandoculis</i>	1834				1	



Gymnosarda unicolor	106	1	1	1	1	
Gymnothorax australicola	27690	1				
Gymnothorax breedeni	7881				1	
Gymnothorax buroensis	6493	1	1		1	
Gymnothorax chilospilus	5390	1	1	1		1
Gymnothorax euostus	6662	1		1		1
Gymnothorax fimbriatus	6495		1	1	1	1
Gymnothorax flavimarginatus	5392	1	1	1	1	1
Gymnothorax formosus	58588				1	
Gymnothorax fuscomaculatus	6496	1	1	1	1	1
Gymnothorax gracilicauda	6497		1	1	1	1
Gymnothorax javanicus	6380		1	1	1	
Gymnothorax kontodontos	58597		1	1		
Gymnothorax margaritophorus	5393		1	1	1	1
Gymnothorax melatremus	7284	1	1	1	1	1
Gymnothorax meleagris	5394	1	1		1	1
Gymnothorax moluccensis	27334		1			
Gymnothorax monostigma	14688				1	
Gymnothorax pictus	6395		1	1		
Gymnothorax pindae	7447			1		
Gymnothorax porphyreus	27501	1				
Gymnothorax reevesii	10159		1			
Gymnothorax rueppelliae	5396	1	1		1	
Gymnothorax shaoi	64161				1	
Gymnothorax thyrsoides	8252	1			1	
Gymnothorax undulatus	4905		1	1		1
Gymnothorax zonipectis	5397		1		1	
Halichoeres claudia	65073	1	1	1	1	1
Halichoeres hortulanus	12663	1	1	1		1
Halichoeres margaritaceus	5630	1	1	1	1	1
Halichoeres marginatus	5631	1	1	1		1
Halichoeres melanurus	4858			1		
Halichoeres melasmapomus	4856	1	1	1	1	
Halichoeres trimaculatus	5634	1	1	1		1
Helcogramma capidata	8502		1			
Hemigymnus fasciatus	5635	1	1	1	1	1
Hemigymnus melapterus	5636			1		
Hemiramphus depauperatus	7507	1	1		1	
Hemitaurichthys multispinosus	25435	1				
Hemitaurichthys polylepis	5586	1	1	1		1
Hemitaurichthys thompsoni	5587	1	1	1	1	
Heniochus acuminatus	5588		1	1	1	1
Heniochus chrysostomus	5589	1	1	1		1
Heniochus monoceros	5590	1	1	1		1
Heteroconger lentiginosus	55150		1			
Heteropriacanthus cruentatus	1150	1	1	1	1	1
Himantura fai	12587		1			
Hipposcarus longiceps	5539		1	1		
Hologymnosus annulatus	5637	1	1	1		1
Hyporhamphus acutus	7505	1		1		
Hyporhamphus affinis	7710			1		
Hyporhamphus dussumieri	12895			1		
Iniistius auropunctatus	59859				1	
Iniistius pavo	5613		1			
Iracundus signifer	7780	1				
Isocirrhites sexfasciatus	5834	1		1		
Istiblennius edentulus	6049		1	1	1	1
Kaupichthys brachychirus	17390		1	1		
Kaupichthys diodontus	25703	1	1	1	1	1
Kuhlia malo	60749		1			
Kuhlia marginata	5789	1	1	1		
Kuhlia mugil	5790	1	1			
Kuhlia sandvicensis	5157	1	1	1		1
Kyphosus bigibbus	5804	1		1		
Kyphosus cinerascens	5805		1	1	1	
Kyphosus ocyurus	3598				1	
Kyphosus pacificus	62424	1		1		1
Kyphosus sectatrix	2498	1				
Kyphosus vaigiensis	5806	1	1	1	1	1
Labroides bicolor	5650	1	1	1	1	1
Labroides dimidiatus	5459	1	1	1	1	1
Labroides pectoralis	5651			1		
Labroides rubrolabiatus	23530	1	1	1	1	1
Labropsis australis	4868			1		
Labropsis polynesica	4864	1	1	1		
Lachneratus phasmaticus	12671				1	
Lactoria cornuta	6399		1			
Lactoria diaphana	6554	1				
Lactoria fornasini	7837	1				
Leiuranus semicinctus	7473	1	1		1	1

