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Thèse de Doctorat
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Evaluation du potentiel biologique, économique et social de la coralliculture dans le sud-ouest de Madagascar

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Evaluation du potentiel biologique, économique et social de la coralliculture dans le sud-ouest de Madagascar

Thèse présentée en vue de l'obtention du grade de Docteur en Sciences

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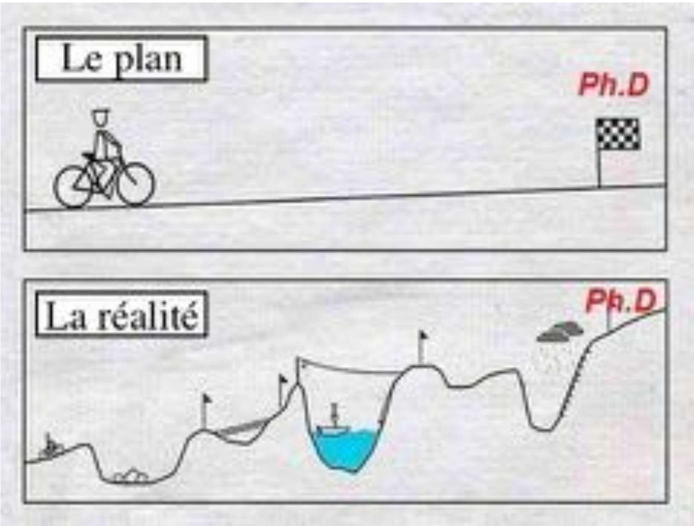
« Ny fianarana no lova tsara indrindra »

« Tsy misy mafy tsy laitry ny zoto »

Proverbes malagasy



Entre les sorties en mer, les séjours dans les villages de pêcheurs, les tâches plus administratives à Madagascar, d'une part. Et d'autres part les travaux en laboratoire et la rédaction souvent jusqu'à ne pas sortir de sa chambre pendant tout le weekend à Mons, Belgique, les quatre années de thèse sont passées tellement vite qu'à la fin, je me rends compte que c'est une expérience qui condense toutes les années d'études et d'éducation, toutes les difficultés qu'on peut rencontrer pendant une vie scolaire et estudiantine, et toutes les émotions qu'un être humain puisse ressentir.

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Je dédie spécialement cette

thèse à notre Mère

et à notre grand-père

Boleslas

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Avant-propos

Cette thèse de doctorat a pour but d'évaluer le potentiel de l'aquaculture de coraux à Madagascar, en particulier dans les villages de pêcheurs de la région sud-ouest du pays. Elle s'intéresse donc aux cnidaires et plus particulièrement aux coraux durs appartenant à l'ordre des Scleractinia. Les recherches de terrain ont principalement été réalisées dans la Baie de Tuléar et celle de Ranobe. Elles ont été réalisées dans le cadre d'un Programme Interuniversitaire Ciblé (PIC) financé par l'Académie de Recherche et d'Enseignement Supérieur, Commission de la Coopération au Développement (ARES-CCD). Le programme intitulé « Développement de la polyaquaculture dans les villages côtiers du sud-ouest et du nord de Madagascar » comportait deux volets principaux, le premier volet se rapportant sur le développement de l'algoculture et le deuxième sur celui de la coralliculture qui est développé dans ce travail.

Le programme dans sa globalité a pour objectif général de favoriser le développement d'aquacultures socio-écologiques (*i.e.* des aquacultures ayant un impact positif sur des communautés à faibles revenus et étant, tant que faire se peut, respectueuses de l'environnement) sur les côtes de Madagascar en tant qu'activités alternatives à la pêche et à la collecte d'organismes sauvages. Depuis une cinquantaine d'années, les récifs coralliens dans toute leur globalité ont subit une dégradation chronique de leur état de santé face aux impacts des activités anthropiques. Les coraux scléractiniaires, principaux constructeurs des récifs coralliens, sont les premières victimes de cette dégradation écosystémique. La pêche côtière, principalement traditionnelle pour le cas de Madagascar, dépend essentiellement de ces récifs coralliens : les pêcheurs s'y déplacent à pieds ou en pirogue et y collectent poissons et invertébrés marins pour leur propre consommation mais aussi pour la chaine commerciale. Cette collecte intensive et la dégradation globale des récifs raréfient considérablement les produits halieutiques au point de diminuer fortement les revenus déjà très faibles des pêcheurs traditionnels (Salimo 1997, Bruggemman et al. 2012).

L'aquaculture villageoise a été développée dans le but de fournir aux pêcheurs une alternative à la pêche, mais également pour pallier aux problèmes de pressions anthropiques pesant sur les récifs coralliens. L'aquaculture villageoise a été initiée en 1998 dans le nord de Madagascar avec l'apparition de l'algoculture sur l'île de Nosy Ankao (espèce aquacultivée : *Kappaphycus alvarezii*) pour ensuite être mise en pratique dans le sud-ouest de l'île. L'holothuriculture, c'est-à-dire l'élevage d'holothuries (espèce aquacultivée : *Holothuria scabra*), a fait suite à l'algoculture. Issue de deux premiers projets PIC (Rasolofonirina 2004 ; Lavitra 2008), elle a été lancée en 1998 dans la région de Tuléar. Le développement des aquacultures villageoises est prometteur : aujourd'hui, plus de 200 familles de villageois côtiers exercent ce type d'activité sur plus de 300 km de côte. Le potentiel de la coralliculture villageoise en tant que générateur de ressources financières est certainement moins évident que l'algoculture et l'holothuriculture pour lesquels un marché d'exploitation existe depuis plusieurs années. Un marché du corail plus étroit et moins connu existe cependant: des coraux se vendent pour l'aquariophilie et d'autres sont récoltés pour la bijouterie. Mon travail de thèse explore ainsi le potentiel biologique mais aussi socio-économique de ce type d'aquaculture lorsqu'il est développé par des villageois pêcheurs.

Résumé

Dans le contexte de la baisse globale de la biodiversité des récifs coralliens et compte tenu du développement du marché des coraux vivants, la coralliculture est une technique prometteuse à développer dans un futur proche. A Madagascar, les aquacultures villageoises représentent une alternative à la pêche et aux collectes des organismes sauvages. La présente étude a été menée dans le cadre du programme PIC ("Programme Interuniversitaire Ciblé") de l'ARES-CCD intitulé "Développement des polyaquacultures au niveau des villages côtières du sud-ouest et du nord de Madagascar". Les principaux objectifs de l'étude consistent (i) à identifier la biodiversité des scléractiniaires, afin d'évaluer leur potentiel de recrutement et de choisir les premières espèces, meilleures candidates pour la coralliculture (ii) à identifier la meilleure technique de transport pour l'exportation des coraux d'élevage et (iii) à évaluer le potentiel de la coralliculture dans les villages du Sud-Ouest de Madagascar.

La biodiversité des scléractiniaires à Madagascar est principalement connue à partir d’une étude réalisée dans la baie de Tuléar (sud-ouest de Madagascar) dans les années septante. Dans la présente étude, nous avons réalisé une nouvelle étude de cette biodiversité 40 ans plus tard. Nous avons établi une base de données moléculaire basée sur des fragments d'ADN 18S afin de l’utiliser comme outil facile pour l'identification des adultes et des recrues. Les résultats ont montré une diversité spécifique plus faible par rapport aux études précédentes et par rapport à des sites similaires dans la région de l'Océan Indien. Cependant, la plupart des genres bien représentés ont été enregistrés. L'apparition d'espèces non comptabilisées antérieurement suggère que les communautés de scléractiniaires changent de composition spécifique au lieu de seulement se dégrader. En outre, nous avons obtenu des fragments de séquence d'ADN 18S pour 20 des espèces les plus dominantes. La comparaison appariée a permis de distinguer 15 groupes d'espèces: 13 sont monospécifiques, 1 comprend 5 espèces et le dernier comprend 2 espèces. Une séquence de 13 recrues a également été obtenue et la comparaison avec la base de données génotypique des adultes a permis d'augmenter la résolution de l'identification des recrues du niveau de la famille (avec la méthode d'identification traditionnelle) au niveau de l'espèce ou du genre. Les recrues identifiées appartenaient aux espèces *Pocillopora sp., Porites profondus, P. rus, Pavona clavus* et *Lobophyllia corymbosa.* Enfin, une discussion sur l'utilisation de la base de données génétique a été apportée.

Nous avons ensuite évalué la période de reproduction des scléractiniaires dans la région sud-ouest par un suivi hebdomadaire de la présence de larves de corail (planula) dans le plancton, par une évaluation mensuelle des recrues (1 an < Recrues) et une estimation du taux de recrutement des juvéniles (1 <Juveniles <2 ans). Les larves de corail ont été observées dans le plancton 9 mois sur 12. Leur abondance a été plus élevée au début de la saison chaude et humide (Septembre à Novembre). La densité annuelle enregistrée des larves variait de 1,30 planula m^{-3} à 16,17 planula m^{-3} selon les stations. Des pics de densité des larves ont été observés en Novembre et Décembre suggérant que la plupart des coraux libèrent leurs œufs fécondés quelques jours ou quelques semaines avant cette période. Par rapport à d'autres régions, le taux de recrutement observé dans le sud-ouest de Madagascar était élevée (100 à> 1000 recrues m^{-2} an^{-1}). Il varie aussi selon les saisons. Nous avons observé des pics de recrutement entre Octobre et Décembre. Nous avons également observé une différence significative entre l'abondance des recrues et celle des juvéniles. Les résultats de l'évaluation de l'abondance des juvéniles ont révélé des taux élevés (> 10 juvéniles de m^{-2}) par rapport à d'autres régions et par rapport au seuil théorique, mais il a également permis de relever une forte mortalité des recrues.

Les espèces *Acropora nasuta* et *Seriatopora caliendrum* ont été utilisées pour expérimenter la coralliculture villageoise à Madagascar. Nous avons identifié les techniques d'élevage (de bouturage) appropriées pour les villageois. La survie et le taux de croissance des boutures de corail ont été suivis pendant les deux saisons: chaude et humide, fraiche et sèche. Les expériences d'élevage ont été réalisées sur un site près du village de Sarodrano à une profondeur de 1 m, avec une température de 26,31 ± 2,07 ° C, une salinité de 32,67 ± 1,19 psu, et un taux de sédimentation de 0,55 ± 0,28 mg cm^{-2} j^{-1}. Pendant la saison chaude et humide, les taux de survie finaux étaient de 67 ± 6% et 57 ± 4% respectivement pour *A. nasuta* et *S. caliendrum*, tandis que pendant la saison fraiche et sèche, les taux de survie étaient respectivement de 85 ± 7% et 69 ± 1%. Le taux de survie de l'espèce *A. nasuta* était significativement plus élevé que celui de *S. caliendrum* au cours des deux saisons. Pendant la saison chaude et humide, les taux de croissance ont été respectivement de 0,46 ± 0,16% j^{-1} et 0,54 ± 0,16% j^{-1} pour *A. nasuta* et *S. caliendrum*. Pendant la saison fraiche et sèche, le taux de croissance de l'espèce *A. nasuta* était de 0,63 ± 0,18% j^{-1}, tandis que *S. caliendrum* de 0,65 ± 0,15% j^{-1}. Une différence significative a été observée entre les deux espèces au cours de la saison chaude et humide, mais pas pendant la saison fraiche et sèche. En outre, le taux de croissance était plus élevé pour les deux espèces pendant la saison fraiche et sèche. Ces résultats correspondent à des taux de croissance de référence pour les coraux.

Le transport des coraux vivants (les boutures) est l'une des contraintes les plus importantes dans le commerce de ces animaux. Actuellement, ils doivent être transportés par voie aérienne, et de préférence en moins de 20 heures en utilisant de l'oxygène concentré, sinon, la mortalité des coraux après le transport augmente considérablement. Afin de mieux comprendre l'effet des conditions de transport sur la physiologie des boutures et leur mortalité après le transport, nous avons effectué des séries de simulations de transport sur *Seriatopora hystrix* et testé différents volumes d'eau (dont la méthode de transport à sec et la méthode immergée avec dans 125 ml, 190 ml et 325 ml d'eau de mer), différentes concentrations d'oxygène dans la phase gazeuse du récipient de transport (21%, 40% et 85%)

Les boutures ont continué à croître pendant le transport et ont consommé les carbonates de calcium, ce qui a réduit rapidement l'alcalinité de l'eau et par conséquent le pH. L'oxygène dissous a également été rapidement réduite. La concentration d'azote inorganique, en particulier les ions ammonium augmente brusquement après 24 h et a atteint des valeurs maximales et létales à 48 h. La méthode à sec était inappropriée par rapport à la méthode immergée. Pour la méthode immergée et pour un transport de moins de 48 heures, plus le volume d'eau est élevé, plus le taux de croissance des boutures après le transport était élevé. En outre, en moins de 48 heures, plus la concentration en oxygène était élevée, plus le taux de croissance des boutures après le transport était également élevé. Au-delà de 48h, dans tous les cas, les conditions de l'eau de transport deviennent brusquement critiques pour les coraux et peuvent induire leur mort.

Pour déterminer la faisabilité économique de la coralliculture, le marché du corail a été étudié et les rendements ont été calculés en utilisant les paramètres techniques, biologiques et sociaux de la production. Ensuite, un "business model" approprié a été déterminé et les clients potentiels identifiés. L'activité peut être rentable à partir de 30 boutures de corail vendues par mois. Les bénéfices peuvent être perceptibles à partir de la deuxième année et un total de plus de € 27000 peut être gagné après 5 ans de production pour un investissement initial de € 1978. Les vendeurs détaillants d'animaux marins et les ONG de conservation de la biodiversité sont les clients et les partenaires potentiels appropriés pour la coralliculture à Madagascar. Les résultats de la présente étude ont montré que cette forme d'aquaculture est techniquement et biologiquement faisable en utilisant des matériaux moins chers et un temps de travail négligeable pour les villageois par rapport à la pêche et aux autres types d'aquaculture comme l'holothuriculture et l'algoculture. En outre, l'évaluation économique d'un projet d'élevage de corail a également prouvé qu'il pouvait être profitable à petite échelle, notamment à l'échelle communautaire. De ce fait, il pourrait être une autre source de revenus pour les communautés de pêcheurs et contribuer à réduire les pressions de pêche sur les récifs coralliens. Mais son intégration dans une structure de polyaquaculture villageoise est suggérée afin d'assurer sa viabilité.

Summary

In the context of the global decline of coral reef biodiversity and considering the development of live corals marketing, the coral aquaculture is a promising technique to develop in a near future. In Madagascar, community-based aquacultures are alternative to fishing and to wild organisms harvesting. The present study was conducted within the PIC ("Programme Interuniversitaire Ciblé") ARES-CCD program titled "Development of community-based coastal polyaquaculture in the Southwest and the North of Madagascar". The main objectives of the study consisted (i) to identify the biodiversity of the most common scleractinians, to evaluate their recruitment potential and to choose the first best candidates for coral farming (ii) to find out the best method of transport for exporting live farmed corals and (iii) to evaluate the potential of coral farming in the villages of the South-West of Madagascar.

The scleractinian biodiversity of Madagascar is mainly known from one study performed in the Bay of Toliara (SW of Madagascar) in the seventies. In the present study, we reinvestigated this biodiversity 40 years later and we initiated the implementation of a molecular database based on 18S rDNA fragments as an easy tool for identification of adults and recruits. Results showed lower species diversity compared to the previous studies and to similar sites in the Indian Ocean region. However, most of the well-represented genera were recorded. The appearance of previously unrecorded species suggests that the scleractinian communities are changing instead of only declining. In addition, we obtained 18S rDNA sequence fragments for 20 of the most dominant species. Fifteen groups are distinguishable by pairwise comparison: 13 are monospecific, 1 includes 5 species and the last includes 2 species. Sequence fragment of 13 recruits were also obtained and BLAST searches against the adult genotypic database permitted to increase the resolution of recruit's identification from the level of family (with the traditional taxonomic key) to the level of species or genus. Identified recruits were *Pocillopora sp., Porites profundus, P. rus, Pavona clavus and Lobophyllia corymbosa*. We finally discuss about the use of the genetic database.

The reproduction period of scleractinians in the SW region was evaluated by a weekly monitoring of the presence of coral larvae (planula) in plankton, by a monthly evaluation of the new settled corals (1 year < Recruits) and a monitoring of the juveniles' recruitment (1< Juveniles < 2 years). Planula was present in plankton 9 months a year. It was abundant from the beginning of the warm wet season (September to November). The annual recorded density of planula varied from 1.30 planula m^{-3} to 16.17 planula m^{-3} depending on the studied stations, with a peak larval density in November and December suggesting that most of corals release their fertilized eggs few days or weeks before November/December. Compared to other regions, the recruitment rate observed in the SW of Madagascar was high (100 to > 1000 recruits m^{-2} $year^{-1}$). It also varied from seasons and peaks of recruitment was observed between October and December. We observed a huge difference of recruit records and juvenile records between the stations. Results of juveniles monitoring revealed high rates (> 10 juveniles m^{-2}) compared to other regions and to the threshold, but it revealed high mortality of the recruits.

The coral species *Acropora nasuta* and *Seriatopora caliendrum* were used to experiment community-based coral aquaculture in Madagascar. Suitable rearing techniques were experienced. Survival and growth rate of the coral nubbins were monitored during wet, warm and dry, cold seasons. Coral nubbins were reared at a depth of 1m, with a temperature of 26.31±2.07°C, a salinity of 32.67±1.19 psu, and a sedimentation rate of 0.55±0.28 mg cm^{-2} d^{-1}. Coral nubbins reared during the wet, warm season showed a final survival rate of 67±6% and 57±4% respectively for *A. nasuta* and *S. caliendrum*, while in the dry, cold season, the survival rates were respectively of 85±7% and 69±1%. *A. nasuta* had a significantly higher survival rate than *S. caliendrum* during both seasons. During the wet, warm season, growth rates were respectively 0.46±0.16%d^{-1} and 0.54±0.16%d^{-1} for *A. nasuta* and *S. caliendrum*. In the dry, cold season, *A. nasuta* had 0.63±0.18%d^{-1} of growth rate, while *S. caliendrum* grew 0.65±0.15%d^{-1}. Significant difference was observed between both species during the wet, warm season, but not during the dry, cold season. Furthermore, both species grew faster during the dry, cold season. These results are in the range of reference values for corals.

Transporting live coral nubbins is one of the most important constraints in coral economy. Nowadays, they must be transported by air, and preferably in less than 20h using concentrated oxygen, if not, post-transportation coral mortality drastically increases. In order to better understand the effect of the transportation conditioning the physiology of the nubbins and their mortality after transportation, we performed series of transportation simulations on *Seriatopora hystrix* and tested different volumes of water (including dry method, 125 ml, 190 ml and 325 ml), different oxygen concentrations in the gas phase of the container (21%, 40% and 85%)

Nubbins continued to grow during transportation and pumped calcium carbonates, which rapidly reduced the alkalinity of the water and therefore the pH. Dissolved oxygen was also rapidly reduced. The concentration of inorganic nitrogen, particularly the ammonium ions increased after 24h and abruptly reached maximum and lethal values at 48h. The dry method was inappropriate for small coral nubbins rather than wet methods. In less than 48h, the higher the water volume was, the better the nubbin grow after transportation. Yet, in less than 48h, the higher the oxygen concentration was, the better the nubbin grew after transportation. Beyond 48h, in all cases, the water conditions became abruptly critical for the nubbins and can induce their death.

To determine economical feasibility, the coral market was investigated and the yields were also calculated using the technical, biological and social parameters of the production. Then, the appropriate business model and appropriate clients were determined. The activity is profitable from less than 76 coral nubbins sold per month. Profit can already be perceivable from the second year and a total of more than EUR 27,000 is earned after 5 years of developing project, for an initial investment of EUR 1,978. Marine animals retailer companies and biodiversity conservation NGOs are the appropriate clients and partners for coralliculture farming in Madagascar. The findings of the present study proved that community-based coral aquaculture is technically and biologically feasible using very low coast materials and spending negligible working time for the community compared to fishing and practicing other types of aquaculture like sea cucumber or algae farming. Also, the economical evaluation of a coral farming project also proved that it could be fully profitable at a small-scale production, notably a community scale. Thereby, it could be an alternative source of revenue to the fishermen communities and contribute to reduce the fishing pressures to the coral reefs. But the integration of the coral farming within existing and well-established community-based polyaquaculture is suggested to ensure its viability.

Chapitre 1
Introduction générale

CHAPITRE 1 : Introduction générale

1.1 Biologie et cycle de vie des scléractiniaires

1.1.1 Classification phylogénétique et caractères généraux

Les coraux *sensu stricto*[1] appartiennent à l'ordre des Scleractinia. Ce sont tous des animaux marins, solitaires ou coloniaux. *Sensu lato*, le terme « corail » englobe les scléractiniaires mais aussi l'ensemble « des cnidaires à squelette dur » dont on retrouve des représentants dans d'autres ordres d'hexacoralliaires, chez des octocoralliaires et chez des hydrozoaires.