Lepadichthys frenatus	24186	1			1	1
Lepidozygus tapeinosoma	5683		1	1	1	
Leptomelanosoma indicum	4469		1			
Leptoscarus vaigiensis	4360	1	1		1	
Lethrinus amboinensis	1853		1	1		
Lethrinus atkinsoni	1854			1		
Lethrinus erythracanthus	1862			1		
Lethrinus laticaudis	1857			1		
Lethrinus microdon	1845		1	1		
Lethrinus olivaceus	1864		1	1	1	
Lethrinus xanthochilus	1852		1	1	1	
Limnichthys fasciatus	13514					1
Limnichthys nitidus	16931	1	1		1	
Liopropoma lunulatum	12862		1			
Liopropoma mitratum	8432			1		
Liopropoma pallidum	7316	1	1	1		1
Liopropoma tonstrinum	12869		1			
Lotella phycis	23157	1				
Lutjanus bohar	1417	1	1	1	1	1
Lutjanus fulviflamma	261			1		
Lutjanus fulvus	262	1	1	1	1	1
Lutjanus gibbus	265		1	1	1	
Lutjanus kasmira	156	1	1	1	1	1
Lutjanus monostigma	166	1	1	1	1	1
Lutjanus rivulatus	173			1		
Lutjanus vitta	184		1			
Lycengraulis limnichthys	61556				1	
Macropharyngodon meleagris	4984	1	1	1	1	1
Macropharyngodon pakokom	67486				1	
Malacanthus brevirostris	5795	1	1		1	1
Manta birostris	2061				1	
Medusablennius chani	67036		1			
Megalops cyprinoides	227		1			
Melichthys niger	966		1	1	1	
Melichthys vidua	5838	1	1	1	1	1
Micrognathus andersonii	5977	1				1
Monopenchelys acuta	9037					1
Monotaxis grandoculis	1869	1	1	1	1	1
Moolgarda engeli	5658		1			1
Moringua javanica	15801		1			
Mugil cephalus	785		1	1		
Mulloidichthys flavolineatus	5983	1	1	1	1	1
Mulloidichthys mimicus	25437				1	
Mulloidichthys vanicolensis	5984	1	1	1	1	1
Muraenichthys gymnopterus	17345					1
Myrichthys colubrinus	8053				1	
Myrichthys maculosus	2650	1			1	
Myripristis adusta	6506		1	1	1	
Myripristis amaena	7773	1	1	1	1	1
Myripristis berndti	4910	1	1	1	1	1
Myripristis earlei	61370		1		1	
Myripristis kuntee	7306	1	1	1	1	1
Myripristis murdjan	5408	1	1	1		
Myripristis pralinia	7308	1	1	1		1
Myripristis randalli	12753	1				
Myripristis tiki	17189	1			1	
Myripristis violacea	7309	1	1	1		1
Myripristis vittata	6505				1	
Myripristis woodsi	17190	1	1			
Myrophis microchir	22602		1	1	1	1
Nannosalarias nativitatis	6053		1	1		1
Naso annulatus	6019		1	1		
Naso brachycentron	6020		1		1	
Naso brevirostris	6021	1	1	1	1	1
Naso caesius	15628			1	1	
Naso hexacanthus	1263	1	1	1	1	1
Naso lituratus	1264	1	1	1	1	1
Naso thynnoides	6932			1		
Naso unicornis	1265	1	1	1	1	1
Naso vlamingii	6024	1	1	1	1	1
Nebrius ferrugineus	5895		1	1		
Nectamia bandanensis	5763		1			
Nectamia fusca	59777			1		
Nectamia luxuria	63750		1			
Nectamia savayensis	5764		1	1		1
Negaprion acutidens	896		1			
Nemateleotris magnifica	6629	1	1	1	1	1
Neocirrhites armatus	5832	1	1	1		1
Neoglyphidodon melas	5707			1		
Neoglyphidodon nigroris	5708			1		