L'évolution de la classification phylogénétique des coraux est fonction de l'évolution des méthodes de recherche. Daly et al. (2007) classe l'ordre des Scleractinia se classe comme suit:

Règne: Animalia
- Phylum : Cnidaria
  - Classe : Anthozoa
    - Sous-classe : Hexacorallia
      - Ordre : Actiniaria
      - Ordre : Antipatharia
      - Ordre : Ceriantharia

[1] Le terme « corail » utilisé dans ce travail fera référence à cette définition stricte

Ordre : Corallimorpharia

Ordre : **Scleractinia**

Ordre : Zoanthidea

Sous-classe : Octocorallia

Classe : Cubozoa

Classe : Hydrozoa

Classe : Scyphozoa

Classe : Staurozoa

Les coraux se retrouvent dans tous les océans du milieu intertidal aux fosses abyssales. Ils seront cependant plus abondants dans les eaux de surface de certaines régions intertropicales. Le terme « corail hermatypique » est communément utilisé pour désigner les espèces bâtisseuses de récifs. Ces coraux hermatypiques sont en symbiose avec des zooxanthelles du genre *Symbiodinium* qui permettent à leur hôte d'accélérer la formation de leur squelette calcaire.

Un corail est constitué d'un ou de plusieurs individus, les polypes. Chaque polype est un cylindre muni d'un orifice unique dans sa partie supérieure, l'orifice gastrovasculaire (souvent appelé bouche mais jouant également le rôle d'anus). L'orifice gastrovasculaire est entouré de tentacules disposés en couronnes régulières.

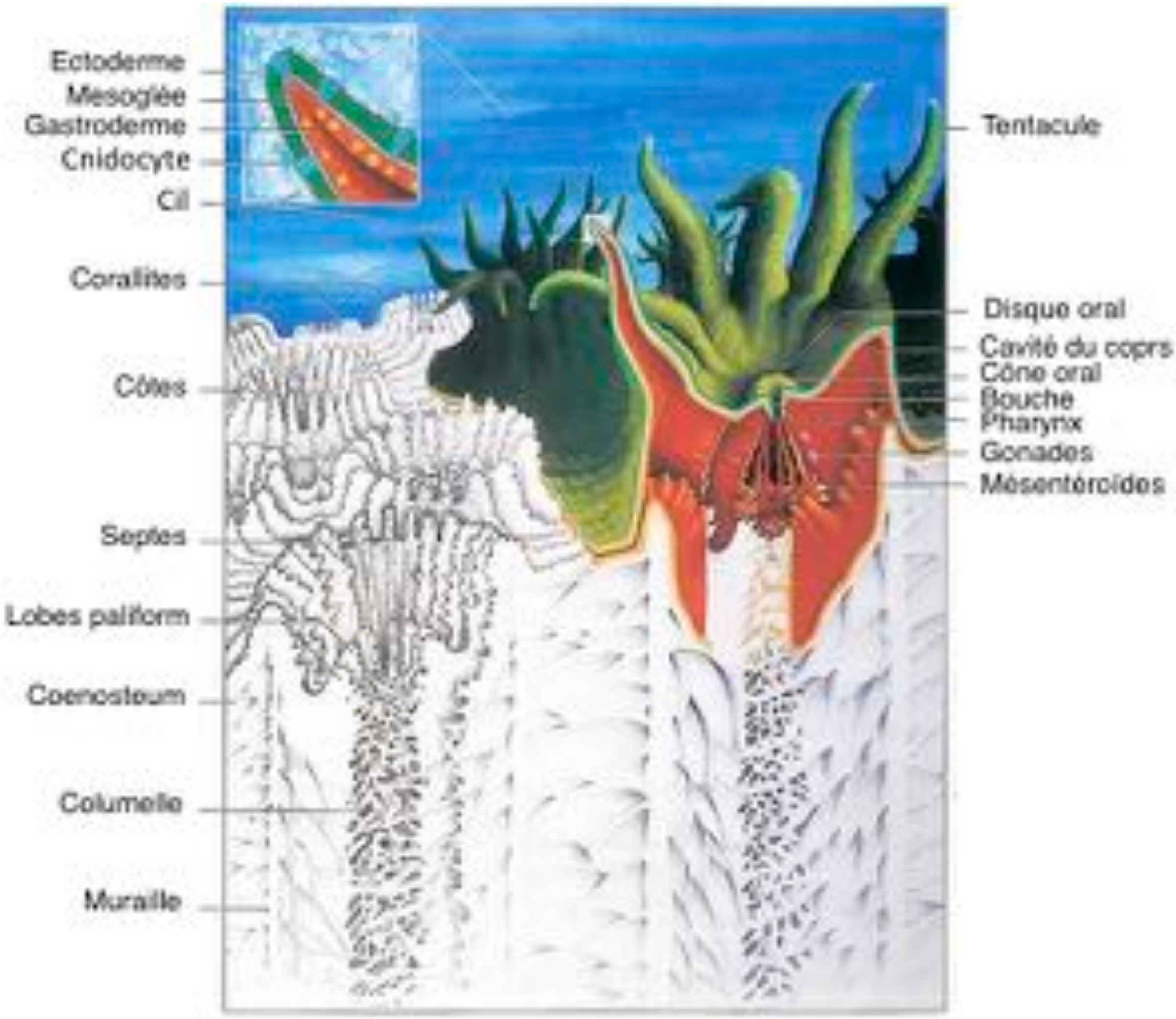


Figure 1: Structure générale d'un polype et de son squelette (d'après Veron 2000)

Les coraux sont des organismes diploblastiques : ils possèdent deux feuillets embryonnaires qui vont se différencier en épiderme (la face externe) et en gastroderme (la face interne) et entre lesquels se trouve la mésoglée, une couche anhyste composée de matériel extracellulaire (Figure 1). L'épiderme oral se compose de diverses cellules dont des cellules ciliées ainsi que des cellules particulières aux cnidaires, les cnidocytes. L'épiderme aboral, ou calicoderme, est constitué de cellules permettant la formation du squelette calcaire sous-jacent (Tambutté et al. 2011).

Le squelette des scléractiniaires est externe. Le squelette sous le polype porte le nom de corallite, l'ensemble des corallites, lorsqu'il s'agit d'une colonie, est le corallum. Au contact avec les tissus vivants, le corallite présente de nombreux septes et côtes de divers ordres, la forme et l'arrangement des septes et des côtes étant un critère taxonomique (Veron 2000). Entre les polypes d'une colonie se trouvent le coenosarc, tissu vivant, et le coenosteum, partie calcaire sécrétée par le coenosarc. Chaque famille, genre et espèce de corail diffèrent par la présence/absence et l'aspect de ces éléments constitutifs du squelette du corail.

1.1.2 Cycle de vie et croissance

Comme l'ensemble des anthozoaires, les coraux n'ont pas de phase méduse. Leur cycle de vie inclut une phase dominante benthique dans laquelle on retrouve un polype ou une colonie de polypes et une phase larvaire, pélagique et très courte (Harrison 2011). La phase larvaire, caractérisée chez les cnidaires par la larve planula, assure la dispersion des espèces. La métamorphose et la fixation des larves planula sur un substrat adéquat se poursuivent par le développement d'un polype fondateur. Lorsqu'il s'agit de colonies, le polype nouvellement recruté bourgeonne et forme la nouvelle colonie qui produit continuellement l'exosquelette calcaire. La colonie adulte devient ensuite sexuellement mature, fermant ainsi le cycle de vie du corail (Harrison et Wallace 1990).

La majorité des coraux (70% des espèces étudiées jusqu'à maintenant) sont des hermaphrodites simultanés (Harrison 2011). Certaines espèces sont incubantes : la fécondation a lieu dans la cavité gastrovasculaire du polype qui relâche directement un œuf fécondé (Harrison 2011). La production d'une larve planula lors de la reproduction sexuée n'est pas le seul mode de dispersion d'un corail, la reproduction asexuée assure également la dispersion. Celle-ci a lieu par exemple lors du détachement de morceaux de la colonie suite à l'impact des vagues, lors de tempêtes ou lors du piétinement effectué par des pêcheurs ou encore à cause des ancres des bateaux. L'existence de ce mode de reproduction permet aussi la transplantation d'une partie d'une colonie. La transplantation permet le déplacement d'une colonie en mauvais état de santé dans un nouvel emplacement lui donnant la possibilité de reprendre une croissance normale (Bowden-Kerby 1999).

Les recherches sur la reproduction et sur la ponte des scléractiniaires ont pris un essor considérable depuis la découverte de pontes massives synchronisées sur la Grande Barrière de corail : plus de 140 espèces participent à ce phénomène (Harrison et al. 1984; Willis et al. 1985; Babcock et al. 1986; Oliver et al. 1988). Dans la majorité des cas, la ponte (et à fortiori la production des larves planula) se produit une fois l'an (Rosser et Baird 2008). Toutefois, plusieurs espèces sont connues pour pondre et donner des larves, plusieurs fois sur une année (Tableau 1). La ponte des coraux, quelle que soit la saison de l'événement, s'observe de 0 à 14 jours après la pleine lune et l'heure de la diffusion des gamètes semble dépendant du cycle de la lumière solaire (Brady et al. 2009).

Tableau 1: Principales périodes connues de ponte des coraux à diverses latitudes

Pays / Région	Coordonnées	Mois de la ponte												Références
		J	F	M	A	M	J	J	A	S	O	N	D	
Australie	18°S - 23°S											■		Harrison et al. (1984); Wallace (1985); Babcock et al. (1986); Nozawa et Harrison (2000); Miller et Mundy (2003)
											■	■		Willis et al. (1985)
				■	■									Babcock et al. (1994)
Polynésie Française	17°S											■		Carroll et al. (2006)
Kenya	3°S		■						■					Mangubhai et Harrison (2008)
La Réunion	21°S		■	■										Massé (2014)

Afrique du Sud	27°S		Massé (2014)
Japon	26°N - 30°N		Hayashibara et al. (1993)
Singapour	1°N		Guest et al. 2002
Malaisie	2°N		Chelliah et al. (2015)
Madagascar	22°S		Gress et al. 2015
Mer rouge	21°N		Bouwmeester et al. 2014
Mer des Caraïbes	15°N		Szmant 1986

Dans le sud-ouest de Océan Indien, la ponte des coraux s'observe aussi bien en été qu'en hiver (*e.g.,* au Kenya, Mangubhai et Harrison 2008 ; à La Réunion et en Afrique du Sud, Massé 2014). La période de ponte des coraux est très peu connue à Madagascar. A ce jour, la seule observation fructueuse et publiée, a été réalisée sur les récifs coralliens d'Andavadoaka (Gress et al. 2015) et aucune étude fine sur le recrutement des coraux n'a été faite.

D'un point de vue pratique, le terme « recrutement » désigne chez les coraux deux périodes qui suivent la fixation des larves et leur métamorphose, la première pendant laquelle les recrues, qui correspondent au polype originel ou à une petite colonie, ne sont pas encore visibles à l'œil nu (Figure 2) (Babcock et Mundy 1996 ; Banks et Harriott 1996 ; Gleason 1996 ; Baird et Hughes 1997 ; Dunstan et Johnson 1998 ; Hughes et al. 1999 ; Mundy 2000 ; Kojis et Quinn 1984) et la seconde qui fait suite, où les colonies, encore nommées colonies juvéniles, deviennent visibles à l'œil nu sur le substrat naturel (ce qui correspond à un stade où les colonies ont une taille supérieur de l'ordre de 1 cm et un âge supérieur à un an ; Figure 2) (Connell 1973 ; Bak et Engel 1979 ; Sakai et Yamazato 1984 ; Wittenberg et Hunte 1992 ; Chiappone et Sullivan 1996 ; Smith 1997 ; Edmunds 2000 ; Miller et al. 2000). Au stade « recrue », l'identification des coraux demeure très difficile car les critères servant à la détermination des adultes leur sont difficilement appliquables (Veron 2000). Pour les recrues, seules 3 familles sont clairement identifiables pour les récifs de l'Indo-

Pacifique : les Acroporidae, les Pocilloporidae et les Poritidae (Babcock 1992 ; Babcock et al. 2003).

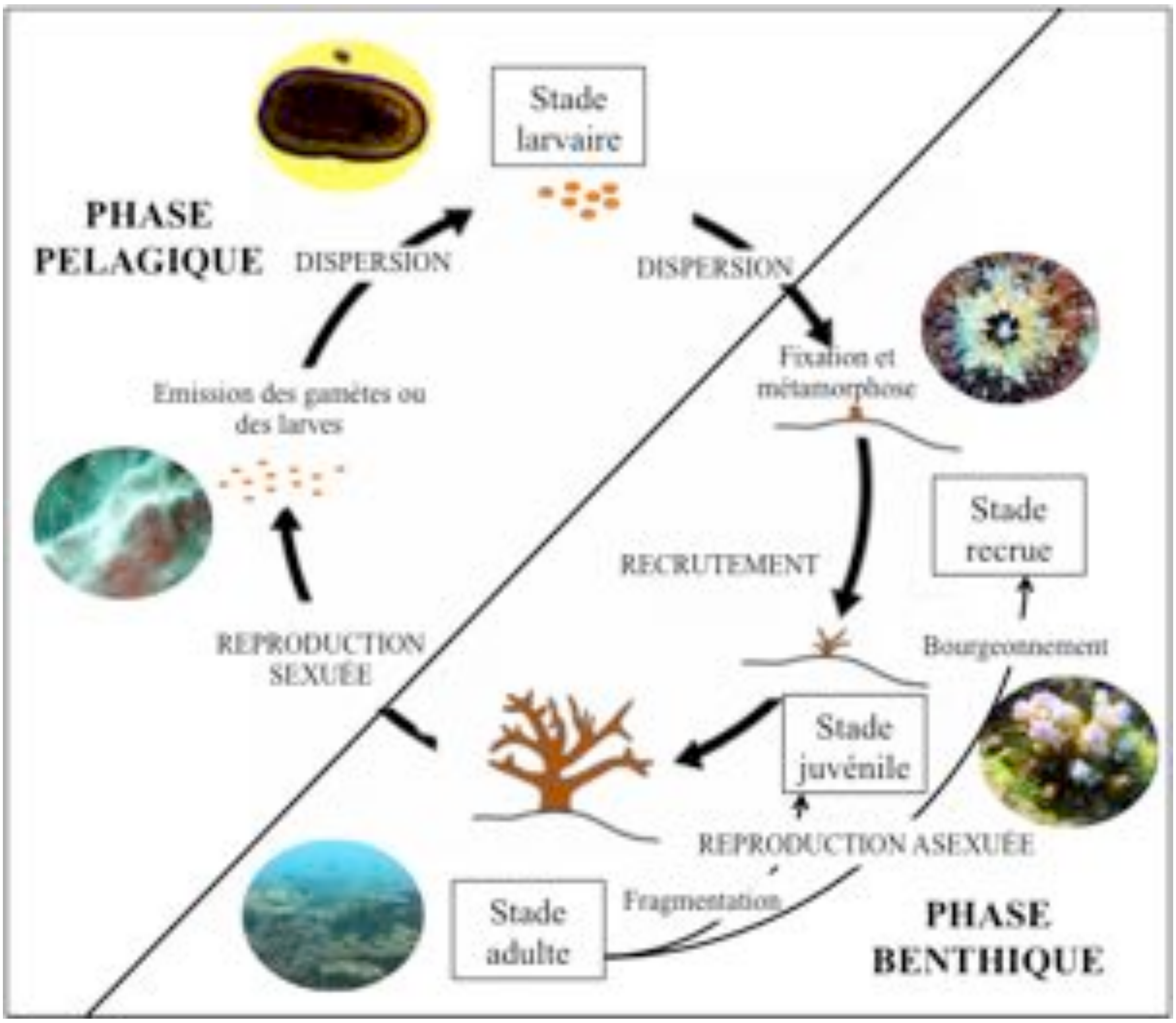


Figure 2: Cycle de vie des scléractiniaires (adapté de Adjeroud et al. 2016).

Les méthodes d'évaluation du recrutement impliquent généralement l'utilisation de substrats artificiels sous forme de plaque, généralement en terre cuite ou en céramique pour les recrues, et la méthode des quadrats pour les juvéniles (Hill et Wilkinson 2004). La fixation des larves planula sur les plaques peut varier en fonction de la nature de la surface et de la position des plaques utilisées (Pénin 2007 ;

Urvoix et al. 2013 ; Baird et al. 2012). La durée de l'immersion des plaques ainsi que la région de l'étude influencent également le taux de fixation. En ce qui concerne les coraux qui seront abordés dans ce travail, le recrutement d'espèces du genre *Acropora* est surtout observé entre octobre et novembre (Australie, Baird et al. 2012). Tandis que la période de recrutement d'espèces des genres *Pocillopora, Seriatopora* et *Stylophora* s'étale sur toute l'année (Australie, Baird et al. 2012 ; La Réunion, Massé 2014).

1.2 Récifs coralliens et diversité corallienne

1.2.1 Formation et définition des récifs coralliens

Les récifs coralliens sont des écosystèmes marins édifiés par les coraux hermatypiques. Ce sont des massifs solides de grandes surfaces, constitués par le squelette des coraux morts mais aussi et surtout par les agrégations calcaires des algues corallines. Ils sont tapissés en surface, d'une fine couche de coraux vivants qui assurent par leur croissance l'extension et le renforcement même des récifs. Il existe plusieurs types de récifs coralliens dont les principaux sont les atolls, les récifs barrières, les récifs frangeants, et les bancs coralliens (Figure 3) (Lieske et Myers 1994 ; Veron 1986 ; Laboute et Forges 2004 ; Veron 2000).

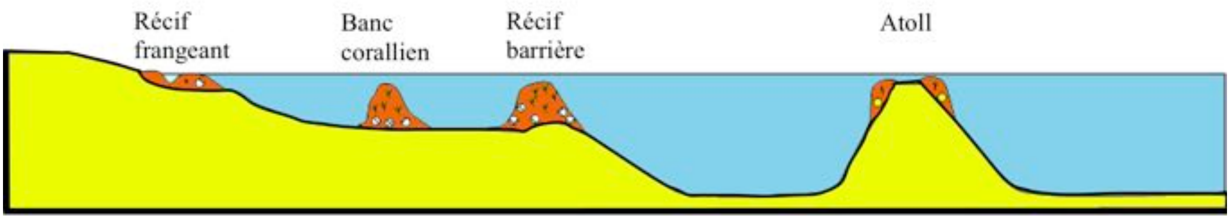


Figure 3: Les principaux types de récifs coralliens

Les récifs coralliens sont présents là où les conditions naturelles favorisent la croissance des coraux hermatypiques. Aussi, les récifs coralliens « vivants » se retrouvent dans des eaux à faible profondeur, avec généralement un maximum de 30 mètres, pour permettre à la lumière d'atteindre les coraux hermatypiques et en particulier les *Symbiodinium* associés. Ce besoin en lumière implique également que la turbidité de l'eau doit être faible. En outre, la température doit être comprise entre 18 et 34°C toute l'année. L'eau doit être riche en carbonate de calcium pour favoriser la calcification. Toutefois, elle doit être oligotrophe car une augmentation de la concentration en nutriments tels que les nitrates peut avoir des effets néfastes sur cette calcification (Erez et al. 2011). A l'échelle mondiale, toutes ces conditions sont remplies dans certaines régions situées entre la latitude 30° nord et la latitude 30° sud (Figure 4).

Figure 4: Répartition géographique des récifs coralliens au niveau mondial (Veron 2000).

Madagascar fait partie du domaine indo-pacifique tropical où les récifs coralliens constituent l'écosystème marin littoral type (Pichon 1978). La partie Est de l'île, exposée à l'Océan Indien est beaucoup moins riche en récifs coralliens que l'Ouest, du côté du Canal du Mozambique. A l'Ouest, les récifs coralliens sont surtout développés depuis Androka (au sud) limité par le fleuve Linta jusqu'à Antsiranana au nord. A l'est, les récifs coralliens se répartissent depuis le cap d'Ambre (Antsiranana) jusqu'à Toamasina (Figure 5). Au total, les récifs coralliens s'étendent sur environ

1400 km de côte, en plus des bancs coralliens et des hauts fonds du large. Ils couvrent, au total, une superficie estimée à 2400 km^2 (Cook et al. 2000).

La région sud-ouest de l'île (entre le fleuve Manombo au nord - latitude 22°58' S - et le fleuve Onilahy - latitude 23°34' S - au sud, Figure 11) se caractérise par la présence de plusieurs types de récifs coralliens (Figure 5) qui se répartissent en trois zones, du nord au sud : (1) la Baie de Ranobe qui regroupe des récifs barrières, et des bancs coralliens; (2) la zone entre le village d'Ifaty et le fleuve Fiherenana qui est caractérisée par un long récif frangeant et (3) la Baie de Tuléar qui se distingue par la présence de la plus grande barrière corallienne de l'Océan Indien, le Grand Récif de Tuléar (GRT) derrière lequel se situent plusieurs bancs coralliens et le récif frangeant de Sarodrano. Au total, la région renferme plus de 20 récifs coralliens : plus de 10 dans la Baie de Ranobe, un entre Ifaty et le fleuve Fiherenana, et 10 dans la Baie de Tuléar (Clausade et al. 1971).