Neomyxus leuciscus	5652	1		1		1
Neoniphon argenteus	7310		1	1		1
Neoniphon opercularis	6582	1	1	1		1
Neoniphon sammara	4911	1	1	1		1
Neosynchiropus ocellatus	7981				1	
Norfolkia thomasi	47191	1	1	1		1
Novaculichthys taeniourus	5610	1	1	1	1	1
Odontanthias tapui	56328		1			
Odonus niger	1311		1		1	
Onigocia bimaculata	61099					1
Onuxodon fowleri	12785				1	
Ophidion muraenolepis	10526				1	
Oplopomus oplopomus	7218					1
Oreochromis mossambicus	3		1			
Ostorhinchus angustatus	5766	1	1		1	1
Ostorhinchus apogonoides	10294		1		1	
Ostorhinchus cyanosoma	4600		1			
Ostorhinchus fleurieu	4838			1		
Ostorhinchus nigrofasciatus	4836	1	1	1		1
Ostorhinchus novemfasciatus	5768	1	1			
Ostorhinchus relativus	59453		1		1	
Ostorhinchus sinus	59454				1	
Ostorhinchus taeniophorus	5767	1				1
Ostracion cubicus	6555	1	1	1		1
Ostracion meleagris	6556	1	1	1	1	1
Ostracion whiteyi	7862				1	
Oxycheilinus bimaculatus	5596	1	1		1	
Oxycheilinus digramma	5599	1		1		
Oxycheilinus unifasciatus	5605	1	1	1	1	1
Oxymonacanthus longirostris	6559		1			
Oxyurichthys rapa	51700	1				
Palutrus pruinosa	61312		1			
Paracaesio sordida	192				1	
Paracentropyge multifasciata	5666		1		1	
Paracirrhites nesus	56330			1		
Paracirrhites xanthus	49449			1		
Paracirrhites arcatus	5835	1	1	1	1	1
Paracirrhites forsteri	5952	1	1	1	1	1
Paracirrhites hemistictus	5953	1	1	1		1
Paracirrhites nesus	56330			1		
Paracirrhites xanthus	49449			1		
Paradiancistrus acutirostris	63231					1
Paragobiodon echinocephalus	7219	1		1	1	1
Paragobiodon lacunicolus	22476		1	1		
Paragobiodon modestus	22477		1	1		1
Paramugil georgii	15756					1
Parapercis cephalopunctata	27593		1			
Parapercis millepunctata	6670	1	1	1	1	1
Parapercis multiplicata	10753	1				
Parapercis schauinslandii	7872		1		1	
Parascorpaena mcadamsi	5809	1		1	1	1
Parascorpaena mossambica	5810	1		1	1	1
Parioglossus galzini	62032	1				
Parupeneus barberinoides	5986			1		
Parupeneus barberinus	5987	1	1	1		1
Parupeneus chrysopleuron	10470				1	
Parupeneus ciliatus	5989	1	1	1	1	1
Parupeneus crassilabris	60947		1	1		
Parupeneus cyclostomus	5990	1	1	1	1	1
Parupeneus indicus	5992				1	
Parupeneus insularis	60849	1	1	1	1	1
Parupeneus multifasciatus	5993	1	1	1	1	1
Parupeneus pleurostigma	5994	1	1	1	1	1
Parupeneus trifasciatus	5988		1	1		
Pascua sticta	62976	1				
Pempheris otaitensis	60241			1		
Pempheris oualensis	5802	1	1	1	1	1
Pempheris rapa	50769	1				
Pempheris vanicolensis	10350			1		
Pervagor aspricaudus	4367	1	1	1		1
Pervagor janthinosoma	4368			1	1	
Pervagor marginalis	4369	1		1	1	
Pervagor melanocephalus	4370		1			
Petroscirtes xestus	6077		1			1
Phyllophichthys xenodontus	7470		1		1	
Plagiotremus rhinorhynchus	6071		1		1	
Plagiotremus tapeinosoma	6072	1	1	1	1	1
Platax orbicularis	5737		1			
Platybelone argalus argalus	1150		1	1		
Plectorhinchus picus	6370	1		1		