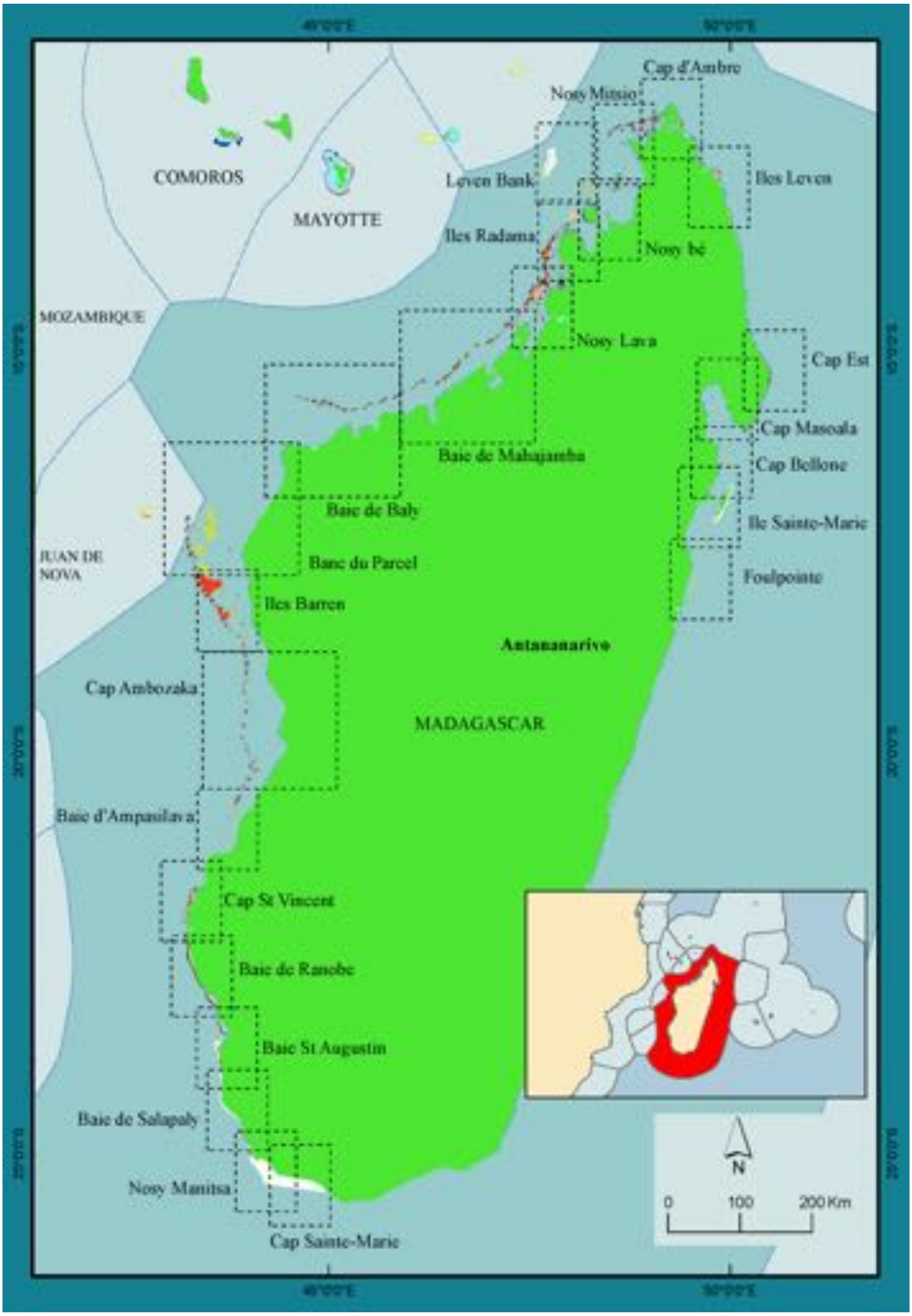


Figure 5: Répartition des récifs coralliens de Madagascar.

1.2.2 Diversité des scléractiniaires

Les scléractiniaires forment un des ordres parmi les cnidaires où les taxons sont les plus complexes en terme d'identification. Cet ordre regroupe plus de 30 familles reconnues dont les plus communes sont celles des Acroporidae, Astrocoeniidae, Pocilloporidae, Euphyllidae, Oculinidae, Meandrinidae, Siderastreidae, Agariciidae, Fungiidae, Rhizangiidae, Pectiniidae, Merulinidae, Dendrophylliidae, Caryophylliidae, Mussidae, Favidae, Trachyphylliidae, et Poritidae (Hoeksema et Cairns 2015). Parmi ces familles, les Acroporidae abritent le plus grand nombre d'espèces, avec plus de 300 recensées. Trois des quatre genres qui composent cette famille sont exclusivement Indo-Pacifique, tandis que trois espèces du genre *Acropora* sont rencontrées en Atlantique (Veron 2000). Par ailleurs, plusieurs études démontrent que le genre *Acropora* est le plus complexe en ce qui concerne l'identification morphologique (Wells 1954 ; Veron et Wallace 1984 ; Sheppard 1998).

La région corallienne de l'Indo-Pacifique abrite le plus large des habitats marins, sachant qu'il s'étend de la Mer Rouge à l'est de l'Océan Pacifique (Sheppard 1998). Toutefois, la distribution des espèces dans cette région est telle que plusieurs écorégions peuvent être distinguées en fonction du nombre d'espèces et de leur affinité (Veron et al. 2015). Le Triangle de corail (traduction littérale de « Coral Triangle ») est le cœur de la distribution globale des scléractiniaires. La bande entre la mer de Sulu et la « Tête d'Oiseau » (« Bird Head ») qui se trouve dans l'extrême ouest de la Nouvelle Guinée représente l'épicentre de la diversité corallienne (Figure 6).

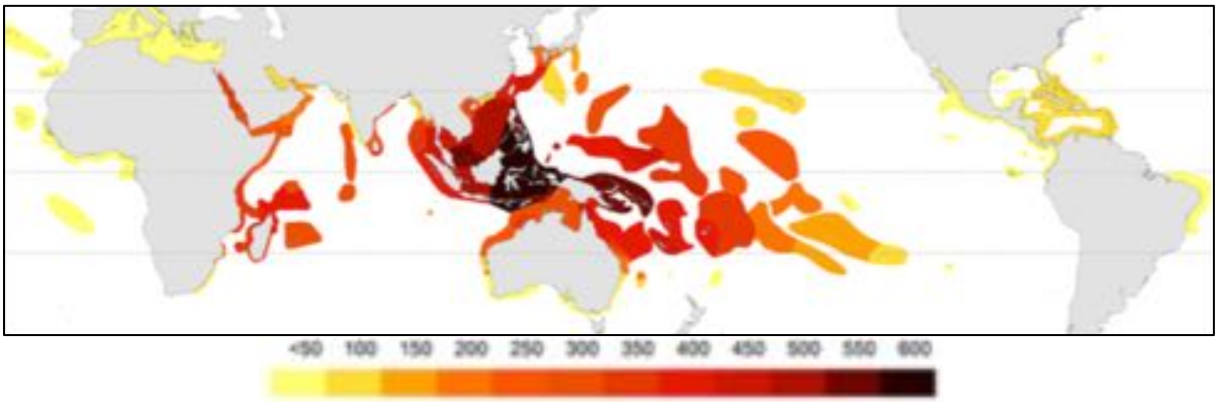


Figure 6: Diversité globale des scléractiniaires traduisant toutes les apparitions notées de chaque espèce.

Les valeurs de la diversité ont été déduites des données cartographiques de toutes les espèces (Veron et al. 2015). D'après Sheppard (1998), 491 espèces de scléractiniaires reparties sur 87 genres sont rencontrées dans l'Océan Indien (études sur 26 sites, Tableau 2). Le nombre de genres et d'espèces semble similaire pour toutes les subdivisions géographiques de l'Océan Indien, mais les études de l'affinité liée à la diversité montrent que la région sud-ouest constitue à elle seule une écorégion (Veron et al. 2015).

Tableau 2 : Résumé du nombre d'espèces et genre dans 26 sites de l'Océan Indien (Sheppard 1998)

Site	Nombre d'espèces	Nombre de genre	Références taxonomiques
Total des sites	491	87	
Gulf of Aqaba, Gulf of Suez	138	54	Sheppard et Sheppard (1991)
Central Red Sea (Yanbu)	150	50	Sheppard et Sheppard (1991)
South Red Sea Jeddah-Jizan, Sudan	115	49	Sheppard et Sheppard (1991)
Arabian Gulf	62	27	Sheppard et Sheppard (1991)
Gulf of Oman	77	34	Sheppard et Sheppard (1991)
South Oman, Gulf of Aden, Socotra	101	43	Sheppard et Sheppard (1991); Salm (1993); Sheppard et Salm (1998)
Gulf of Kutch	37	20	Bakus (1994); Patel (1988)
Somalia	52	22	Carbone et al. *(*1994)

Kenya / Tanzania	112	50	Hamilton et Brakel (1984)
Mozambique	110	44	Reigl (1993, 1995)
Tulear Madagascar	112	57	Pichon (1978)
South Africa	89	39	Reigl (1993)
Aldabra, Cosmoledo, Farquhar	95	40	Rosen (1979, 1992b)
Granitic Seychelles, Amirantes	174	55	Rosen (1992b); Hoeksema (1993)
SE India, Sri Lanka	182	55	Pillai (1972, 1983); Bakus (1994); Rajasuriya et De Silva (1988); Mergner et Scheer (1974)
Lakshadweep	95	34	Bakus (1994); Pillai (1971a,b)
Maldives	187	57	Sheppard (1998)
Chagos	220	58	Sheppard (1981)
La Réunion	124	43	Bouchon (1981); Faure (1997)
Mauritius	133	47	Faure (1977)
Rodriguez	84	36	Faure (1997)
Cocos Keeling	94	29	Veron (1990)
Nicobars, Andamans	131	50	Scheer et Pillai (1974); Bakus (1994); Reddiah (1997); Mukherjee (1985)
Thailand, Mergui Archipelago (Myanmar)	214	64	UNESCO (1984)
Northwest Australia	311	71	Veron et Marsh (1988); Veron (1993)
Southwest Australia	192	47	Veron et Marsh (1988); Veron (1993)

A Madagascar, la diversité des scléractiniaires a été réalisée par Pichon (1978). Cette étude, effectuée sur les récifs du sud-ouest de l'île, donne un aperçu détaillé de la répartition de toutes les espèces existantes sur tous les étages et les biotopes des écosystèmes récifaux. Les résultats démontrent que sur les 147 espèces citées, le genre *Acropora* est le plus diversifié avec 13 espèces rencontrées, suivis de *Pavona* (8), *Fungia* (7), *Pocillopora* (7), *Porites* (7) et *Leptoseris* (6) (Tableau 3).

Tableau 3: Liste des genres et nombre d'espèces de scléractiniaires rencontrées au niveau des récifs de la région sud-ouest de Madagascar (Pichon 1978). NE = nombre d'espèces.

Genre	NE	Genre	NE	Genre	NE	Genre	NE
Acropora	13	*Dendrophyllia*	2	*Balanophyllia*	1	*Merulina*	1
Pavona	8	*Echinopora*	2	*Caryophillia*	1	*Montastrea*	1
Fungia	7	*Galaxes*	2	*Caulastrea*	1	*Oxypora*	1
Pocillopora	7	*Goniastrea*	2	*Culicia*	1	*Paracyathus*	1
Porites	7	*Goniopora*	2	*Cycloseris*	1	*Parascolymia?*	1
Leptoseris	6	*Hydnophora*	2	*Cynarina*	1	*Pectinia*	1
Favites	5	*Mycedium*	2	*Diaseris*	1	*Physogyra*	1
Montipora	5	*Oulophyllia*	2	*Diploastrea*	1	*Platygyra*	1
Turbinaria	5	*Pachyseris*	2	*Echinophyllia*	1	*Plerogyra*	1
Favia	3	*Platygyra*	2	*Gyrosmilia*	1	*Podabacia*	1
Leptastrea	3	*Plesiastrea*	2	*Halomitra*	1	*Polycyathus*	1
Lobophyllia	3	*Turbastraea*	2	*Herpolitha*	1	*Seriatopora*	1
Psammocora	3	*Acanthastrea*	1	*Heterocyathus*	1	*Siderastrea*	1
Stylophora	3	*Agariciclla*	1	*Heteropsamia*	1	*Sphenotrochus*	1
Blastomussa	2	*Alveopora*	1	*Horastrea*	1	*Stylocoeniella*	1
Coscinarea	2	*Anomastrea*	1	*Leptoria*	1	*Symphyllia*	1
Cyphastrea	2	*Astreopora*	1	*Madracis*	1	*Trachyphyllia*	1

1.2.3 Identification des scléractiniaires et données moléculaires

La difficulté et la complexité de l'identification chez les Scleractinia constituent une des multiples raisons du développement des données moléculaires sur les coraux. Cela est particulièrement valable pour l'étude des recrues pour lesquels les critères morphologiques d'identification se limitent à quelques familles (Baird et al. 2012), et pour les larves qui présentent pour toutes les espèces une morphologie très similaire qui rend impossible une identification taxonomique spécifique. Beaucoup d'études phylogénétiques sur base de données moléculaires (séquences d'ADN) ont à ce jour été réalisées pour la création de banques de données, l'identification d'espèces et pour la caractérisation de relations intra- et inter-spécifiques (*e.g.,* Fukami et al.

2000; van Oppen et al. 2000; Forsman 2003; Fukami et Knowlton 2005 ; Benzoni et al. 2007 ; Knittweis et al. 2009 ; Gittenberger et al. 2011 ; Huang et al. 2011 ; Kitano et al. 2013). Ces données moléculaires sont utilisées pour effectuer des analyses phylogénétiques de taxons infra-ordres (*e.g.,* Flot et Tillier 2006) ou de l'ensemble des Scleractinia, pour une meilleure compréhension de la structure phylogénétique des espèces (Kitahara et al. 2010) ou pour des analyses génétiques des populations (*e.g.,* Odorico et Miller 1997).

Parmi les données moléculaires les plus utilisées pour l'identification des coraux, on retrouve les gènes codant pour la Cytochrome Oxydase I (COI), les Internal Transcribed Spacers (ITS) et le gène 18S rDNA codant pour l'ARN ribosomial inclus dans la petite sous unité. Les deux premiers sont mitochondriaux, le troisième est nucléaire. Le COI, l'ITS et le 18S rDNA montrent 1652, 1732 et 2670 entrées sur la banque de données GenBank. Parmi ces gènes, le COI représente maintenant le standard planétaire pour le barcoding des espèces animales (Hebert *et al.* 2003). Pour l'identification des scléractiniaires au niveau spécifique, ce gène présente cependant deux désavantages majeurs. Le premier est qu'il montre extrêmement peu de variabilité génétique entre espèces (parfois 0%) et est donc peu utile pour l'identification des coraux aux niveaux « espèces » et « genres » (Shearer et Coffroth 2008). Le second lors de l'étude d'espèces appartenant à différentes familles, son amplification nécessite l'emploi d'une multitude de couples d'amorces lors des réactions de polymérisation en chaîne (PCRs) (Lin et al. 2011). Les ITS sont des régions non codantes qui accumulent beaucoup de mutations au cours de leur histoire. Ils sont surtout utilisés lors d'études phylogénétiques intraspécifiques (Takabayashi et al. 1998). Le 18S rDNA quand à lui montre aussi peu de variabilité entre les espèces de même genre. Son amplification est cependant plus aisée car elle demande l'utilisation de moins de couples d'amorces.

1.3 Importance des coraux et des récifs coralliens

1.3.1 Intérêts environnementaux et sociaux

Morts ou vivants, les récifs coralliens sont des biotopes très diversifiés qui constituent des abris et des supports pour une multitude d'organismes vivants extrêmement variés phylogénétiquement (Pichon 1963 ; Veron 1986; Vasseur et al 1988 ; Gabrié et al 2000). Les régions coralliennes les plus riches comptent plus de 700 espèces de coraux, plus de 6000 espèces de mollusques et près de 4000 espèces de poissons (Weinberg 1996). A Madagascar, plus de 1000 espèces de poissons récifaux et plus de 2500 invertébrés marins ont été répertoriés (Baumeister, 1997; Laboute et Maharavo 1998).

Les récifs coralliens, tout particulièrement ceux de la région sud-ouest de Madagascar, jouent un rôle important dans la protection de la côte contre l'érosion, en brisant l'action de la houle et des vagues. Ceci permet, en outre, l'installation d'autres écosystèmes côtiers qui ont besoin d'une eau calme et protégée, notamment les herbiers de phanérogames et les mangroves qui présentent un intérêt colossal pour la reproduction de certains animaux marins tels que, entre autres, les crevettes et les crabes (Kaiser et al. 2011). A travers la photosynthèse, les phanérogames des herbiers contribuent fortement à la production de la matière organique en milieu côtier. Les herbiers sont des zones d'alimentation de plusieurs espèces marines d'importance écologique et socio-économique, telles que les tortues et les dugongs. La présence des nattes des herbiers permet la stabilisation des sédiments et favorisent l'oxygénation des eaux (Ratsifandrihamanana 2010).

Du point de vue social, la diversité et l'abondance des ressources marines vivrières sur les récifs coralliens en font des garde-mangers indispensables pour la plupart des pays qui pratiquent la pêche traditionnelle et artisanale. Au niveau mondial, la production potentielle des ressources marines d'origine récifale est estimée à 12% des captures totales (Ifrecor 1999). La quasi-totalité de la production de la pêche traditionnelle provient directement des récifs coralliens ou des écosystèmes adjacents, dont l'installation est conditionnée par la présence des récifs coralliens (lagons, mangroves). A Madagascar, la population côtière, et plus particulièrement la population des pêcheurs vit étroitement avec la mer et les récifs coralliens. En 1988, le nombre total de pêcheurs traditionnels à Madagascar était estimé à 42556 (Andrianaivojaona et al. 1992). Ce nombre qui n'a cessé d'augmenter témoigne de l'importance des activités liées à la pêche au niveau des récifs coralliens. Représentant plus de la moitié de la production halieutique marine, la pêche traditionnelle ravitaille la totalité des villes du pays, en particulier Tuléar où la consommation hebdomadaire est dominée par le poisson (Leva 1991).

Les récifs coralliens et leur extraordinaire biodiversité constituent encore un attrait écotouristique important. Le tourisme est un des secteurs du travail qui connaît le plus fort taux de croissance dans les pays en voie de développement, l'écotourisme représentant un moyen puissant pour valoriser et protéger la biodiversité. A Madagascar, le tourisme amène quelque 200000 étrangers non résidents par an et génère environ 300 millions d'euros/an (Ministère du tourisme de Madagascar 2014a, 2014b). Le nombre d'emplois générés par le secteur du tourisme a augmenté de 73% en 9 années, l'écotourisme étant le segment le plus développé sur l'île.

1.3.2 Intérêts des coraux en médecine

Les coraux ont été utilisés comme matériaux de remplacement osseux à l'échelle expérimentale vers 1975 (Chiroff et al. 1975) pour combler des trous de trépans crâniens ou ceux laissés par des prises de greffe iliaque (Loty et al. 1990 ; Vuola 2001). Depuis lors, les expérimentations animales qui s'en sont suivies ont montré une tolérance encourageante. En 1990, Loty et al. (1990) ont rapporté après 5 années d'utilisation du squelette du genre *Porites* sur l'homme, que le corail est un matériau de substitution osseuse intéressant, aisément disponible, facilement stérilisable et d'un coût modéré. Le comblement de trous de trépans crâniens et des zones de prises de greffes osseuses iliaques est assuré d'une bonne tolérance pour le patient (Loty et al. 1990). D'autres espèces comme *l'Acropora palmata* qui ont également été testées comme substituts osseux ont montré une efficacité notable (Chamberlain 1978).

Chez les cnidaires en général, incluant les coraux et les coraux mous, environ 3000 nouveaux extraits naturels ont été isolés d'environ 300 espèces (soit ~ 4.3%, Leal et al. 2012) depuis les deux dernières décennies (Leal et al. 2013), parmi lesquelles plusieurs ont potentiellement des propriétés pharmaceutiques prometteuses (anti-microbienne, anti-tumorale, anti-inflammatoire, anti-fouling ; Rocha et al. 2011). Chez les scléractiniaires (sur environ 30 espèces ; Leal et al. 2013), on a surtout découvert des molécules anti-inflammatoires et anti-tumorales (*e.g.,* chez les espèces *Tubastrea sp.*, *Cladocora caespitosa* ; Rocha et al. 2011)

1.3.3 Bijouteries et autres intérêts

A Madagascar comme partout dans le monde, les coraux sont exploités pour leur utilisation comme objets décoratifs, comme matériaux de construction et comme bijoux. Depuis 1984, le corail est utilisé comme matériau de confection de souvenirs aux îles Salomon. D'après Lal et Kinch (2005), le Ministère des pêches et des ressources marines de ce pays a reporté 20000 pièces de corail exportées en 2004 vers les Etats-Unis d'Amérique où ils ont été vendus en tant que souvenirs. Cette activité représente une source considérable de revenus pour les communautés côtières. Ces dernières collectent sur les récifs des spécimens des genres *Acropora*, *Pocillopora*, *Turbinaria*, *Heliopora* et *Seriatopora*, puis les laissent sécher et blanchir au soleil. A

Madagascar, aucune donnée sur la collecte et le commerce de coraux à des fins décoratives n'est disponible. Cependant, il est connu que depuis plusieurs décennies, les squelettes de coraux blanchis et nettoyés sont vendus aux touristes comme souvenirs. En parallèle avec les réglementations internationales pour la protection des récifs coralliens et d'espèces récifales (IUCN et CITES), cette activité y est interdite depuis une dizaine d'années. Toutefois, des squelettes de coraux, incluant les coraux noirs (Antipatharia), sont toujours observés sur les marchés de souvenirs, notamment de Tuléar à Nosy Be (*observations personnelles*). Les espèces les plus souvent observées appartiennent aux genres *Acropora* et *Pocillopora*.