Plectranthias cirrhitoides	26729	1					
Plectranthias flammeus	66972					1	
Plectranthias fourmanoiri	12797	1	1				1
Plectranthias longimanus	7322		1				
Plectranthias nanus	15118	1	1	1		1	1
Plectranthias winniensis	12799		1				1
Plectroglyphidodon dickii	5709	1	1	1		1	1
Plectroglyphidodon flaviventris	10242		1	1			
Plectroglyphidodon imparipennis	5710	1	1	1			1
Plectroglyphidodon johnstonianus	5711	1	1	1		1	1
Plectroglyphidodon lacrymatus	5712	1	1	1		1	1
Plectroglyphidodon leucozonus	5713	1	1	1		1	1
Plectroglyphidodon phoenixensis	5714	1	1	1		1	1
Plectroglyphidodon sagmarius	55481					1	
Plectropomus leopardus	4826			1			
Plectropomus laevis	7372	1		1			1
Plectrypops lima	12893	1	1	1		1	1
Pleurosicya australis	59334	1					1
Pleurosicya coerulea	56839	1					
Pleurosicya fringilla	26318			1		1	1
Pleurosicya labiata	59437		1			1	
Pleurosicya micheli	25509	1	1				1
Pleurosicya mossambica	23079		1			1	
Pleurosicya plicata	27570					1	
Poecilia reticulata	3228		1				
Pogonoperca punctata	12727			1		1	
Polydactylus plebeius	7901		1				
Polydactylus sexfilis	6416	1	1			1	
Pomacanthus imperator	6504	1	1	1			1
Pomacentrus moluccensis	5724			1			
Pomacentrus coelestis	5720		1	1		1	
Pomacentrus imitator	12489					1	
Pomacentrus moluccensis	5724			1			
Pomacentrus pavo	5726		1	1		1	1
Pomacentrus vaiuli	5730	1					1
Pomachromis fuscidorsalis	10282	1	1	1			1
Pomachromis richardsoni	6923			1			
Praealticus caesius	61224	1		1			
Priacanthus hamrur	5791			1		1	1
Priolepis ailina	59325		1			1	
Priolepis cincta	7221		1				
Priolepis compita	26317		1	1		1	1
Priolepis inhaca	8032		1				
Priolepis kappa	27354	1					1
Priolepis nocturna	25525					1	
Priolepis pallidicincta	56842					1	
Priolepis semidoliata	12885	1	1	1			1
Priolepis squamogena	56844	1	1	1		1	1
Priolepis triops	59408		1			1	
Pristiapogon exostigma	5756	1	1	1			1
Pristiapogon fraenatus	5757		1	1			1
Pristiapogon kallopterus	5758	1	1			1	1
Pristiapogon taeniopterus	5755		1	1		1	1
Pristipomoides auricilla	200		1				
Pristipomoides filamentosus	201		1				
Pseudamia gelatinosa	4362	1	1				
Pseudamiops gracilicauda	5788	1	1			1	1
Pseudamiops phasma	59455					1	
Pseudanthias bicolor	7874		1				
Pseudanthias hiva	60821					1	
Pseudanthias mooreanus	59194		1	1			
Pseudanthias olivaceus	46510	1	1	1			1
Pseudanthias oumati	66973					1	
Pseudanthias pascalus	6934	1	1	1			1
Pseudanthias regalis	26872					1	
Pseudanthias ventralis ventralis	12700		1	1			1
Pseudechidna brummeri	10216		1				
Pseudobalistes flavimarginatus	6027	1	1	1			1
Pseudobalistes fuscus	4466	1		1			1
Pseudocaranx dentex	1002	1		1			1
Pseudocheilinus citrinus	55229	1					
Pseudocheilinus evanidus	5616	1	1	1			
Pseudocheilinus hexataenia	5617		1	1			
Pseudocheilinus ocellatus	55234		1	1			1
Pseudocheilinus octotaenia	5618	1	1	1		1	1
Pseudocheilinus tetrataenia	5619	1	1	1			1
Pseudocoris aurantiofasciata	25783		1	1		1	
Pseudodax moluccanus	5594		1			1	
Pseudogramma polyacantha	7320	1	1	1		1	1
Pseudogramma xantha	49428						1

<i>Pseudojuloides atavai</i>	4849	1	1	1		1
<i>Pseudojuloides cerasinus</i>	4851	1	1	1		
<i>Pseudojuloides pyrius</i>	4850				1	
<i>Pseudolabrus fuentesi</i>	46949	1				
<i>Pseudolabrus torotai</i>	46959	1				
<i>Pseudoplesiops revellei</i>	15021	1	1	1		1
<i>Pseudoplesiops rosae</i>	14270		1			
<i>Pteragogus enneacanthus</i>	52464	1		1		1
<i>Ptereleotris evides</i>	4375	1	1	1		1
<i>Ptereleotris heteroptera</i>	4378		1		1	
<i>Ptereleotris melanopogon</i>	4380				1	
<i>Ptereleotris microlepis</i>	4381		1			1
<i>Ptereleotris monoptera</i>	4382		1			1
<i>Ptereleotris zebra</i>	4384		1		1	
<i>Pterocaesio marri</i>	935				1	
<i>Pterocaesio tile</i>	939	1	1	1	1	1
<i>Pterois antennata</i>	4914	1	1	1	1	1
<i>Pterois mombasae</i>	10288		1			
<i>Pterois radiata</i>	4913	1	1	1		1
<i>Pterois volitans</i>	5195				1	
<i>Pygoplites diacanthus</i>	6572		1	1		
<i>Remora remora</i>	1751				1	
<i>Rhabdoblennius nitidus</i>	13762				1	
<i>Rhabdoblennius rhabdotrachelus</i>	6056	1	1	1		
<i>Rhinecanthus aculeatus</i>	5839	1	1	1	1	1
<i>Rhinecanthus lunula</i>	13774	1	1			1
<i>Rhinecanthus rectangulus</i>	5840	1	1	1	1	1
<i>Rhinecanthus verrucosus</i>	6028		1			1
<i>Rhinopias cea</i>	50318	1				
<i>Saloptia powelli</i>	7374		1			
<i>Samariscus triocellatus</i>	8568		1		1	1
<i>Sarda orientalis</i>	114			1		
<i>Sardinella marquesensis</i>	1512				1	
<i>Sargocentron caudimaculatum</i>	4907		1	1	1	
<i>Sargocentron diadema</i>	4699	1	1	1		1
<i>Sargocentron hormion</i>	50111	1	1			1
<i>Sargocentron iota</i>	50117			1		
<i>Sargocentron ittodai</i>	6573					1
<i>Sargocentron lepros</i>	27348	1		1		
<i>Sargocentron microstoma</i>	5841	1	1	1	1	1
<i>Sargocentron punctatissimum</i>	4906	1	1	1	1	1
<i>Sargocentron rubrum</i>	6625			1		
<i>Sargocentron spiniferum</i>	6507	1	1	1		1
<i>Sargocentron tiere</i>	4908	1	1	1	1	1
<i>Sargocentron tiereoides</i>	7311		1	1		
<i>Sargocentron violaceum</i>	4909		1		1	
<i>Saurida flamma</i>	7772	1	1	1		1
<i>Saurida gracilis</i>	4534	1	1	1	1	1
<i>Saurida nebulosa</i>	8119			1	1	1
<i>Scarus altipinnis</i>	5540	1	1	1		1
<i>Scarus chameleon</i>	5543			1		
<i>Scarus festivus</i>	5544		1	1		
<i>Scarus forsteni</i>	5545	1	1	1	1	1
<i>Scarus frenatus</i>	5546	1	1	1		1
<i>Scarus ghobban</i>	5548	1	1	1		
<i>Scarus globiceps</i>	4970	1	1	1		1
<i>Scarus koputea</i>	4980				1	
<i>Scarus longipinnis</i>	4981	1	1	1		1
<i>Scarus niger</i>	5550	1	1	1	1	1
<i>Scarus oviceps</i>	5551	1	1	1		1
<i>Scarus psittacus</i>	5553	1	1	1	1	1
<i>Scarus rivulatus</i>	4969			1		
<i>Scarus rubroviolaceus</i>	5555	1	1	1	1	
<i>Scarus schlegeli</i>	4975	1	1	1		1
<i>Schedophilus velaini</i>	26371	1				
<i>Schismorhynchus labialis</i>	17410	1	1			
<i>Schultzidia johnstonensis</i>	7471		1		1	
<i>Scolecenchelys gymnota</i>	7288		1	1		1
<i>Scolecenchelys laticaudata</i>	15672	1	1	1		1
<i>Scolecenchelys macroptera</i>	7289	1	1			
<i>Scomberoides lysan</i>	1951		1	1	1	
<i>Scomberoides tol</i>	1953			1	1	
<i>Scorpaenodes albaiensis</i>	7313	1				
<i>Scorpaenodes evides</i>	59562	1			1	
<i>Scorpaenodes guamensis</i>	5819	1	1	1		
<i>Scorpaenodes hirsutus</i>	5815	1			1	1
<i>Scorpaenodes kelloggi</i>	5816			1	1	
<i>Scorpaenodes minor</i>	5817		1			
<i>Scorpaenodes parvipinnis</i>	4915	1	1	1	1	1
<i>Scorpaenodes quadrispinosus</i>	60274	1		1	1	