Les coraux noirs représentent un cas particulier (voir annexe 1 ; Todinanahary et al. 2016). La collecte et la commercialisation de corail noir ont toujours existé à travers le monde, mais son exploitation a augmenté avec le développement des techniques de plongée en scaphandre autonome, au point de devenir une importante source de devise de plusieurs pays tels que les îles Cayman, Cuba, Mexique, Taïwan, les Philippines et la République Dominicaine (Castorena et Metaca 1979 ; Guitart et al. 1997). A Madagascar, notamment dans la partie sud de l'île (Région Androy et Région Anosy), la pêche et le commerce de corail noir se sont développés depuis seulement quelques années avec la forte demande du marché. Cependant, le manque d'informations biologiques et écologiques de base, ainsi que l'absence de politique de gestion bien déterminée dans le pays a conduit le gouvernement à interdire l'exploitation de corail noir dans tout le pays depuis 2014 (Todinanahary et al. 2016). Etant donné que c'est une activité illégale, aucune statistique sur la production des coraux noirs n'est disponible. Cependant, nous avons estimé à partir des données collectées à travers les enquêtes et les données officielles sur les saisies du Centre de Surveillance des Pêches, qu'une activité de collecte de 4-5 mois permet aux exploitants une vente de 5 tonnes de coraux noirs (Todinanahary et al. 2016). La production de coraux noirs dans ces deux régions pourrait passer la barre des 10 tonnes par an.

Les coraux sont également utilisés pour la fabrication de chaux à l'échelle artisanale. La littérature qui rapporte l'utilisation des squelettes de coraux à cette fin est très rare néanmoins quelques informations témoignent du cas de la collecte du squelette des coraux « cornes de cerf » (*Acropora spp.*) et la fabrication de chaux aux îles Salomon (Lal et Kinch 2005). Dans ce pays, la chique de bétel est une coutume ancestrale très répandue, et la chaux faite de squelette de corail en est un des ingrédients, avec le « daka » (feuilles de bétel) et la noix d'arec. Cette pratique fait partie intégrante de la culture salomonaise et joue un rôle social fort au sein des communautés locales (Teitelbaum 2007). A Madagascar, la chaux fabriquée à partir des coraux est destinée à l'industrie artisanale de construction (Figure 7). Elle est notamment utilisée dans la construction de maison et des petits travaux de bâtiment. Cependant, dans ce pays, les squelettes de coraux utilisés pour cette production de chaux sont des fossiles, qui viennent des terres fermes, dans les sédiments anciennement colonisés par les récifs coralliens. La chaux vive, la chaux éteinte, le carbonate de calcium et la dolomie sont également utilisés dans le domaine de l'aquaculture de crevette, pour la correction du pH du sol et l'assainissement des fonds de bassin. Mais les entreprises crevetticoles de Madagascar n'utilisent pas les chaux fabriquées localement avec des coraux vivants. Le domaine d'aquaculture de crevette biologique exige des conditions physiques et chimiques particulières, ce qui explique l'importance des importations de chaux (Randrianarivelo et al. 2014).

Figure 7: Fabrication artisanale de chaux vive à partir du corail fossile à Soalara Sud (~ 40 km au sud de la ville de Tuléar).

Les blocs de coraux fraichement collectés sur les récifs coralliens sont aussi utilisés dans la construction des puisards, pour leur propriété poreuse qui permet la filtration des eaux grises et des eaux noires. Cette pratique est cependant interdite depuis plusieurs années.

1.3.4 Pêche au niveau des récifs coralliens

Les récifs coralliens constituent la principale zone de collecte des pêcheurs traditionnels de la région sud-ouest de Madagascar. Dans la baie de Tuléar, plus de 1500 pêcheurs traditionnels, répartis sur trois principaux villages y pratiquent leurs activités (Brenier 2009). Long de 18 km, le Grand Récif de Tuléar constitue un complexe récifal comprenant des bancs coralliens internes (Harmelin-Vivien 1979; Andréfouët et al. 2009). La biodiversité y est élevée avec plus de 6000 espèces recensées (ONE 2003). D'après Harmelin-Vivien (1974,1977 et 1979) et Rasoarimalala (2001), 714 espèces de poisson récifaux y ont été recensées, avec une biomasse de 1200 kg/ha (Laroche et Ramananarivo 1995). Les techniques de pêche sont très diverses dans cette zone : le filet maillant, la ligne, le fusil et la senne de plage sont embarqués dans des pirogues monoxyles à voile conduites en général par les hommes adultes (Rejela 1993; Angin 2007). Les sennes qui sont déployées au niveau des plages ou au niveau du platier récifal, représentent 43% de la capture de pêche en terme de poids (Bruggemman et al. 2012). Cette pratique est très destructive pour les récifs coralliens (Vasseur 1997). La pêche à pied pratiquée par les femmes et les enfants, s'ajoute également à cette pratique destructive pour les récifs coralliens. Depuis plusieurs dizaines d'années, les jeunes pêcheurs utilisent les « voloso » (piquet en bois avec un à 4 crochets sur l'extrémité) pour chercher les poulpes, les gastéropodes et les poissons, cachés sous les blocs de coraux (Koechlin 1984). Cette pratique est particulièrement hostile pour les coraux du fait que les pêcheurs retournent les blocs et ne les remettent pas en place. La destruction d'habitat corallien causée par ces techniques destructives sur le platier du GRT a été estimée à 1 $km^2.an^{-1}$ (Salimo 1997). Actuellement, on assiste à un changement majeur des habitats récifaux dû essentiellement aux pressions de la pêche, aux facteurs climatiques et aux facteurs externes tels que la sédimentation (Andréfouët et al. 2013; Sheridan et al. 2014).

La production de la pêche traditionnelle était auparavant assez conséquente, mais en 50 ans, un déclin notable de cette production a été observé. Dans les années 1950, la capture par unité d'effort (CPUE, désigne la quantité de produits pêchés par rapport à une unité d'effort de pêche qui correspond souvent en une sortie de pêche) a été estimée entre 50 à 100 kg j^{-1} pour la pêche au filet maillant et > 1000 kg j^{-1} pour la pêche au filet de senne. Dans les années 2000, cette production a diminué jusqu'à respectivement, 6,5 à 7,4 kg j^{-1} et 14,5 à 18,0 kg j^{-1} (Laroche et al. 1997 ; Lagouin 1959 ; Bruggeman et al. 2012). Cette diminution est proportionnelle à la diminution de la biomasse qui, elle aussi, est essentiellement due à l'augmentation de la pression de pêche sur le récif (Vasseur 1997).

La composition de la capture de la pêche traditionnelle dans les milieux récifaux est essentiellement constitué de poissons, appartenant, entre-autres, aux familles des Acanthuridae, Carangidae, Siganidae, Engraulidae, Caesionidae, Lethrinidae, Pomacentridae, Lutjanidae, Serranidae, Gerreidae, Hemiramphidae, Labridae, Holocentridae et des Mullidae (Brenier 2009; Davies et al. 2009). Les petits pélagiques comme les Clupeidae, les Carangidae, les Scombridae sont également exploités (Rakotoarinivo 1998). Les poissons de la famille des Chaetodontidae ont été rarement capturés par les pêcheurs qui les considéraient comme des captures de deuxième catégorie. Depuis les premières évaluations de capture, dans les années 1970, la diversité de cette composition n'a jamais cessé de diminuer (Figure 8) (Ranaivomanana 2006) et les Chaetodontidae commencent aussi à être pêchés. Depuis une dizaine d'années, ces poissons ont de plus en plus rempli la capture des pêcheurs et sont de plus en plus observés sur le marché local (Maharavo J, *com. pers.*). Bruggeman et al. (2012) rapporte qu'en 30 ans, plusieurs familles de poissons ont perdu de leur richesse spécifique. Leur observation visuelle de 2008-2009 a montré que les Acanthuridae et Siganidae ont perdu respectivement 2 et 1 espèces, tandis que les Scarinae sont passés de 13 à 7 espèces observées. Les Chaetodontidae et les Serranidae qui étaient composé de 20 espèces auparavant, ont perdu respectivement 6 et 7 espèces (Bruggeman et al. 2012).

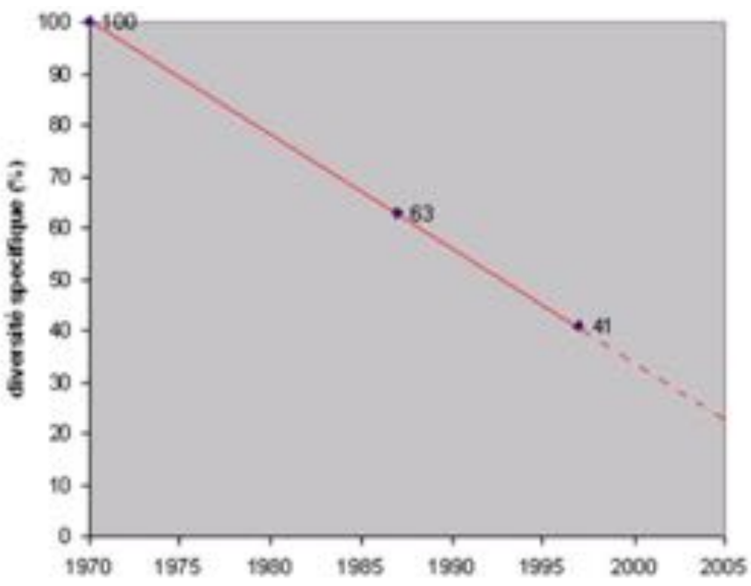


Figure 8: Diminution de la diversité spécifique en poissons (%) dans la Baie de Tuléar entre 1970 et 1995 (Pichon 1972 ; Vasseur et al. 1988 ; Rasoarimalala 2001). Source : Ranaivomanana 2006

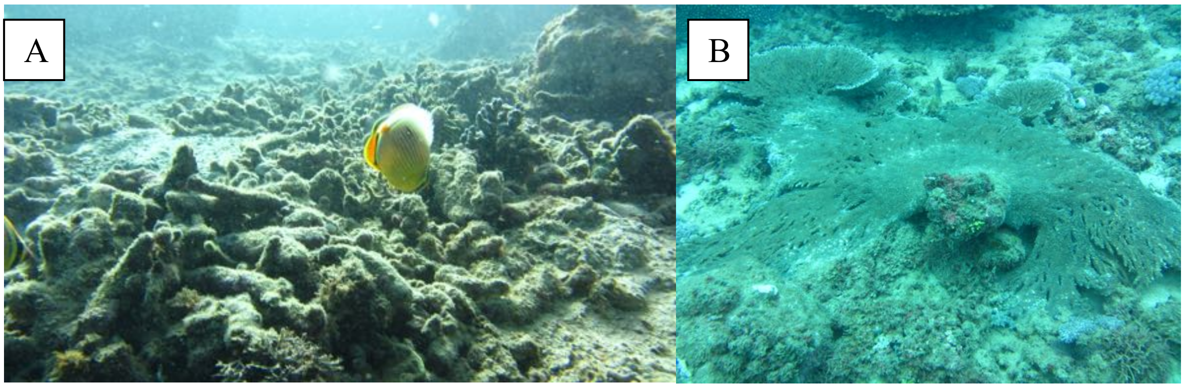


Figure 9: A. Platier récifal dégradé sur le GRT (Grande Vasque) ; B. Corail tabulaire (*Acropora*) retourné, sur le site de Nosy Arakaivo (Sarodrano)

1.4 Marché aquariophile

Le marché des coraux est à ce jour très méconnu, le débouché économique le plus évident étant le marché aquariophile. Le commerce des coraux vivants (coraux d'aquaculture et sauvages confondus) a approximativement été multiplié par 40 en 23 ans. Il est passé d'environ 50000 coraux (nombre) en 1990, à plus de 2000000 en 2013 (CITES 2016)[2]. Les aquariums à coraux vivants sont apparus en Europe avant 1986, année à partir de laquelle ce type d'aquarium a gagné l'Amérique du Nord (Smit 1986) (Figure 10). Depuis lors, la popularité des aquariums n'a cessé de gagner du terrain, notamment aux Etats-Unis qui sont devenus les plus gros importateurs d'animaux récifaux au monde (Green et Shirley, 1999). Les Etats-Unis ont importé plus de 115000 coraux d'aquaculture entre 1990 et 2013, suivis de près par le Japon (23301), la France (6225), le Mexique (2479) et le Sri Lanka (2400) (CITES 2016).

[2] Ces nombres incluent toutes les sources des coraux commercialisés : sauvages ou issus de l'aquaculture.

Figure 10 : Illustrations de coraux dans des aquariums récifaux. A. un aquarium personnel à Miami (Veron 2000) ; B. Un aquarium avec *Acropora* en Norvège. C et D. Coraux en pleine croissance dans un aquarium du laboratoire d'Ecologie Numérique des Milieux Aquatiques (ECONUM) de l'Université de Mons, Belgique.

A partir des années 1990, la collecte et le commerce des coraux sauvages sont devenus règlementés, du moins au niveau international. En effet, depuis un peu plus de 20 ans, beaucoup d'espèces de coraux et d'autres organismes récifaux sont répertoriés dans le livre rouge de l'Union Internationale de la Conservation de la Nature (UICN) et se retrouvent dans les listes CITES (Convention sur le commerce international des espèces de faune et de flore sauvages menacées d'extinction) (Ifrecor 1999). Toutes les espèces appartenant à l'ordre des Scleractinia sont inscrites à l'Annexe II de la liste CITES (Tableau 4), qui stipule que l'exportation d'un spécimen d'une espèce inscrite dans cet annexe nécessite la délivrance et la présentation préalable d'un permis d'exportation, et l'importation nécessite la présentation préalable d'un permis d'exportation (CITES 1973).

Tableau 4 : Les espèces de cnidaires inscrites dans les annexes de CITES. Les fossiles ne sont pas soumis aux dispositions de la Convention (CITES 2016)

Annexe I	**Annexe II**	**Annexe III**
Phylum : Cnidaria Classe : Anthozoa (coraux et anémones de mer)		
Antipatharia (Coraux noirs)		
	Antipatharia spp.	
Gorgonaceae		
Corallidae		
		Corallium elatius (Chine) *Corallium japonicum* (Chine) *Corallium konjoi* (Chine) *Corallium secundum* (Chine)
Helioporacea		
Helioporidae (Corail bleu)		
	Helioporidae spp. (inclus seulement l'espèce *Heliopora coerulea*)	
Scleractinia (Coraux durs)		
	Scleractinia spp.	
Stolonifera		
Tubiporidae (Orgues de mer)		
	Tubiporidae spp.	
Classe hydrozoa (hydres, coraux de feu et physalies)		
Milleporina		
Milleporidae (Coraux de feu)		
	Milleporidae spp.	
Stylasterina		
Stylasteridae (Stylastérides)		
	Stylasteridae spp.	

1.4.1 Aquaculture de coraux

Depuis l'inscription des cnidaires aux annexes de la CITES, l'aquaculture de ces animaux a commencé à voir le jour (Department of Fisheries of Australia 2009) afin de satisfaire la demande tout en préservant les coraux et les récifs coralliens. L'aquaculture de coraux a depuis été pratiquée à différentes échelles en France, aux Pays-Bas, en Allemagne, en Chine, en République Dominicaine, aux îles Fiji, en Indonésie, aux îles Marshall, aux Philippines, à Singapour, en Tanzanie, aux Etats-Unis, à Porto-Rico, à Palau, aux îles Salomon, au Japon et en Australie (CITES 2002 ; Hernández-Delgado et al. 2014). Les méthodes utilisées diffèrent en général selon la latitude. Dans les pays intertropicaux, les coraux sont cultivés la plupart du temps en milieu naturel (Ellis et Sharron 1997; Albert et al. 2012) tandis que les pays tempérés pratiquent plutôt la coralliculture en aquariums sur la terre ferme (Wijgerde et al. 2014 ; Leblud et al. 2014).

Dans les deux cas, les méthodes se basent généralement sur la technique de bouturage. Une bouture composée d'une ou quelques branches est coupée d'une colonie mère, puis fixé fermement sur un support dur en plastique, en ciment ou en matériaux spécialement conçu par l'aquaculteur. La taille de la bouture dépend du but et de sa destination finale après élevage. Le support est ensuite arrimé à une structure plus large qui contient plusieurs boutures à l'aide de fil élastique ou en encastrant le support dans la structure préalablement conçu pour le recevoir. La fixation de la bouture sur le support est également différente selon l'aquaculteur et ses objectifs (Shafir et al. 2006 ; Shafir et Rinkevich 2008). Parmi les plus utilisés, on distingue le ciment prompt, la colle cyanoacrylate ou simple fil élastique (*e.g.,* Shafir et Rinkevich 2008 ; Forsman et al. 2011 ; Ng et al. 2012). En milieu naturel, une table de coralliculture en métal est la structure la plus communément utilisée tandis qu'en aquarium, cette structure est souvent en plastique ou en pierre. L'utilisation de stimulant électrique est connu pour améliorer de façon significative la survie, croissance et le stress des organismes marins incluant les coraux (Goreau 2014). Toutefois, l'utilisation de cette technique est encore limité au programme de restauration de récifs dégradé et/ou stressé pour augmenter leur capacité de résilience (van Treeck et Schuhmacher 1997 ; Goreau 2012). L'efficacité de cette méthode en aquaculture est très limitée du fait de la nécessité d'une formation adéquate pour les praticiens (Goreau 2014).

Il est connu que la production de coraux d'aquaculture dans le monde augmente et de plus en plus de pays la pratiquent tant à l'échelle industrielle qu'artisanale (Delbeek 2001). L'Indonésie reste le plus grand producteur et exportateur de coraux vivant dans le monde (Raymakers 2001 ; CITES 2016).

1.4.2 Difficultés liées à l'aquariophilie

Malgré son essor, l'aquaculture de coraux et l'aquariophilie ne sont pas sans difficulté. Les coraux peuvent tolérer un intervalle assez large de conditions environnementales, mais ils sont très sensibles à un changement brusque des paramètres tels que la température, la salinité, le pH et l'oxygène dissous (Osinga et al. 2011; Wijgerde et al. 2014). En aquariophilie, le maintien de ces paramètres constitue une des plus grandes contraintes. Cela nécessite de gros investissements afin de maintenir une bonne santé et une croissance normale des coraux. Le total des coûts indispensables pour un système de coralliculture ex-situ peut aller jusqu'à plus de 11 Euros par m^2 (*e.g.*, NAUSICAA, Osinga et al. 2011). Ce coût peut aussi changer en fonction du régime d'alimentation adopté les espèces aquacultivées. Par exemple, la production de 100 g (poids immergé obtenu en 1 an environ) de *Seriatopora caliendrum* nécessite entre 25.40 Euros et 30.20 Euros par colonie respectivement pour un régime à faible alimentation et à alimentation élevée (Osinga et al. 2011).

En outre, l'obtention des colonies souches est aussi un défi considérable pour chaque aquariophile (particulier) ou chaque producteur/vendeur de plus grande envergure tels que les magasins d'aquariums et les aquariums publics. Souvent installés dans des pays tempérés, ces aquariums doivent importer des colonies souches depuis les pays tropicaux ou intertropicaux producteurs de coraux d'aquaculture ou collecteurs de coraux sauvages (suivants les règlementations CITES). La distance entre les exportateurs et les importateurs est souvent très longue et implique que les coraux soient transporté pendant parfois plus de 25 heures (Delbeek 2008). Il existe plusieurs méthodes de transport de coraux selon le stade de développement et la taille des colonies transportées mais en général ces méthodes implique un transport à sec (la colonie est transportée dans un conteneur remplis de bandelettes en plastique imbibées d'eau de mer ; Petersen et al. 2004) ou un transport immergé (chaque colonie est immergée dans de l'eau de mer filtrée ; Delbeek 2008). Ce dernier type de transport est également utilisé pour les larves en gardant une certaine densité pour permettre une plus grande survie et une plus longue durée de transport (Petersen et al. 2005).

Le transport reste un facteur déterminant pour le commerce de coraux. Il limite l'accessibilité des importateurs à la biodiversité tropicale et intertropicale, mais aussi l'accessibilité des pays producteurs à un marché en plein essor. Les coraux étant des animaux très sensibles, une augmentation du temps de transport causé par un retard ou une annulation de vol peut provoquer une mortalité post-transport très élevée, voire totale. Par ailleurs, même si elles survivent à un transport de longue durée, les colonies coralliennes peuvent présenter des stress dont les effets néfastes (blanchissement ou mort) peuvent ne surgir que plusieurs semaines après le transport.

Les études sur les méthodes et les types de transport des coraux sont pour la plupart basées sur des expériences empiriques des importateurs et des chercheurs (*e.g.,* Petersen et al. 2004, 2005 ; Delbeek 2008). Elles offrent une description technique et pratique plus ou moins détaillée de chaque méthode, mais ne donnent pas un aperçu des changements des paramètres de l'eau qui provoque la mortalité ou le stress des colonies transportées. L'influence de la variation de chaque paramètre reste donc méconnue et sa compréhension permettrait d'adopter des méthodes et des techniques plus performantes (techniquement et économiquement) qui amélioreraient la résistance des coraux à une durée de transport plus élevée.