Scorpaenodes scaber	7314	1	1				1
Scorpaenodes varipinnis	5818	1					
Scorpaenopsis diabolus	4921	1	1	1	1		1
Scorpaenopsis macrochir	5820		1	1	1		
Scorpaenopsis oxycephala	5822					1	
Scorpaenopsis papuensis	56815			1	1		
Scorpaenopsis possi	59500	1	1		1		1
Scorpaenopsis pusilla	59501				1		
Sebastapistes fowleri	5821		1	1	1		1
Sebastapistes galactacma	5812				1		1
Sebastapistes mauritiana	5813	1			1		1
Sebastapistes strongia	5814			1	1		
Sebastapistes tinkhami	16869	1	1	1	1		1
Selar crumenophthalmus	387	1	1	1	1		1
Seriola lalandi	382	1	1				
Seriola rivoliana	1007		1				
Sicyopterus lagocephalus	9994		1				
Sicyopterus pugnans	26942		1				
Sicyopterus rapa	26938	1					
Siganus argenteus	4614	1	1	1	1		1
Siganus spinus	4457		1	1			
Sphyræna barracuda	1235	1	1	1	1		1
Sphyræna forsteri	5734		1	1			
Sphyræna helleri	6649	1			1		
Spratelloides gracilis	1458						1
Stanulus seychellensis	6061	1	1	1			1
Stanulus talboti	12642	1					1
Stegastes apicalis	4344			1			
Stegastes albifasciatus	4340	1	1	1			
Stegastes aureus	4345			1	1		
Stegastes emeryi	4346	1		1			1
Stegastes fasciolatus	4347	1	1	1			1
Stegastes lividus	58951			1	1		
Stegastes nigricans	4352	1	1	1	1		1
Stegastes punctatus	4351	1	1				
Stenogobius randalli	58656	1					
Stethojulis bandanensis	5640	1	1	1	1		1
Stethojulis interrupta	6633		1				
Stethojulis marquesensis	57372				1		
Stethojulis strigiventer	5641	1	1	1			1
Stethojulis trilineata	6622			1			
Stiphodon elegans	22507		1				
Stonogobiops medon	4309				1		
Strongylura incisa	8121		1	1			
Sufflamen bursa	6029	1	1	1	1		1
Sufflamen chrysopterum	5842			1	1		
Sufflamen fraenatum	1312		1	1	1		
Sunagocia otaitensis	12903	1	1		1		1
Suttonia lineata	49436	1	1				
Synanceia verrucosa	5825		1				
Synodus binotatus	7292	1	1		1		1
Synodus capricornis	55101	1					
Synodus dermatogenys	12620	1	1	1	1		1
Synodus jaculum	7943		1		1		1
Synodus myops	2724				1		
Synodus variegatus	5398	1	1	1	1		1
Taenianotus triacanthus	5824		1	1			
Taeniura meyeri	6482				1		
Thalassoma amblycephalum	5642	1	1	1	1		1
Thalassoma hardwicke	5643		1	1			1
Thalassoma heiseri	56820	1	1	1			1
Thalassoma lunare	5645			1			
Thalassoma lutescens	5646	1	1	1	1		1
Thalassoma purpureum	5647	1	1	1	1		1
Thalassoma quinquevittatum	5648	1	1	1	1		1
Thalassoma trilobatum	5649	1	1	1			1
Thysanophrys chiltonae	12902		1				
Trachinotus baillonii	1978		1		1		1
Triaenodon obesus	907	1	1	1	1		1
Trimma emeryi	25541		1				1
Trimma milta	61011		1				
Trimma taylori	12752				1		
Trimma unisquamis	58501	1	1				1
Trimma woutsi	61014				1		
Trimmatom eviotops	22494	1					1
Trimmatom nanus	25620		1				1
Tylosurus crocodilus	977	1	1	1			1
Upeneus taeniopterus	5995			1			
Upeneus vittatus	4821		1				
Uropterygius fuscoguttatus	7286		1		1		