1.5 Gestion des récifs coralliens à Madagascar

Face à la situation alarmante que connaissent les récifs coralliens, les différents services du gouvernement malgache, les institutions de recherche et les ONGs ont commencé à prendre des mesures de gestion, de protection et de restauration des écosystèmes récifaux à partir des années 2000. Parmi ces mesures, la plus répandue et la plus connue est la création d'Aires Marines Protégées (AMPs) dont les parcs marins et les réserves marines (Mahafina 2011 ; Todinanahary et al. 2013).

Les parcs marins sont rares à Madagascar. Les plus connues sont situées dans le nord, notamment, entre autres, les parcs marins de Sahamalaza, de Masoala et de Nosy Tany Hely (Madagascar National Parks, 2016). Dans la Région sud-ouest, le long de la côte entre le fleuve Mangoky (latitude 21°24' S) et le fleuve Onilahy (latitude 23°34' S), 59 réserves marines dont 56 récifs coralliens et 3 mangroves, ont été mises en place par le projet d'Appui aux Communautés de Pêcheurs (PACP) entre 2006 et 2012 (Figure 11). La surface totale des réserves de récifs coralliens est de 5.146 ha. Toutefois, parmi toutes ces réserves marines, seules la réserve du Jardin des Roses, à Ifaty et la réserve « Nosy Masaka » à Sarodrano sont des réserves permanentes. Les autres réserves sont des réserves de poulpes, de calmar et de poissons (Voajanahary 2011 ; Todinanahary et al. 2013).

Figure 11: Réserves marines de la région sud-ouest de Madagascar (Todinanahary et al. 2013)

La mise en place des réserves marines a été réalisée avec une approche participative qui comprend plusieurs étapes afin de faciliter l'implantation et l'appropriation par la population locale. La première étape consistait en une sensibilisation au niveau de chaque village, par des organismes partenaires telles que les ONGs Blue Ventures au nord de la Baie de Ranobe, Reef Doctor, SAGE et WWF dans la Baie de Ranobe et WCS et SAGE dans la Baie de Tuléar (Mahafina 2011). En tout, 7 communautés de pêcheurs ont été impliquées dans cette mise en place ce qui, en théorie, devrait permettre le transfert du processus de gestion aux communautés elles-mêmes. Ce transfert n'est cependant faisable et efficace que si les communautés concernées s'approprient les réserves et les perçoivent comme une forme de gestion efficace de la pêche et des récifs coralliens (Mahafina 2011).

La gestion des récifs coralliens a toujours été associée avec la gestion de la pêche. Par conséquent, elle est complexe parce que plusieurs paramètres socio-économiques doivent être pris en compte afin d'assurer son efficacité. En somme, la complexité des récifs coralliens ne se limite pas à leur écologie ou à la biologie des organismes qui les constituent. Etant donné que ces écosystèmes sont des patrimoines gérés par l'Homme, les facteurs sociaux et économiques deviennent sans équivoque des paramètres clés pour une bonne gestion. Les recherches réalisées actuellement sur la gestion des récifs coralliens dans le monde s'articulent souvent avec ces enjeux. Le cas de Madagascar est souvent mis en évidence dans l'Océan Indien car il s'y distingue par le développement de projets de recherche qui travaillent sur le développement de l'aquaculture villageoise.

But du travail

Cette thèse a pour but général d'estimer le potentiel de la coralliculture villageoise à Madagascar, en particulier dans la région sud-ouest de l'île. La coralliculture pourrait en effet, dès lors qu'elle montrerait une certaine rentabilité, faire partie des aquacultures villageoises développées depuis plus de 15 années dans cette région du pays. La rentabilité économique de la coralliculture semble à priori moins évidente que l'holothuriculture et l'algoculture (qui sont les deux aquacultures déjà bien établies dans les villages malgaches) mais certains débouchés existent et méritent d'être étudiés. La mise en place d'une coralliculture villageoise demandait tout d'abord une connaissance plus poussée de la biologie des scléractiniaires dans la région ciblée. Dans ce contexte, quatre objectifs spécifiques ont été définis et ont été développés dans les quatre chapitres qui forment le corps de cette thèse.

Le chapitre 2 a pour but de déterminer quels sont les scléractiniaires les plus communs de la Baie de Tuléar et d'initier une banque de données génétique permettant l'identification des recrues de ces coraux. La seule investigation effectuée sur la diversité des scléractiniaires date de 1978 ; elle ne consiste qu'en une liste des espèces rencontrées sur le Grand Récif de Tuléar sans apporter de données quantitatives. Nous avons étudié la biodiversité des scléractiniaires en effectuant de nombreux transects sur divers sites, identifié ensuite les coraux avec des outils taxonomiques traditionnels et estimé enfin l'efficacité de la nouvelle banque de données génétiques en identifiant quelques recrues.

Le troisième chapitre évalue le potentiel de recrutement naturel des coraux scléractiniaires. Aucune étude sur le recrutement n'a été réalisée jusqu'à présent et celle-ci nous permet d'estimer la dynamique des coraux de la région. Nous avons pour cela effectué des traits de plancton pour identifier là ou les périodes d'apparition des larves planula, analysé périodiquement des plaques de recrutement et effectué des observations *in situ* pour le comptage des juvéniles.

Le quatrième chapitre a pour objectif d'estimer la meilleure méthode de transport pour les coraux vivants. Le transport de coraux vivants est une des contraintes majeures pour tous ceux qui ont besoin de déplacer ces organismes (les acteurs du marché aquariophile et les personnes impliquées dans la conservation des récifs coralliens). Nous avons ici travaillé dans des mésocosmes afin de comprendre la dynamique éco-physiologique des coraux dans un petit volume d'eau afin d'optimaliser leur résistance par rapport aux conditions de transport et de maximiser leur taux de survie.

Le cinquième chapitre analyse le potentiel d'élevage des coraux par des villageois pêcheurs. Nous avons mis en étude des différentes techniques d'aquaculture de coraux applicables et accessibles aux pêcheurs dans le but d'en sélectionner la plus efficace. Nous avons déterminé les taux de croissance et de mortalité de deux espèces de coraux-cibles mises en culture sur site et couplé ces paramètres biologiques avec les paramètres économiques nécessaires pour estimer le potentiel de la coralliculture dans cette région.

Chapitre 2

Scleractinian biodiversity in the Bay of Toliara (SW of Madagascar) with the construction of an 18S rDNA database for adults and recruits identification

CHAPITRE 2 : Scleractinian biodiversity in the Bay of Toliara (SW of Madagascar) with the construction of an 18S rDNA database for adults and recruits identification[3]

Abstract

The scleractinian biodiversity of Madagascar is mainly known from one study performed in the Bay of Toliara (SW of Madagascar) in the seventies. In the present study, we reinvestigated this biodiversity 40 years later and we initiated the implementation of a molecular database based on 18S rDNA fragments as an easy tool for identification of adults and recruits. Results showed lower species diversity compared to the previous studies and to similar sites in the Indian Ocean region, however most of the well-represented genera were recorded. The appearance of previously unrecorded species suggests that the scleractinian communities are changing instead of only declining. In addition, we obtained 18S rDNA sequence fragments for 20 of the most dominant species. Fifteen groups are distinguishable by pairwise comparison: 12 are monospecific, 1 includes 5 species and the last includes 2 species. Sequence fragment of 13 recruits were also obtained and BLAST searches against the adult genotypic database permitted to increase the resolution of recruit's identification from the level of family (with the traditional taxonomic key) to the level of species or genus. Identified recruits were *Pocillopora sp., Porites profundus, Porites rus, Pavona clavus and Lobophyllia corymbosa*. The findings of the present study constitute the baseline of high-resolution scleractinian diversity and recruitment studies in Madagascar.

[3] Ce chapitre sera soumis pour publication: Todinanahary GGB, Refoty ME, Terrana L, Lavitra T, Eeckhaut I (*In prep*) Scleractinian biodiversity in the Bay of Toliara (SW of Madagascar) with the construction of an 18S rDNA database for adults and recruits identification.

2.1 Introduction

Coral reefs of Madagascar occupy an area of 2,400 km^2 along 1,400 km of the coastline (Cook et al. 2000). Thanks to the particular geomorphology of the coastline, most of the coral reef types (barrier reef, fringing reef, patch reef, coral bank) setup into complex reef systems (Clausade et al. 1972) dominated by the Great Reef of Toliara (GRT) situated in the SW region of Madagascar. The GRT is among the most studied reef of the Indian Ocean. It houses one of the most diverse marine flora and fauna communities of Madagascar with more than 6,000 species (ONE 2003), including pelagic reef fishes (714 species, Harmelin-Vivien 1979; Rasoarimalala 2001) and benthic organisms such as sponges (125 species, Vacelet and Vasseur 1971) and scleractinians (112 species, Pichon 1978; Sheppard 1998).

It is well known that the coral reefs of Madagascar, especially those in the SW, are subjects to wicked social-ecological problems that force unprecedented change. In less than 50 years, the coral cover decreased from >50 to 5% (reported by Bruggemann *et al.* 2012), reef fish specific diversity dropped from 100 to < 30% (Ranaivomanana 2006), while the anthropic pressures by destructive fishing continued to raise due to the increasing demography (Vasseur et al. 1988; Toany 1995; Salimo 1997; Vasseur 1997). In the years 2006-2011, more than 50 marine protected areas (MPAs) were created as solutions to coral reef degradation and to fishery products decline (Voajanahary 2011; Todinanahary 2013). These MPAs were socially well perceived and accepted by fishermen communities, which were the main users and became the principal managers (Mahafina 2011). Mahafina (2011) reported some success and benefits generated by MPAs to the communities however most MPAs are not properly managed and their status as protected areas are often not respected except in some of them where there is a strong implication of non-governmental organizations (NGOs) (Rocliffe and Peabody 2012; Belle et al. 2009; Shane 2012).

The study of Pichon (1978) is the only one that relates the species richness and diversity of scleractinians in Madagascar and especially in the SW region of the country. Since then, new data about the reef building corals are very few and used only data from Pichon (1978) (*e.g.,* Sheppard 1987; Sheppard 1998; Obura 2012; Bruggemann 2012). In addition, there is a total lack of knowledge about coral recruitment. One of the main reasons why coral recruitment studies have never been performed is certainly the difficulty encountered in identifying coral recruits. A recruit is a stage existing between the time of larval settlement and the time when the colony became observable to the naked eyes. It is generally considered to be less than 1 year in age (Kojis and Quinn 1984; Babcock and Mundy 1996; Banks and Harriott 1996; Gleason 1996; Baird and Hughes 1997; Dunstan and Johnson 1998; Hughes et al. 1999; Mundy 2000) and recruit identification by traditional taxonomic keys is limited to only 3 families, the Acroporidae, Pocilloporidae, and Poritidae (Babcock et al. 2003).

The progress in molecular biology offers new tools to improve biological and ecological investigations including identification of scleractinian adults and recruits. The mitochondrial cytochrome oxidase 1 gene (CO1) is commonly used as the standard barcode for identifying species in almost all animal groups (Hebert 2003) although, for scleractinians, this gene was proved to be inappropriate due to an overlap between intraspecific and interspecific variations: analyses of scleractinians CO1 sequences showed almost no genetic divergence among species (Shearer and Coffroth 2008). Other genes used in scleractinian relationships are the internal transcribed spacers (ITS) of the ribosomal DNA (*e.g.*, Flot and Tillier 2006; Gittenberger et al. 2011; Huang et al. 2011). These regions are known to be highly variable in terms of sequence length among species but also in terms of intraspecific divergence (Takabayashi et al. 2006) and they are consequently, not suggested to be used in species identification. On the other hand, amongst the genes that are easy to amplify and that can thus routinely be used by any laboratories of zoology is the 18S rDNA gene. It is a slow evolving gene and it thus has a very low substitution rate (Hadziavdic et al. 2014). If 18S rDNA gene is not a good candidate for estimating the phylogenetic history between the species, a single substitution existing between two species is enough for differentiating these species and this molecular marker has already been used for distinguishing among the major groupings within the Class Anthozoa (Berntson et al. 1999) and also for first species characterization (Straub and Harmer Luke 2008).

The general aim of the present study is to settle the baselines for the construction of an 18S rDNA database to allow identifying scleractinian adults and recruits in the SW of Madagascar. For that purpose, the study pursued three specific goals: (i) to determine the present scleractinian biodiversity in the Bay of Toliara, (ii) to obtain 18S rDNA signatures of the most representative scleractinians of the Bay and (iii) to test if the genotypic database allows identifying scleractinian recruits more accurately than the classical morphological taxonomic keys.

2.2 Materials and methods

2.2.1 Area of study

Two distinct sites were chosen for the biodiversity analysis and the samplings (Figure 12). The first was the “Grande Vasque” (GV here after). The Grande Vasque is a basin of 1 km in diameter situated in the flat of the Great Barrier Reef of Toliara. GV is well protected from the swell, of 15 m deep and its slopes are colonized by sceractinians, mainly on the first 8 m. GV is located in front of the main harbour of the region, near Toliara city. Two stations in the GV were defined and sampled: one in its southern part (GV South), the other in its northern part (GV North). The second site of the study was Nosy Tafara. Nosy Tafara is a complex of patch reefs located between the southern tip of the Great Barrier Reef of Toliara and the sandy coast of Sarodrano village. Nosy Tafara is well exposed to the swell and the waves generated by the dominant SW wind. Two stations were also defined and sampled at Nosy Tafara: the outer slope of Arakaivo exposed to the open sea and Velomitahy, a station protected by Arakaivo. Both sites were chosen for the existence of old and up-to-date data (*e.g.,* Voajanahary 2011; Mahafina 2011; Bruggemann et al. 2012; Andréfouët 2013; Sheridan et al. 2014a, 2014b; Todinanahary 2013) and because they are among the most accessible sites in the Bay at every times of the year.

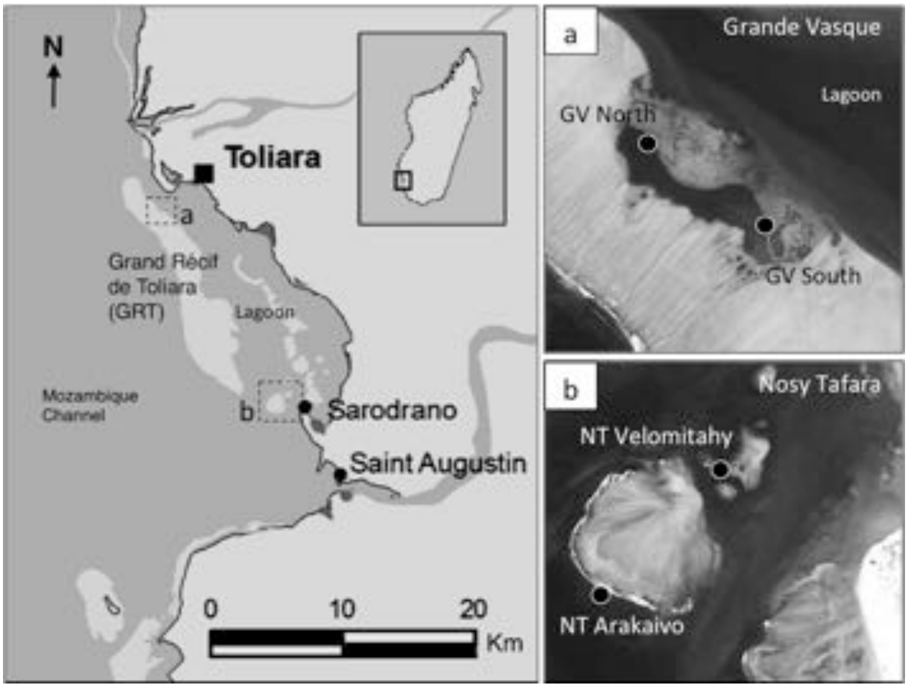


Figure 12: Localisation of the sites and stations

2.2.2 Monitoring the diversity

In the WIO Region, the PRE-COI ("Programme Régional Environnement de la Commission de l'Océan Indien") method is recommended for coral cover monitoring (Conand et al. 1997). This method based on a combination of transects and quadrats, was widely used for coral reefs studies in Madagascar, but was limited to category levels for coral identification (see details in Conand et al. 1997). In the present study, we used the Point Intersept Transect (PIT) (Hill and Wilkinson 2004). Several coral reef research programs used the PIT method (*e.g.*, Rogers et al. 1994), recommended by English et al. (1997), and adapted by others to fit with regional aspects and research focuses (Beenaerts and Berghe 2005). It was chosen and adapted for its efficiency to coral species diversity monitoring (Beenaerts and Berghe 2005).

At each station, 15 transects of 10 m were placed to the reef slope, at 8 to 15 m depth, by 3 to 4 divers between January and August 2015. The transect line was a flexible measuring tape, marked in millimetres. The line was kept closer to the benthic communities using small weights. To allow record of small coral colonies (< 10 cm including juveniles which are abundant on the sites), the line was marked every 5 cm and the sessile benthic organism or substrate directly beneath the mark was recorded. During the survey (*in situ*), the WIO common set of cover categories (see details of categories in Conand et al. 1997) were used. Live coral species were identified to at least genus level using the *in-situ* Coral finder identification guide (Kelley 2011), followed by an in-lab skeletal morphology analysis based on Veron's works (2000). All the observed colonies were photographed and 2 x 2 to 5cm branch were sampled respectively for skeletal morphology analysis and for DNA sequencing.

2.2.3 Calculation of ecological parameters

Coral species richness, species dominance and diversity were calculated for each station. Richness was calculated as the total number of species under the transect line. Species dominance was calculated as the ratio of the abundance of each species and the total number of recorded colonies on the transect reported as percentage. The Shannon diversity index (Shannon and Weaver 1964) was calculated at the level of coral species.

To characterize the community at each station, constancy and fidelity index of each species in the coral community (station) were also calculated. Constancy was calculated by dividing the number of transects containing the species by the total number of transects within the station. Fidelity was deduced by dividing the constancy of a species by the sum of the constancy of that species to all the stations.

$C_{A/1} = (R_A/R_1)*100$

$F_{A/i} = (C_{A/1} / \sum^{n}_{1} C_A)*100$

$C_{A/1}$: constancy of the species A to the station 1

R_A: number of transects containing the species A

R_1: total number of transects for the station 1

F_{Ai}: fidelity of the species A to the station i

The most characteristic species and common or rare species were identified for each station using the constancy and fidelity values on the basis of the following categories.

Constancy index:

- 75% - 100%: Constant species
- 50% - 74.9%: Common species
- 25% - 49.9%: Less common species
- < 24.9%: Rare species

Fidelity index:

- 75% - 100%: Selective species
- 50% - 74.9%: Preferential species
- 25% - 49.9%: Indifferent species
- < 24.9%: Occasional species

2.2.4 Statistical analysis

All statistical analyses were performed using the R software (R Core Team 2015). Descriptive statistics were calculated first. Normality of the data was determined using a Shapiro-Wallis test, and homogeneity of the variance was calculated using Levene's test. For specific richness analysis, data were transformation into log(x+1). Significance or not of difference in means were determined using one-way ANOVA, with a level of 5%. Multiple comparison test of Tukey was used for pairwise comparison between stations. Principal component analysis (PCA) and hierarchical cluster dendrogram of species and stations were performed to characterize the distribution of the species and the similarity of the stations.

2.2.5 Establishing the 18S rDNA database

About 2 to 5 cm fragment of each *in-situ* observed sample was fixed with ethanol 100%. 0.5 to 40 mg of tissue was ripped from each sample using a sterile scalpel. Total genomic DNA was extracted from the sampled tissue using the « Invisorb Spin Tissue Mini Kit » (STRATEC Molecular). A 530 bp fragment corresponding to the 5' beginning of the 18S rDNA was targeted for species identification. The variability of the fragment was first tested on two close species *Seriatopora hystrix* and *Stylophora madagascarensis* and revealed a difference of 5 substitutions (and 3 gaps). The variability of the fragment was also tested on 4 samples of different colonies from the same species, *Seriatopora hystrix* and did not revealed intraspecific variability. To amplify the targeted gene, Polymerase Chain Reaction (PCR) was performed using the couple of primers of Eeckhaut et al (2000): the forward 1N: 5'- CTTGTCTCAAAGATTAAGCC – 3' with the reverse: 8WRC: 5'- TTGGAGCTGGAATTACCG – 3'. With these primers, some amplified fragments belonged to the endosymbiotic zooxanthellates *Symbiodinium*. Those samples were reamplified successfully with the couple of primers 1N and the new R546: 5' – CCC TCC AAT GGA TCC TCG – 3'. For amplifications, 25µl of mixture of DNA/RNA free water, 0.5µl (25µM) of each primer and 1to 3µl of genomic DNA was added to the 0.2ml PCR tube containing illustra puReTaq Ready-To-Go PCR Beads. For the 25µl final volume, the concentration of each dNTP was 200µM in 10mM Tris-HCL (ph 9.0 at room temperature), 50mM KCl and 1.5 mM MgCl2. The PCR was performed with a BIORAD iCycler, using the cycling conditions of 5 min denaturing at 95°C; then 35 cycles of 30 s at 95°C, 30 s at 60°C annealing temperature, and 1 min at 72°C; followed by 2 min of final extension at 72°C. The PCR products were purified using the QIAquick PCR Purification Kit. Electrophoresis was performed in 1% agarose gel (TAE), and DNA was stained with ethidium bromide. Purified PCR products were sequenced using the StarSEQ DNA sequencing U-Mix service (http://www.starseq.com/). Obtained forward and reverse sequences of each sample were analysed and quality controlled using Codoncode Aliner version 5.1.5 (CodonCode Corporation, http://www.codoncode.com/) by checking the correspondent pairs of chromatograms. The consensus forward sequence was exported into FASTA file for further treatment. The scleractinian identity of the sequences were checked with Blast searches (Altschul et al. 1990; Madden et al. 1996; Morgulis et al. 2008) and deposited in the GenBank database under the accession numbers KU921625 to KU921644.