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<i>Uropterygius inornatus</i>	58623		1	1		
<i>Uropterygius kamar</i>	15665	1	1	1		1
<i>Uropterygius macrocephalus</i>	7870	1			1	
<i>Uropterygius supraforatus</i>	17388		1			
<i>Uropterygius xanthopterus</i>	7287	1	1	1	1	1
<i>Valenciennea helsdingenii</i>	7224				1	
<i>Valenciennea puellaris</i>	7246	1				
<i>Valenciennea randalli</i>	12613		1			
<i>Valenciennea strigata</i>	6575	1	1			1
<i>Vanderhorstia ornatissima</i>	12784	1	1	1		1
<i>Variola louti</i>	5354	1	1	1	1	1
<i>Wetmorella albofasciata</i>	4869	1	1			
<i>Wetmorella nigropinnata</i>	4870		1	1	1	1
<i>Xanthichthys auromarginatus</i>	6030		1		1	
<i>Xanthichthys caeruleolineatus</i>	6359				1	
<i>Xanthichthys mento</i>	4284	1				
<i>Xenisthmus polyzonatus</i>	13766				1	
<i>Yirrkala moorei</i>	62662		1		1	
<i>Zanclus cornutus</i>	5950	1	1	1	1	1
<i>Zapogon evermanni</i>	5750				1	
<i>Zebrasoma flavescens</i>	6018		1			
<i>Zebrasoma rostratum</i>	25802	1	1	1	1	1
<i>Zebrasoma scopas</i>	5951	1	1	1		1
<i>Zebrasoma velifer</i>	1266	1	1	1		1

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# Etude de la distribution des peuplements ichthyques de Polynésie française

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## Contexte

Dans le Pacifique, il est admis que la biodiversité ichthyque diminue d'ouest en est (Ekman, 1953). Cependant, à l'échelle de la Polynésie française, aucun gradient n'est observé (Fig 1).

La distribution des peuplements ichthyques de Polynésie française peut-elle être expliquée par la surface habitable ?

## Matériel et Méthodes

Les données ont été collectées sur 48 îles selon la même méthode d'observation mais avec un nombre de transects variable. Une analyse Aire-Espèces a été effectuée selon 8 modèles (Table 1) et un modèle moyen (multi-modèle) a été créé en utilisant l'équation suivante :

$$\bar{S} = \sum_{i=1}^M S_i w_i$$

$\bar{S}$  est la richesse prédite du modèle moyen  
 $S_i$ , la richesse prédite du modèle  $i$   
 $w_i$ , le poids du modèle  $i$

Table 1. Utilisation de 8 modèles Aire-Espèces classiques

Nom	Formule	Forme
Puissance	$S = cA^Z$	Convexe
Exponentielle	$S = c + z \log(A)$	Convexe
Exponentielle négative	$S = c(1 - e^{-zA})$	Convexe
Monod	$S = (cA) / (z + A)$	Convexe
Rationnelle	$S = (c + zA) / (1 + fA)$	Sigmoïde
Logistique	$S = c / (1 + e^{-(zA + f)})$	Sigmoïde
Lomolino	$S = c / (1 + (z \log(f/A)))$	Sigmoïde
Weibull cumulative	$S = c(1 - e^{-(zA^f)})$	Sigmoïde

## Résultats

↗ du nombre d'espèces en fonction de la surface échantillonnée jusqu'à atteindre une asymptote (Fig 2A). De même, ↗ du nombre d'espèces en fonction de la surface disponible jusqu'à saturation du milieu (Fig 2B).

## Discussion et perspectives

La surface habitable est un des facteurs primordiaux pour expliquer la distribution de la faune ichthyque comme l'avaient démontré MacArthur et Wilson en 1967. L'utilisation d'un modèle général dynamique (Whittaker, 2008) utilisant l'âge des îles ou d'un modèle de connectivité (Bowen et al., 2006) est souhaitable pour mieux expliquer cette distribution.

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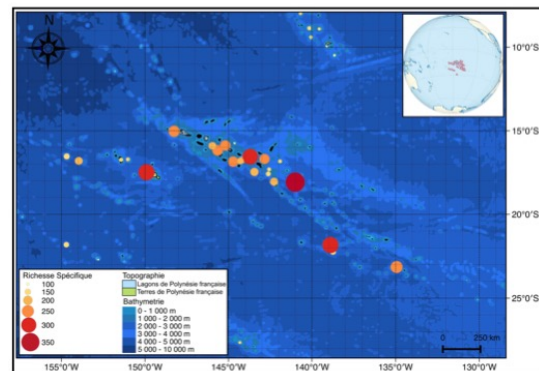


Figure 1. Représentation de la richesse spécifique de la faune ichthyque en Polynésie française

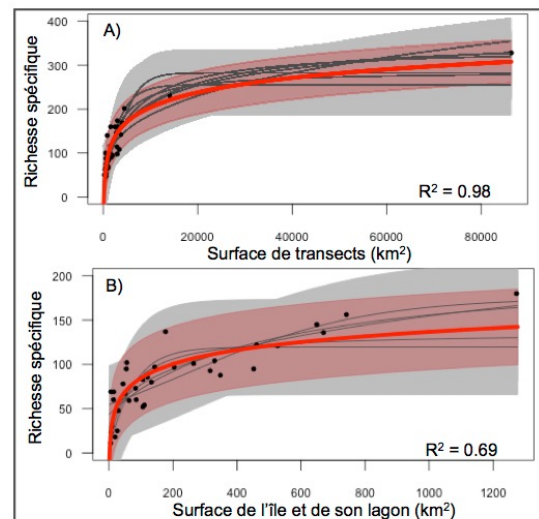


Figure 2. Elaboration de deux multi-modèles Aire-Espèces. A - Richesse spécifique maximale théorique obtenue par courbes d'accumulation d'espèces en fonction de la surface de transects. B - Richesse spécifique pour un nombre de transects proportionnels à la surface habitable en fonction de la surface de l'île et du lagon.



## Appendix V: Abstract and summary of the internship

	Diplôme : Master Approche Ecosystemique de l'Halieutique
	Spécialité : Halieutique
	Spécialisation / option : Ressources et Écosystèmes Aquatiques (REA)
	Enseignant référent : LE PAPE Olivier
Auteur(s) : CARLOT Jérémy	Organisme d'accueil : Centre de Recherches Insulaire et Observatoire de l'Environnement (CRIOBE).
Date de naissance* : 19/06/1992	Adresse : CRIOBE, Papetoai BP 1013 98729, Moorea, Polynesia Française
Nb pages : 22      Annexe(s) : 5	Maître de stage : René GALZIN
Année de soutenance : 2016	
Titre français : Etude de la distribution des peuplements ichthyiques de Polynésie française	
Titre anglais : Study of the fish distribution in French Polynesia	
Résumé (1600 caractères maximum) :	
<p>L'archipel Indo-Australien est décrit depuis des décennies comme le hotspot le plus conséquent d'espèces marines. Il a après été admis que la richesse spécifique diminuait graduellement en fonction de sa distance. Cependant, ce patron ne semble pas s'appliquer en Polynésie française. En utilisant diverses campagnes scientifiques, plusieurs courbes d'accumulations ont pu être mis en place pour déterminer de manière homogène la richesse spécifique de chaque île. Postérieurement, les données de richesse spécifique ont été confrontées à 1) la surface habitable grâce la création d'un multi-modèle Aire-Espèces et 2) à la surface habitable en ajoutant l'ontogénie des îles pour construire un modèle général dynamique. Ainsi, la variation de richesse spécifique est principalement expliquée par la surface habitable. D'autre part, cette dernière diminue en fonction de l'ontogénie des îles soulignant une différence majeure entre les patrons théoriques observés en écologie terrestre et nos résultats observés dans le domaine marin.</p>	
Abstract (1600 caractères maximum) :	
<p>The Indo-Australian-Archipelago has been described for decades as the global biodiversity hotspot of marine species and that species richness tends to decrease regularly as distance increase from this location. However, this pattern does not seem to apply at the scale of French Polynesia. Using data from various scientific investigations, several species accumulation curves have been set up to determine homogeneously the number of fish for each island. Then, the species richness was confronted with 1) the island area, highlighting the creation of a multi-model Species-Area-Relationship and 2) the island area combined with the ontogeny of islands to build a Dynamic General Model. The variation of species richness is mainly explained by the island area. However, the number of species also decreases according to the ontogeny of islands highlighting a major difference between patterns observed in terrestrial ecology and our results observed in the marine domain.</p>	
Mots-clés : Ichthyologie, Biogéographie, Relation Aire-Espèces, Modèle Général Dynamique, Polynésie française	
Key Words: Ichthyology, Biogeography, Species-Area-Relationship, General Dynamic Model, French Polynesia	

\* Élément qui permet d'enregistrer les notices auteurs dans le catalogue des bibliothèques universitaires