2.2.6 Testing the accuracy of the 18S rDNA database on recruits

2.2.6.1 Sampling new settled coral recruits

New settled coral recruits used in this test of accuracy were sampled with ceramic tiles deployed at the same stations during a parallel study that aimed to estimate the distribution and evolution of the coral recruitment (Chapitre 3). The 13 coral recruit samples (Rec1 to Rec13) used in the present study were collected from two different tiles collected in January and May from two different stations: Nosy Tafara (Figure 12) and the Rose Garden marine reserve located in Ifaty. These samples were chosen from among respectively 27 and 5 new settled coral recruits that were present on tiles

2.2.7 Morphological and 18S rDNA identifications

Each coral recruit was photographed directly from the tiles with a trinocular stereoscopic Novex microscope (Euromex microscopes) and identified to the level of families using the scleractinian identification key proposed by Babcock et al. (2003). This identification method suggests 3 distinguishable families that are Acroporidae, Pocilloporidae and Poritidae. Recruits of other families present no different, distinguishable characters (Babcock et al. 2003). One of the samples (Rec1, 1<age<3months) used in the present study was identified as a Pocilloporidae, three others (Rec8, Rec10 and Rec13, age<1month) were identified as Poritidae (Figure 16), and the others (Rec 2 to Rec8, Rec11 and Rec12) were not Acroporidae, Pocilloporidae or Poritidae.

The 18S rDNA sequence fragments of recruits were obtained using the same method as the one applied on adults (see details in section 2.5. Establishing the 18S rDNA database). Each recruit's sequence was compared with the 20 adult sequences using the Basic Local Alignment Search Tool of the National Center for Biotechnology Information (NCBI) (Altschul et al. 1990).

2.3 Results

2.3.1 Characterisation of the scleractinian communities

2.3.1.1 Richness and diversity of coral species

Species richness varied significantly from 4.2 ± 1.4 (mean ± SD) to 9.1 ± 2.2 (mean ± SD) at the studied stations ($p<0.001$). The lowest richness was observed at the Grande Vasque site, while Nosy Tafara presented the highest values (significant difference between both sites, $p<0.001$). Arakaivo station has significantly higher species richness than the three other stations (Table 6 and 7). Species richness on Velomitahy was significantly higher compared to GV North (Table 7). GV North and GV South present no significant difference.

Similarly to richness patterns, Shannon diversity on the studied sites show significantly higher diversity at Nosy Tafara, compared to Grande Vasque ($p<0.001$). This difference was highly influenced by the station Arakaivo, which has the highest and significant diversity index than the three other stations between which no significant difference was observed (Table 5 and Table 6). In addition, GV North and GV South showed no significant difference in richness nor in diversity (Table 6).

Table 5: Average specific richness and diversity at each station. SD: standard deviation (n=15).

	Richness		Diversity	
	Mean	SD	Mean	SD
Arakaivo	9.067	2.017	0.891	0.097
Velomitahy	5.846	1.994	0.668	0.161
GV North	4.200	1.373	0.551	0.149
GV South	4.692	1.109	0.559	0.120
ANOVA (p-value)	< 0.001		< 0.001	

Table 6: Pairwise comparison between stations. Probability was calculated using the multiple comparison test of Tukey (n=15)

	Richness		Diversity	
Comparison	t-value	p-value	t-value	p-value
Arakaivo - Velomitahy	-4.246	< 0.001	-4.433	< 0.001
Arakaivo - GV North	7.270	< 0.001	6.993	< 0.001
Arakaivo - GV South	5.895	< 0.001	6.584	< 0.001
Velomitahy - GV North	2.760	0.0388	2.306	0.110
Velomitahy - GV South	1.594	0.3909	2.079	0.173
GV North - GV South	1.111	0.6846	0.154	0.999

2.3.1.2 Recorded species: abundance, dominance and distribution

A non-exhaustive total of 36 species from 14 genera and 9 families were recorded at the 4 monitored stations (Table 7). Acroporidae is the most represented families with 14 species recorded, followed by Pocilloporidae, which has 9 species represented and Poritidae with 4 species. Agaricidae, Oculidae and Fungidae are represented each by 2 species, and Favidae, Euphyllidae and Mussidae, by 1 species each (Table 7). The overall dominance values place *Porites rus* as the most dominant species (15.9%), followed by *Acropora nobilis* (14.5), *Seriatopora hystrix* (7%), *Fungia repanda* (6.3%) and *Acropora nasuta* (5.8%) (Figure 13). These 5 species dominate 49.5% of the communities. However, the distribution of each species at the stations suggests that the dominance of *Porites rus* is due to its large dominance at GV South (53.7%), of *Acropora nobilis* to GV North (43.5%), while the other species do not show so obvious dominance to any station (Table 7).

Figure 13: Total dominance of each species. Species followed by * were listed by Pichon (1978), including synonymized species name (WoRMS Editorial Board 2016). Species followed by § have been 18S rDNA sequenced in the present study.

The principal component analysis (PCA) and the hierarchical cluster dendrogram of species and stations suggest each station is mostly characterized by one to 3 species. Arakaivo has far different community species composition from the other stations. This station is characterized mostly by the branching species such as *Acropora* and *Pocillopora*, which are, with *Echinopora gemmacea* and *Galaxea fascicularis*, the less common but the most selective species (Figure 14 and Figure 15B). Velomitahy is characterized by less common but indifferent species (Figure 15A), particularly by *Pavona cactus*, *Plerogyra sinuosa* and *Galaxea astreata*. These species, with the other tolerant ones, are common to the region and recorded from at least 3 of the studied stations (Table 7). GV South is largely characterized by the species *Porites rus* whose dominance influences the whole community at this station. GV North presents a similar community than Velomitahy (Table 7, Figure 15B). This station is particularly characterized by the free species *Fungia repanda* and *Herpolita limax*, which are indifferent as well according to calculations.

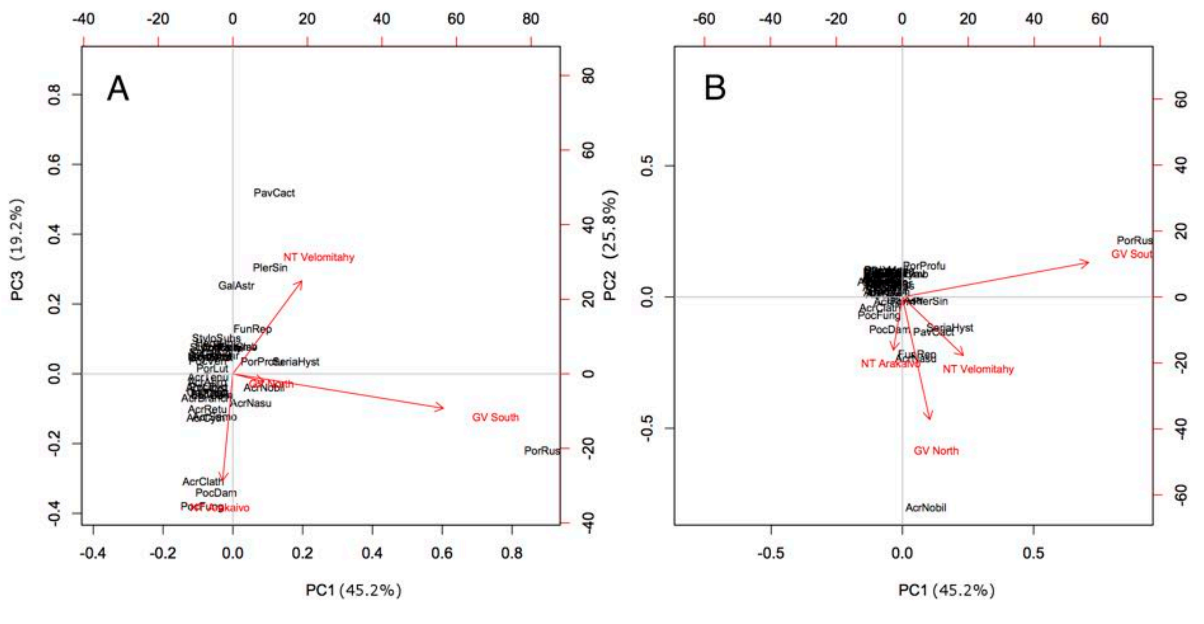


Figure 14: Principal component analysis of the stations and the species. A. According PCA1-PCA3 projection; B. According to the PCA1-PCA2 projection.

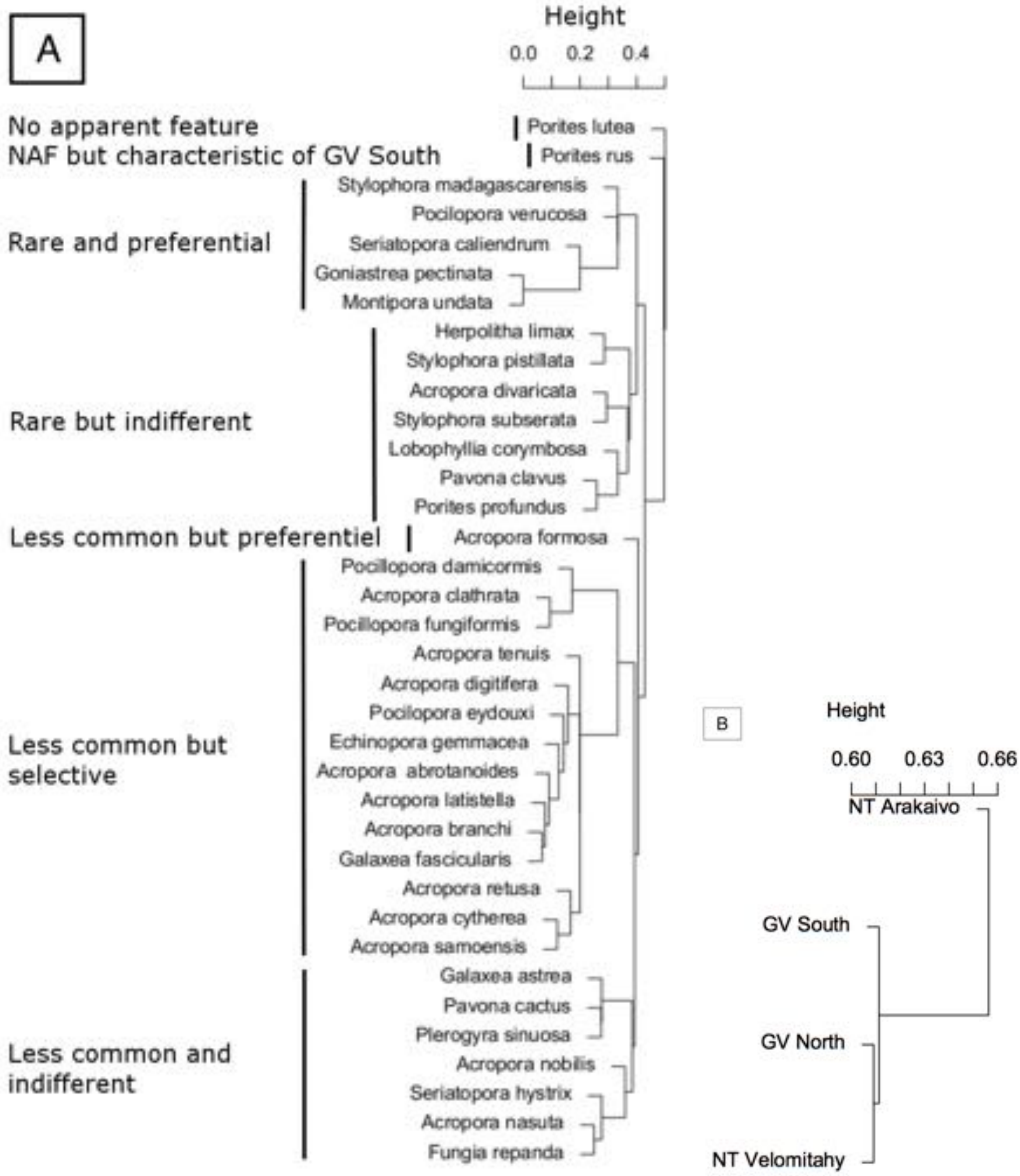


Figure 15: A. Cluster dendrogram of species, based on their abundance to each station. The characteristics of each group of species are based on the results of constancy and fidelity (Table 7). NAF = No apparent feature. B. Cluster dendrogram of the stations.

Table 7: List of species recorded during the survey, total abundance, dominance, constancy and fidelity of each species. TA: total abundance (number of recorded individuals); D: dominance (in%); C: constancy (in%); F: fidelity (in%); OD: overall dominance (in%). Dark grey cells with bold font = C or F > 75% ; Grey cells = 50% < C or F < 74.99% ; Light grey cells = 25% < C or F < 49.99% ; White cells = C or F < 25%.

Species	TA	Arakaivo			Velomitahy			GV North			GV South		
		D	C	F	D	C	F	D	C	F	D	C	F
Acropora abrotanoides	5	2	20	**100**									
Acropora branchi	8	3	33.3	**100**									
Acropora clathrata	24	11.6	73.3	**100**									
Acropora cytherea	12	6.2	53.3	**100**									
Acropora digitifera	11	3.4	46.7	**77.8**				2.8	13.3	22.2			
Acropora divaricata	9	1.4	13.3	28.6	1.6	20	42.9	1.7	6.7	14.3	0.6	6.7	14.3
Acropora formosa	19	4	40	60	9.6	26.7	40						
Acropora latistella	6	2.4	33.3	**100**									
Acropora nasuta	45	6.4	60	36	4.7	33.3	20	9.1	40	24	2.9	33.3	20
Acropora nobilis	83	5.4	20	13	8.1	26.7	17.4	43.5	**100**	65.2	1	6.7	4.3
Acropora retusa	12	4.9	26.7	57.1				1.4	20	42.9			
Acropora samoensis	13	5.4	53.3	**80**							1.5	13.3	20
Acropora tenuis	5	1.8	13.3	66.7				0.6	6.7	33.3			
Echinopora gemmacea	9	3.4	46.7	**77.8**				0.6	6.7	11.1	0.5	6.7	11.1
Fungia repanda	35	0.6	13.3	9.1	5	40	27.3	15.7	73.3	50	3.7	20	13.6
Galaxea astreata	18				14.5	40	75	0.6	6.7	12.5	0.4	6.7	12.5
Galaxea fascicularis	7	2.8	33.3	**100**									
Goniastrea pectinata	2	0.6	6.7	50	0.4	6.7	50						
Herpolitha limax	8				1.1	20	42.9	4.4	26.7	57.1			
Lobophyllia corymbosa	7				2	13.3	50	1	6.7	25	1.7	6.7	25
Montipora undata	2	0.3	6.7	50	1.7	6.7	50						
Pavona cactus	40				14.9	53.3	72.7				1.9	20	27.3
Pavona clavus	11	0.3	6.7	25	2.2	6.7	25				4.1	13.3	50
Plerogyra sinuosa	29				13.9	60.0	64.3				5.9	33.3	35.7
Pocillopora damicormis	34	12	**93.3**	66.7	0.4	6.7	4.8	3	26.7	19	2.3	13.3	9.5
Pocillopora fungiformis	29	11.6	**80**	**100**									
Pocilopora eydouxi	8	1.9	20	75				1	6.7	25			
Pocilopora verrucosa	1	0.4	6.7	**100**									
Porites lutea	3	1.1	13.3	66.7							0.8	6.7	33.3
Porites profundus	16	0.4	6.7	9.1	1.7	6.7	9.1				7.8	60	**81.8**
Porites rus	94	1.4	20	11.1	5	40	22.2	3.7	20	11.1	53.7	**100**	55.6
Seriatopora caliendrum	3	0.6	6.7	33.3	1.2	13.3	66.7						
Seriatopora hystrix	49	4.2	53.3	25	8.1	60	28.1	5.8	33.3	15.6	9.9	66.7	31.3
Stylophora madagascarensis	3				1.3	13.3	66.7				1.3	6.7	33.3
Stylophora pistillata	6							3.7	20	**100**			
Stylophora subserata	8	0.6	6.7	16.7	2.6	20	50	1.7	13.3	33.3			

2.3.2 18S rDNA database

2.3.2.1 Pairwise base difference analysis

After trimming, 427 ± 3 sites of 18S rDNA sequence were obtained for 20 adults (species followed by "*§*" in Figure 13). The alignment results in a database of 433 characters including gaps. Eleven sites (2.7% of complete alignment) were variable and 9 were parsimony informative (2.2% of complete alignment). The resulting database with the 20 aligned sequences showed 14 variable sequences including 12 monospecific groups and 2 polyspecific groups. The first polyspecific group was made of 5 species (*Pocillopora damicornis, Pocillopora eydouxi, Pocillopora verrucosa, Acropora cytherea* and *Acropora samoensis*) and the second polyspecific group of 3 species (*Seriatopora hystrix, Seriatopora caliendrum* and *Acropora clathrata)* (Table 9). The observed substitutions when a given species is compared to all the others vary from 7 bases (*Porites profundus*) to 11 (*Galaxea astreata*), with total of 183 substitutions for all the species (Table 9). The mean transition/transversion ratio was 0.172 (mean over all sequence pairs), with a minimum observed of 0 between *Lobophyllia corymbosa* and *Acropora clathrata* (0 transition, 6 transversions) and a maximum of 2 between *Pocillopora damicornis* and *Galaxea astreata* (2 transitions, 1 transversion).

Table 8: Base differences of the compared 20 18S rDNA sequences obtained from the adult samples. Rows with bold and with italic fonts represent respectively species with no base difference.

Position	1	12	17	58	116	117	118	119	120	121	143	162	163	164	165	173	174	175	177	184	208	214	215	240	391	415	431	432	433	TD
Acropora branchi	A	A	G	A	T	C	T	-	-	-	T	C	-	-	T	G	T	Y	T	T	C	T	-	T	T	-	T	N	C	11
Acropora clathrata	**A**	**A**	**G**	**T**	**G**	**T**	**T**	**C**	**T**	**T**	**G**	**C**	**-**	**-**	**T**	**G**	**T**	**C**	**T**	**A**	**G**	**A**	**A**	**A**	**T**	**-**	**T**	**G**	**C**	**8**
Seriatopora caliendrum	**A**	**A**	**G**	**T**	**G**	**T**	**T**	**C**	**T**	**T**	**G**	**C**	**-**	**-**	**T**	**G**	**T**	**C**	**T**	**A**	**G**	**A**	**A**	**A**	**T**	**-**	**T**	**G**	**C**	**8**
Seriatopora hystrix	**A**	**A**	**G**	**T**	**G**	**T**	**T**	**C**	**T**	**T**	**G**	**C**	**-**	**-**	**T**	**G**	**T**	**C**	**T**	**A**	**G**	**A**	**A**	**A**	**T**	**-**	**T**	**G**	**C**	**8**
Acropora divaricata	A	A	G	A	-	-	-	T	C	T	T	C	-	-	T	G	T	C	T	T	C	T	-	T	T	-	T	A	C	6
Acropora nobilis	A	A	G	A	-	-	-	T	C	T	T	C	-	-	T	G	T	C	T	T	C	T	-	T	T	-	T	A	C	6
Galaxea astreata	A	A	-	T	G	T	C	T	T	C	G	C	-	-	T	G	-	T	G	A	C	T	T	A	C	C				11
Lobophyllia corymbosa	A	-	G	A	-	-	-	T	C	T	T	C	-	-	T	-	T	C	T	T	C	T	-	T	T	-	T	C	C	8
Pavona cactus	A	-	G	A	T	G	T	G	A	A	T	T	C	G	T	-	T	G	T	T	C	T	G	T	T	-	C	-	C	18
Pavona clavus	T	A	G	A	-	-	-	T	C	T	T	C	-	-	T	-	C	A	T	T	C	T	-	T	T	-	T	A	C	10
Platygyra sinuosa	T	-	G	A	-	-	-	T	C	T	T	C	-	-	C	-	T	C	T	T	C	T	-	T	T	-	T	C	C	10
Acropora cytherea	*A*	*A*	*G*	*C*	*A*	*T*	*C*	*T*	*G*	*C*	*G*	*C*	*-*	*-*	*T*	*G*	*-*	*T*	*G*	*A*	*C*	*G*	*T*	*A*	*T*	*-*	*T*	*G*	*C*	*9*
Acropora samoensis	*A*	*A*	*G*	*C*	*A*	*T*	*C*	*T*	*G*	*C*	*G*	*C*	*-*	*-*	*T*	*G*	*-*	*T*	*G*	*A*	*C*	*G*	*T*	*A*	*T*	*-*	*T*	*G*	*C*	*9*
Pocillopora damicornis	*A*	*A*	*G*	*C*	*A*	*T*	*C*	*T*	*G*	*C*	*G*	*C*	*-*	*-*	*T*	*G*	*-*	*T*	*G*	*A*	*C*	*G*	*T*	*A*	*T*	*-*	*T*	*G*	*C*	*9*
Pocillopora eydouxi	*A*	*A*	*G*	*C*	*A*	*T*	*C*	*T*	*G*	*C*	*G*	*C*	*-*	*-*	*T*	*G*	*-*	*T*	*G*	*A*	*C*	*G*	*T*	*A*	*T*	*-*	*T*	*G*	*C*	*9*
Pocillopora verrucosa	*A*	*A*	*G*	*C*	*A*	*T*	*C*	*T*	*G*	*C*	*G*	*C*	*-*	*-*	*T*	*G*	*-*	*T*	*G*	*A*	*C*	*G*	*T*	*A*	*T*	*-*	*T*	*G*	*C*	*9*
Porites profundus	A	A	G	A	-	-	-	T	C	T	T	C	-	-	T	-	T	C	T	T	C	T	-	T	T	-	T	C	C	7
Porites rus	T	A	G	A	-	-	-	T	C	T	T	C	-	-	C	-	T	C	T	T	C	T	-	T	T	-	T	C	C	9
Stylophora madagascarensis	A	A	G	C	G	T	C	T	T	C	G	C	-	-	T	G	-	T	G	A	C	T	G	A	T	-	T	C	A	10
Stylophora subseriata	A	A	G	T	G	T	C	T	T	C	G	C	-	-	T	G	-	T	G	A	C	T	T	A	T	-	T	G	C	8
Total																														183

2.3.2.2 Identification of recruits

Pairwise base differences between recruits and adults show complete likeness of Rec1 to the polyspecific group with the 5 species (*P. damicornis, P. verrucosa*, *P. eydouxi*, *A. cytherea* and *A. samoensis*). Rec2, Rec3 and Rec4 show complete likeness with the species *Porites profundus*, Rec5 with *Porites rus*, Rec6 with *Pavona clavus* and Rec7 with *Lobophyllia corymbosa*. Rec8 to Rec13 did not match totally any of the species present in the database but presented the highest similarity to *Porites profundus* with one substitution (Table 9).

Morphological analysis of Rec1 excluded it from the Acroporidae, the recruits of this family having a porous coenosteum, prominent septa in 2 cycles, and they lacked columella (Babcock et al. 2003). Rec1 also presented prominent septa in 2 cycles, but with a solid coenosteum and prominent columella (Figure 16A) like recruits of Pocilloporidae (Babcock et al. 2003). Mixing molecular and morphological information, Rec1 is likely a *Pocillopora* close to *P. damicornis, P. verrucosa* or *P. eydouxi*.

Morphological analysis of Rec2 to 5 indicated that they are Poritidae. Rec2 (age > 3 months) presented more than 24 prominent septa with vertical tooth each. Thickness and junction of the septa showed that they grew up by six pairs (Figure 16B). Rec3 and Rec4 of <1 month age, presented a distinguishable epitheca, particularly visible on Rec4. Primary septa started to arise from the epitheca of Rec3 (Figure 16C). The deterioration of the skeleton of Rec4 did not permit to distinguish the appearance of its septa. Rec5 also presented a distinguishable epitheca from which 6 primary septa arised (Figure 16E).

Rec6 identified as *Pavona clavus* was characterized by the deep cup formed by its epitheca, and the presence of 6 primary and 6 secondary septa (Figure 16F). Rec7

(< 1 month) identified as *Lobophyllia corymbosa* was characterised by 6 prominent septa originated from the basal plate (Figure 16G). Each septum had robust and nodular spines.

Rec8 to Rec13, which presented the highest similarity to *Porites profundus,* had the distinguishable characters of Poritidae as described above. These recruits belong all to a same species: they had 6 thick primary septa with prominent vertical tooth the first month (Figure 16L), the primary septa grew beyond the epitheca, a 2nd cycle of septa grew at 3 months (Figure 16I), the secondary septa fused with the primary septa to form new pairs (Figure 16D, H, J), and the epitheca is progressively lost (Babcock et al. 2003).

Table 9: Base difference comparison of the recruits and adults. Recruits code followed by * correspond to recruit with 100% identity with adult. #Sub: number of substitutions.

		Rec_1*			Rec_2*			Rec_3*			Rec_4*			Rec_5*			Rec_6*		
#base	*Species*	Gaps	#Sub	Identities (%)	Gaps	#Sub	Identities (%)	Gaps	#Sub	Identities (%)	Gaps	#Sub	Identities (%)	Gaps	#Sub	Identities (%)	Gaps	#Sub	Identities (%)
426	*Acropora branchi*	5	5	98	1	1	99	1	1	99	1	1	99	1	2	99	1	2	99
430	*Acropora clathrata*	3	7	98	5	6	97	5	6	97	5	6	97	5	7	97	5	8	97
429	***Acropora cytherea***	**0**	**0**	**100**	4	7	97	4	7	97	4	7	97	4	8	97	4	7	97
426	*Acropora divaricata*	5	5	98	1	0	99	1	0	99	1	0	99	1	1	99	1	2	99
426	*Acropora nobilis*	5	5	98	1	0	99	1	0	99	1	0	99	1	1	99	1	2	99
429	***Acropora samoensis***	**0**	**0**	**100**	4	7	97	4	7	97	4	7	97	4	8	97	4	7	97
426	*Galaxea astreata*	1	5	99	6	8	97	6	8	97	6	8	97	6	9	96	6	8	97
424	***Lobophyllia corymbosa***	4	7	97	1	0	99	1	0	99	1	0	99	1	1	99	1	2	99
429	***Pavona cactus***	6	8	97	7	2	98	7	2	98	7	2	98	7	3	98	7	3	98
425	***Pavona clavus***	4	7	97	0	2	99	0	2	99	0	2	99	0	3	99	**0**	**0**	**100**
424	*Plerogyra sinuosa*	4	7	97	1	1	99	1	1	99	1	1	99	1	0	99	1	3	99
429	***Pocillopora damicornis***	**0**	**0**	**100**	4	7	97	4	7	97	4	7	97	4	8	97	4	7	97
429	***Pocillopora eydouxi***	**0**	**0**	**100**	4	7	97	4	7	97	4	7	97	4	8	97	4	7	97
429	***Pocillopora verrucosa***	**0**	**0**	**100**	4	7	97	4	7	97	4	7	97	4	8	97	4	7	97
425	***Porites profundus***	4	7	97	**0**	**0**	**100**	**0**	**0**	**100**	**0**	**0**	**100**	0	1	99	0	2	99
425	***Porites rus***	4	7	97	0	1	99	0	1	99	0	1	99	**0**	**0**	**100**	0	3	99
430	*Seriatopora caliendrum*	3	7	98	5	6	97	5	6	97	5	6	97	5	7	97	5	8	97
430	*Seriatopora hystrix*	3	7	98	5	6	97	5	6	97	5	6	97	5	7	97	5	8	97
429	*Stylophora madagascarensis*	0	4	99	4	7	97	4	7	97	4	7	97	4	8	97	4	7	97
429	*Stylophora subseriata*	0	4	99	4	7	97	4	7	97	4	7	97	4	8	97	4	7	97

Table 9 (continued)

#base	*Species*	Rec_7*			Rec_8			Rec_9			Rec_10			Rec_11			Rec_12		
		Gaps	#Sub	Identities (%)	Gaps	#Sub	Identities (%)	Gaps	#Sub	Identities (%)	Gaps	#Sub	Identities (%)	Gaps	#Sub	Identities (%)	Gaps	#Sub	Identities (%)
426	*Acropora branchi*	2	1	99	1	2	99	1	2	99	1	2	99	1	2	99	1	2	99
430	*Acropora clathrata*	6	6	97	5	5	98	5	5	98	5	5	98	5	5	98	5	5	98
429	***Acropora cytherea***	5	7	97	4	7	97	4	7	97	4	7	97	4	7	97	4	7	97
426	*Acropora divaricata*	2	0	99	1	1	99	1	1	99	1	1	99	1	1	99	1	1	99
426	*Acropora nobilis*	2	0	99	1	1	99	1	1	99	1	1	99	1	1	99	1	1	99
429	***Acropora samoensis***	5	7	97	4	7	97	4	7	97	4	7	97	4	7	97	4	7	97
426	*Galaxea astreata*	7	8	96	6	7	97	6	7	97	6	7	97	6	7	97	6	7	97
424	***Lobophyllia corymbosa***	**0**	**0**	**100**	1	1	99	1	1	99	1	1	99	1	1	99	1	1	99
429	***Pavona cactus***	6	2	98	7	3	98	7	3	98	7	3	98	7	3	98	7	3	98
425	***Pavona clavus***	1	2	99	0	3	99	0	3	99	0	3	99	0	3	99	0	3	99
424	*Plerogyra sinuosa*	0	1	99	1	2	99	1	2	99	1	2	99	1	2	99	1	2	99
429	***Pocillopora damicornis***	5	7	97	4	7	97	4	7	97	4	7	97	4	7	97	4	7	97
429	***Pocillopora eydouxi***	5	7	97	4	7	97	4	7	97	4	7	97	4	7	97	4	7	97
429	***Pocillopora verrucosa***	5	7	97	4	7	97	4	7	97	4	7	97	4	7	97	4	7	97
425	***Porites profundus***	1	0	99	*0*	*1*	*99*	*0*	*1*	*99*	*0*	*1*	*99*	*0*	*1*	*99*	*0*	*1*	*99*
425	***Porites rus***	1	1	99	0	2	99	0	2	99	0	2	99	0	2	99	0	2	99
430	*Seriatopora caliendrum*	6	6	97	5	5	98	5	5	98	5	5	98	5	5	98	5	5	98
430	*Seriatopora hystrix*	6	6	97	5	5	98	5	5	98	5	5	98	5	5	98	5	5	98
429	*Stylophora madagascarensis*	5	7	97	4	7	97	4	7	97	4	7	97	4	7	97	4	7	97
429	*Stylophora subseriata*	5	7	97	4	6	97	4	6	98	4	6	98	4	6	98	4	6	98

Table 9 (continued)

#base	*Species*	Rec_13		
		Gaps	#Sub	Identities (%)
426	*Acropora branchi*	1	2	99
430	*Acropora clathrata*	5	5	98
429	***Acropora cytherea***	4	7	97
426	*Acropora divaricata*	1	1	99
426	*Acropora nobilis*	1	1	99
429	***Acropora samoensis***	4	7	97
426	*Galaxea astreata*	6	7	97
424	***Lobophyllia corymbosa***	1	1	99
429	***Pavona cactus***	7	3	98
425	***Pavona clavus***	0	3	99
424	*Plerogyra sinuosa*	1	2	99
429	***Pocillopora damicornis***	4	7	97
429	***Pocillopora eydouxi***	4	7	97
429	***Pocillopora verrucosa***	4	7	97
425	***Porites profundus***	*0*	*1*	*99*
425	***Porites rus***	0	2	99
430	*Seriatopora caliendrum*	5	5	98
430	*Seriatopora hystrix*	5	5	98
429	*Stylophora madagascarensis*	4	7	97
429	*Stylophora subseriata*	4	6	98

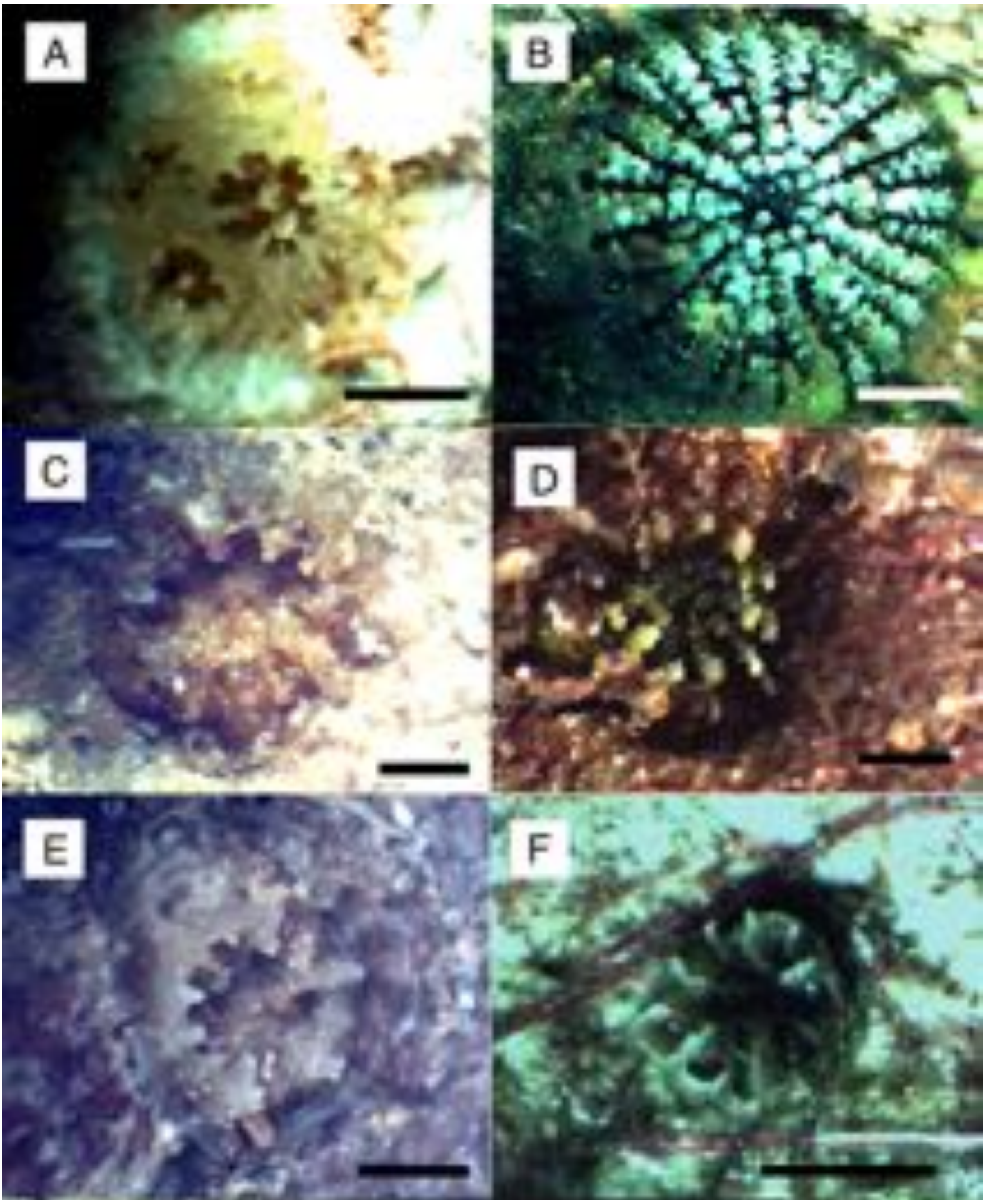


Figure 16: Scleractinian recruits morphotypes. Respectively from A: Rec1; B: Rec2; C: Rec3; D: Rec8; E: Rec5; F: Rec6; G: Rec7; H: Rec8; I: Rec9; J: Rec10; K: Rec11; L: Rec12. Scale bar: 500 µm

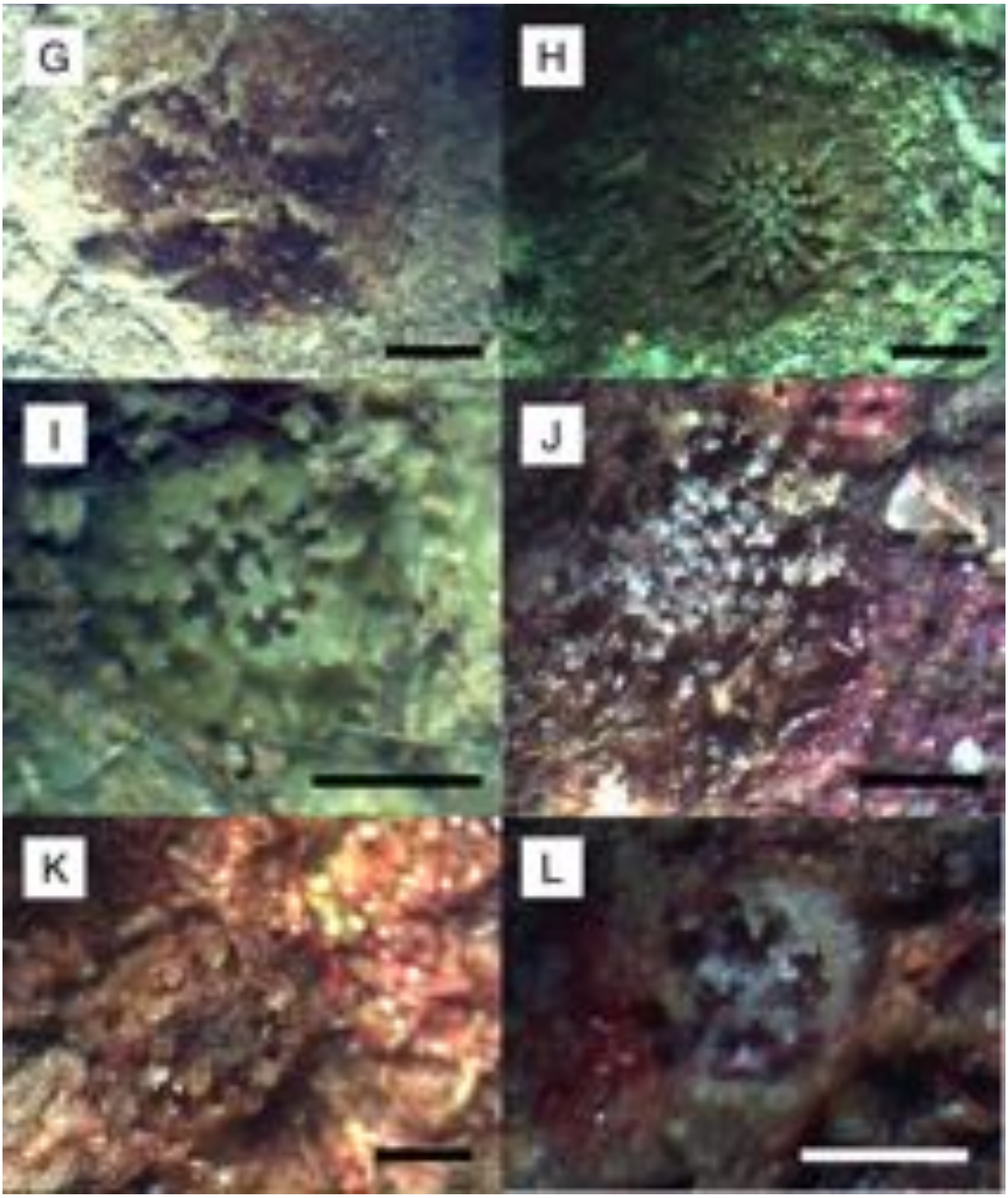


Figure 16 (continued): Scleractinian recruits morphotypes. Respectively from A: Rec1; B: Rec2; C: Rec3; D: Rec8; E: Rec5; F: Rec6; G: Rec7; H: Rec8; I: Rec9; J: Rec10; K: Rec11; L: Rec12. Scale bar: 500 µm

2.4 Discussion

Most studies to date have been limited to identifying coral recruits to the family level. The general aim of the present study was to settle the baselines for the construction of a fast, easy-to-work DNA database that allow identifying scleractinian adults and recruits in the SW of Madagascar. The slow rate of evolution in mitochondrial genomes has called into question the usefulness of COI DNA barcoding for identifying coral species (and anthozoans in general) (France et al. 1996; van Oppen et al. 1999; Shearer and Coffroth 2006). Despite this disadvantage, a few authors used this molecular marker to increase the taxonomic resolution of recruits. Shearer et al. (2006) applied COI and species-specific RFLP patterns to identify some Carribean coral recruits. Rubin et al. (2008) used COI and cytochrome *b* to study coral recruits in damaged reefs in Florida. Suzuki et al. (2008) identified the dominant *Acropora* species recruits in the Ryukyu Archipelago using mitochondrial and nuclear markers. Hsu et al. (2014) tested three DNA-barcoding markers (cytochrome oxidase I gene [COI], open reading frame [ORF], and nuclear *Pax*-*C* intron [PaxC]) for increasing the resolution of coral recruits in Taiwan. In the present study, we checked the efficiency and accuracy of a 18S rDNA fragment in the identification of recruits in the SW of Madagascar. For that purpose, we characterised the structure of the coral communities commonly observed in the Bay of Toliara and we tested if 18S rDNA signatures from the most common adults allow identifying recruits recently settled on experimental plates.

We recorded 36 species from 14 genera and 9 families at the 4 monitored stations. The scleractinian diversity was relatively low compared to similar studies in the WIO region (*e.g.,* Sheppard 1987; Beenaerts and Berghe 2005; Obura 2012) and especially the one of Pichon 1978 (corrected later by Sheppard 1998) who observed on the GRT 112 species belonging to 57 genera. Our results may be due to the surface of the sampled area that was lower than the one in Pichon (1978)'s study. Apart the work of Pichon (1978), the only other study about the global coral biodiversity of the GRT was made in the 2000s and revealed the loss of about 8 to 18 coral genera (Bruggemann et al. 2012) but, as in the present study, this work did not cover all the stations studied in 1978 and comparisons with the study made 40 years ago are difficult to assess.

The present paper reports a total record of 24.6% of the total number of genera recorded before, and 32.1% of the species. Most of the genera observed by Pichon (1978) were recorded in the present study, including essentially *Acropora*, *Pocillopora, Stylophora,* and *Porites*. Fourteen of the presently listed species were not listed by Pichon (1978) (Table 10), including eight species of *Acropora* (*A. branchi, A. clathratha, A. divaricata, A. latistella, A. nasuta, A. retusa, A. samoensis* and *A. tenuis*), two *Porites* (*P. lutea* and *P. profundus*), 1 *Pocillopora* (*P. fungiformis*), one *Seriatopora* (*S. caliendrum*), one *Stylophora* (*Stylophora madagascariensis*) and one *Fungia* (*F. repanda*). *Fungia* is the least represented with only 1/7 species recorded (present study/Pichon 1978). *Acropora* is well represented with 13/13 numbers of species but only 5 of the 13 presently recorded species of *Acropora* are in the list of Pichon (1978).

Table 10: Comparative list of genera and number of species of Scleractinia recorded on the coral reefs of the SW region of Madagascar and the present study (Genera in bold font). P: number of species recorded by Pichon (1978), T: number of species recorded by the authors at the selected stations. nr: not recorded.

Genera	P	T	Genera	P	T	Genera	P	T	Genera	P	T
Acropora	13	13	*Dendrophyllia*	2	nr	*Balanophyllia*	1	nr	*Merulina*	1	nr
Pavona	8	2	***Echinopora***	2	1	*Caryophillia*	1	nr	*Montastrea*	1	nr
Fungia	7	1	***Galaxea***	2	2	*Caulastrea*	1	nr	*Oxypora*	1	nr
Pocillopora	7	4	***Goniastrea***	2	1	*Culicia*	1	nr	*Paracyathus*	1	nr
Porites	7	3	*Goniopora*	2	nr	*Cycloseris*	1	nr	*Parascolymia?*	1	nr
Leptoseris	6	nr	*Hydnophora*	2	nr	*Cynarina*	1	nr	*Pectinia*	1	nr
Favites	5	nr	*Mycedium*	2	nr	*Diaseris*	1	nr	*Physogyra*	1	nr
Montipora	5	1	*Oulophyllia*	2	nr	*Diploastrea*	1	nr	*Platygyra*	1	nr
Turbinaria	5	nr	*Pachyseris*	2	nr	*Echinophyllia*	1	nr	*Plerogyra*	1	1

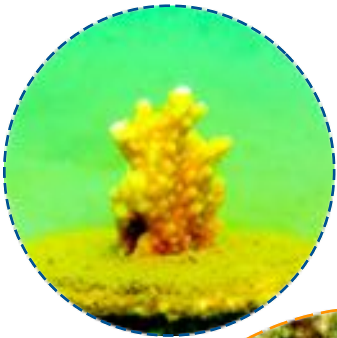
Favia	3	nr	*Platygyra*	2	nr	*Gyrosmilia*	1	nr	*Podabacia*	1	nr
Leptastrea	3	nr	*Plesiastrea*	2	nr	*Halomitra*	1	nr	*Polycyathus*	1	nr
Lobophyllia	3	1	*Turbastraea*	2	nr	***Herpolitha***	1	1	***Seriatopora***	1	2
Psammocora	3	nr	*Acanthastrea*	1	nr	*Heterocyathus*	1	nr	*Siderastrea*	1	nr
Stylophora	3	3	*Agariciclla*	1	nr	*Heteropsamia*	1	nr	*Sphenotrochus*	1	nr
Blastomussa	2	nr	*Alveopora*	1	nr	*Horastrea*	1	nr	*Stylocoeniella*	1	nr
Coscinarea	2	nr	*Anomastrea*	1	nr	*Leptoria*	1	nr	*Symphyllia*	1	nr
Cyphastrea	2	nr	*Astreopora*	1	nr	*Madracls*	1	nr	*Trachyphyllia*	1	nr

Out of the four investigated stations, the richness and diversity in Arakaivo appears very different from the three others. Arakaivo is the most exposed station to the water current and it houses most of the branching species. The richness and diversity in Velomitahy that is only separated from a few hundred meters from Arakaivo, are closer to the ones of the Grande Vasque, a station clearly well protected from the hydrodynamics of the open sea. In the Grande Vasque, the South is dominated by the species *Porites rus* for an unknown reason while the diversity of the North of the Grande Vasque and the one of Velomitahy are very similar. In his work, Pichon (1978) differentiated three coral communities according to the depth of the reef slope: many *Acropora* and species of Pocilloporidae inhabit the upper part of the slope, the massive species (*e.g., Pavona*, *Plerogyra* and *Galaxea*) are restricted to the lower part of the slope and other species like *Porites*, *Montipora* and some *Acropora* occur from the top to the bottom of the slope. In the present paper we investigated a zone between 8 to 15 m depths. Branching colonies were observed in Nosy Tafara and in the Grande Vasque but principally in the hydrodynamically active station, Arakaivo. In addition to hydrodynamics, the difference in coral composition between the studied stations could also be explained by the change in habitat structure due to sedimentation and fishing pressure. Indeed, in 50 years, the sedimentation increased on the GRT and certainly influences the structure of the habitats and consequently the structure of the benthic community, especially the scleractinians (Bruggemann et al. 2012; Andréfouët et al. 2013). Sheridan et al. (2015) shows that the GRT was more affected by diseases than coral reefs of the SW of Madagascar that were not subjected to sedimentation.

Except for Arakaivo, the two other stations are highly accessible to fishermen and are the most frequented fishing zones. These stations are subjects to frequent trampling due to destructive fishing techniques (Salimo 1997).

From the 36 species recorded, a fragment of the 18S rDNA was successfully sequenced for 20 of them with two pairs of primers. For the other species, the sequences obtained either belong to *Symbiodinium* or their resolution was too low to be considered without error. A fragment of 427 ± 3 base pairs (about 23% of the total length of the 18S rDNA gene) was used. The actual database differentiates 14 variable sequences. Amongst the 14 variable sequences one characterizes five species and a second one characterizes three species. Nonetheless, pairwise comparison of 13 recruits having different morphotypes revealed informative specific matching. With the traditional morphological criteria, recruits were identified as Acroporidae, Pocilloporidae or Poritidae or to a group of morphologically non-distinguishable families (excluding Acroporidae, Pocilloporidae and Poritidae) (Babcock et al. 2003). Using the database, 6 recruits matched a monospecific sequence. The results means that they are likely the species retrieved from the database although the extension of this database in the future will indicate if these sequences are truly monospecific or not. The present database does not present enough variation to identify one recruit, Rec1, which matched the polyspecific group including 5 species. To solve this problem, the length of the sequences may be increased or other molecular markers may be mixed with the 18S rDNA although this will also increase the complexity of the method. Finally, the present database does not have enough adult sequences to identify six of the recruits: Rec8 to Rec13, which differ from one base with *P. profundus*. This problem may also be solved in extending the number of adult sequences in the database.

In conclusion, even if the 18S rDNA is poorly informative in scleractinians, a single difference in a molecular marker is enough to identify a species in a particular region under the assumption that the informative sites are not subject to homoplasic events. The results of the present study prove that an 18S rDNA sequences database of scleractinians adult, presently those of the SW region of Madagascar, can be used as an easy tool to improve the identification resolution of scleractinian recruits. The database should be extended to get a maximum of species to increase its reliability. The database could be used with other molecular markers though this step will increase the time and difficulty of the identifications.



Chapitre 3

First records on recruitment of corals in Madagascar. Distribution of scleractinian larvae, recruits and juveniles in the southwest region

CHAPITRE 3: First records on recruitment of corals in Madagascar. Distribution of scleractinian larvae, recruits and juveniles in the southwest region[4]

Abstract

The reproduction period of scleractinians in the SW region of Madagascar was evaluated between October 2013 and September 2014. We monitored the presence of coral larvae (planula) in plankton by a weekly sampling using plancton net and evaluated the recruitment rate by a monthly sampling of the new settled corals (1 year < Recruits) with recruitment tiles and by a monitoring of the juveniles' recruitment (1< Juveniles < 2 years) using the quadrat method. Planulae were present in plancton 9 months during the survey. It was abundant from the beginning of the warm and wet season (September to November). The annual recorded density of planula varied from 1.30 planula m^{-3} to 16.17 planula m^{-3} depending to studied stations with a peak larval density in November and December. These results suggest that most of corals release their fertilized eggs few days or weeks before November/December. Compared to other regions, the recruitment rate observed in the SW of Madagascar was high (100 to > 1000 recruits m^{-2} $year^{-1}$). It also varied from seasons and peaks of recruitment was observed between October and December. We observed a huge difference of recruit records and juvenile records between the stations. Results of juveniles monitoring revealed high rates (> 10 juveniles m^{-2}) compared to other regions and the threshold, but it revealed high mortality of the recruits. Results relate an important mortality post-settlement but the abundance of survived juvenile still represent higher rate compared to other regions. The coral recruitment in the SW region is high and could result in good resilience of the coral reef assemblages but several post-settlement factors may induce an important mortality of coral recruits and juveniles.

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[4] Ce chapitre sera soumis pour publication: Todinanahary GGB, Hasintantely N, Lavitra T, Eeckhaut I (*In prep*) First records on recruitment of corals in Madagascar. Distribution of scleractinian larvae, recruits and juveniles in the southwest region.

3.1 Introduction

Recruitment processes are important in the dynamics and resilience of coral reef assemblages (Adjeroud et al. 2016). Even so, development of coral recruitment and spawning studies is very recent due to difficulties in observing and identifying the very punctual spawning phenomenon and very small size coral recruits that are invisible to naked eyes. Researches on scleractinian sexual reproduction and spawning started in the early 1980s (*e.g.,* Baggett and Gright 1985, Brazeau and Lasker 1989, Babcock et al. 1994, de Graaf et al. 1999), while the studies of new settled recruits and juveniles started earlier (*e.g.,* Lewis 1974, Goreau et al. 1981).

The spawning of the corals are known in several region of the world, occurring few days after the full moons of the warm season, for example, generally in October and November (spring) on the Great Barrier Reef and in March to April (autumn) on the Western Australian coast (Rosser and Baird 2008). In the Western Indian Ocean (WIO), the first spawning studies were performed more recently. In South Africa and in La Réunion *Acropora austera* and *Platygyra daedalea* spawnings were observed in February, and the study of their sexual reproduction suggested an extended spawning period between September and March (Massé 2014). In Madagascar, only spawnings of *Acropora* were recorded in scientific literature: the study was made in the coral reefs of Andavadoaka, in the southwest region (Gress et al. 2015).

The first studies in the WIO region report a recruitment period that covers the summer and winter seasons in South Africa and La Réunion (Massé 2014). Notable differences in spatial variations of recruitment patterns have been recorded at a regional scale, notably between Indo-Pacific and Atlantic reefs (Ritson-Williams et al. 2009), and at local scale within reefs or between sites of the same region. In the Pacific, the recruitment rate is much lower (*e.g.,* ~40 recruits $m^{-2}year^{-1}$ at the Mo'orea (French Polynesia), Adjeroud 2007) than in the Western Pacific reefs where ~200 to

700 recruits m^{-2} $year^{-1}$ and even up to 4,590 recruits m^{-2} $year^{-1}$ were recorded (Hughes et al. 1999). The recorded recruitment rates in the WIO are comparable to the higher rates, but proven to be higher in subtropical latitude (548 recruits m^{-2} $year^{-1}$ in South African reefs) than in tropical latitude (305 recruits m^{-2} $year^{-1}$, La Réunion Island) (Massé 2014).

There is also a very few papers reporting on the distribution patterns of coral juveniles, despite the relatively developed observation methods (Baird et al. 2006). Zahir et al. (2002) reported a juvenile (< 10 cm size) recruitment rate of 30 – 49 m^{-2} in the Maldives Islands. In Mayotte and the Glorieuses Islands, the observed juvenile recruitment rate was < 30 juveniles m^{-2}, but it concerned only juveniles of < 5 cm size.

One of the most constraining factors in recruitment studies is the difficulty of recruit identification. The used methods generally depend in the survey level. At the level of new settled recruits, unglazed terracotta and ceramic tiles are the most widely used, while for the juveniles that are observable *in situ* (mostly < 5 cm size), the method of *in situ* quadrat is usual (Hill and Wilkinson 2004). Based on morphological characteristics, recruits are only observable to the level of 3 families, Acroporidae, Pocilloporidae and Poritidae (Babcock et al. 2003). Since a few years, development of molecular phylogeny permitted new higher resolution methods to identify newly settled scleractinians. The mitochondrial cytochrome oxydase sub-unit 1 (CO1) is the most used genetic marker for barcoding (*e.g.,* Shearer and Coffroth 2006, Rubin et al. 2008, Roth and Knowlton 2009). The uses of fluorescence census techniques were also suggested to increase the *in situ* early detection of coral juveniles (Baird et al. 2006). More recently, Hsu et al. (2014) combined both fluorescence and molecular phylogeny to increase the identification level of the recruits. Recently, we identified the 36 most frequent scleractinians in the bay of Toliara and we initiated a 18S rDNA data base with which we combined morphological characters that allowed us to identify (Chapitre 2).

The present paper is the first to record scleractinian recruitments in Madagascar. It aims at characterizing the spatial and temporal distribution of coral larvae, recruits and juveniles in coral reefs of the SW region, using the most recent survey methods and recruits identification techniques.

3.2 Materials and methods

3.2.1 Studied stations

The present study was performed on coral reefs of the Southwest Region of Madagascar, between the latitude 22°58'S in the North and the latitude 23°34'°S in the South (Figure 17). Three distinct stations were chosen for the recruitment study. The first station was located on the coral reef of Nosy Tafara (at Nosy Velomitahy, NT here after) (latitude 23°30'S), which is a complex of patch reefs located between the southern tip of the Great Barrier Reef of Toliara (GRT here after) and the sandy coast of Sarodrano village. The second station was located in the "Grande Vasque" (latitude 23°22' S), a basin of 1 km in diameter situated in the flat of the GRT. These two reefs are located in the Bay of Toliara. The third station was the reef of Rose garden, located in the Bay of Ranobe (latitude 23° 8' S), which is a reef patch dominated by *Montipora* species and is a protected area.

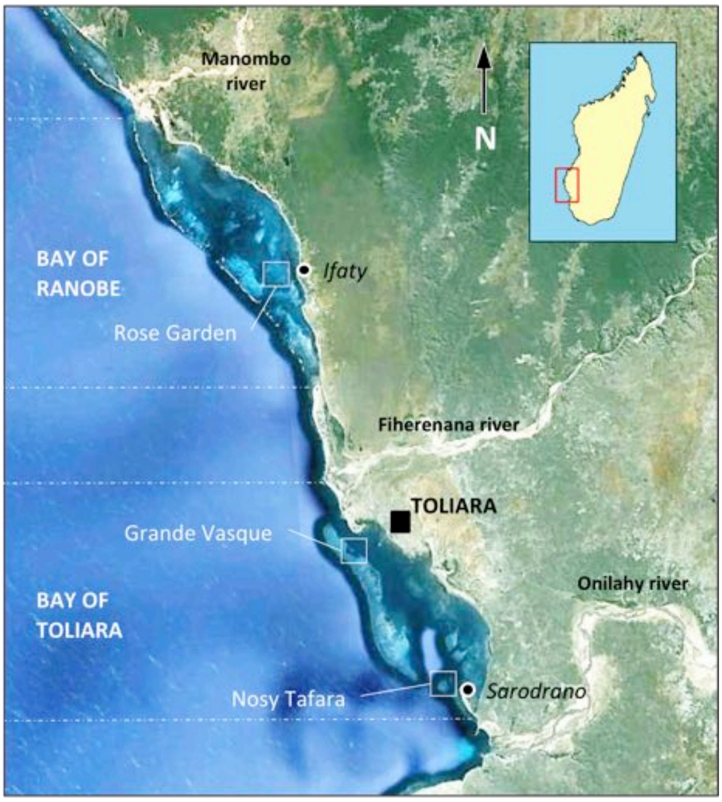


Figure 17: Location of the studied stations

At each station, temperature of the bottom water (at the same depth that the recruitment tiles, see *Recruitment monitoring* below) was measured every hour with the HOBO data logger from which data were downloaded and calculated using the ONSET HOBOware Pro version 3.7.0 (Onset Computer Corporation, 2002-2014). Salinity, pH and water visibility were weekly measured using respectively a refractometer, pH meter (sensION+, precision = 0.01) and Secchi disc.

3.2.2 Planula records

Weekly, the sampling of zooplankton was performed to record the planula larvae for one year (from October 2013 to September 2014). Samplings were performed at the surface (< 1 m depth) every morning between 6 am and 8 am depending to the tide. We used a 63 µm mesh plankton net with a 25 cm diameter mouth that was dragged by a small boat (7 m long) during 15 mn, covering a distance of ~900 m. For each sample, the filtered seawater was 44 m^3. Samples were filtered to separate the plankton of different size using sieves (63 µm, 80 µm, 100 µm and 250 µm). The filtration aimed to facilitate the observation and counting of the planula larvae within the sampled zooplankton. Eight replicates of 50 µL per sample of different size were observed and coral larvae were counted using a Euromex Oxion photonic microscope.

3.2.3 Recruitment monitoring

In this chapter, we use the term "recruit" to describe the first period corresponding to the metamorphosis of the primary polyp and to the small colony following larval settlement. During this period, they are not yet visible to the naked eye (Babcock and Mundy 1996; Banks and Harriott 1996; Gleason 1996; Baird and Hughes 1997; Dunstan and Johnson 1998; Hughes et al. 1999; Mundy 2000; Kojis and Quinn 1984). The term "juvenile" is used to denote the period when colonies become visible to the naked eye on the natural substrate. This period corresponds to a stage where colonies have a size of about 1 cm or more and age older than one year (Connell 1973; Bak and Engel 1979; Sakai and Yamazato 1984; Wittenberg and Hunte 1992; Chiappone and Sullivan 1996; Smith 1997; Edmunds 2000; Miller and al. 2000).

Ceramic tiles were used to estimate the distribution of the coral recruitment. The tiles were installed in July 2013. About 3 months of conditioning are needed to allow settlement substratum (Erwin et al. 2008, Massé 2014). We collected 4 conditioned tiles per station per month. We could observe the first recruits on October 2013 using the following identification method. During the 12 months, from October 2013 to September 2014, 48 tiles per station were observed (144 in total). The tiles were fixed horizontally, unglazed face down on a Polyvinyl chloride (PVC) cross-system that we confectioned after pre-research experiments that revealed the resistance of the system against waves and other conditions in the stations. Each system was fixed on the substrate by iron rod induced of antirust, which was planted into the substrate. Each tile measured 30 x 30 cm^2. In total, 43.2 m^2 of surface was covered in each station.

In addition, *in situ* observation of recruitment was performed to estimate coral juveniles on two of the three stations: Nosy Tafara and Grande Vasque. The survey was performed in September and October 2013 at Nosy Tafara, while at Grande Vasque it was performed in January 2014. Juveniles were not recorded at Rose Garden as it was considered as a monospecific site with dominance of *Montipora* species. Juveniles are observable *in situ* and typically aged of at least 1 year (Adjeroud et al. 2016). The method, described below, provided a reliable estimation of future coral species assemblages and allows estimating the post-settlement rates of mortality that are often very high during the first weeks following the settlement and mainly due to predation, competition, sedimentation and stress (Adjeroud et al. 2016). We used the recruitment quadrat method known as the method of Atlantic and Gulf Rapid Reef Assessment (AGRRA) (Hill and Wilkinson 2004) and we adapted it to the characteristics of the studied stations. We swam along of 50 x 2 meters transect and placed the 25 cm x 25 cm quadrat on the substratum in areas lacking large (> 25 cm diameter) sessile invertebrates. We counted all small (two classes: < 2 cm diameter and 2 cm < diameter < 5 cm) scleractinians within the quadrat separated in four groups - Acroporidae, Pocilloporidae, Fungidae and a 4^{th} group including other massive, encrusting or foliose species - that were reliably distinguishable in these *in situ* observations.

3.2.4 Identification method

Once at the laboratory, each coral recruit was photographed directly on the tiles using a trinocular stereoscopic Novex microscope (Euromex microscopes). Based on the morphology of the first skeleton, recruits were identified to the level of 3 distinguishable families that are Acroporidae, Pocilloporidae and Poritidae using the scleractinian recruits identification key proposed by Babcock et al. (2003). We here classified the recruits into 5 families: the Acroporidae, Agariciidae, Lobophyllidae, Pocilloporidae, Poritidae, and the unidentified ones that were grouped as "others". This classification was based on the skeletal characteristics of recruits (Babcock et al. 2003) refined in using also the characteristics of the 6 species genetically distinguished by Todinanahary et al. (submitted). Todinanahary *et al.* (2016)'s method permitted to identify 6 recruits at the level of species, especially two of the identified species belong to the families Agariciidae and Lobophyllidae. We used the morphological characters of these two species to identify recruit samples as belonging to these families and classified them by age accordingly (Table 11).

Table 11: The main morphological characters used to distinguish the studied families

Family	Coenosteum or epitheca	Basal ridge and primary septa	Columella	Number of polyps row (< 1 month)	Main difference of aged recruits (> 1 month) compared to early recruits (<1 month)
Acroporidae	Porous coenosteum	Prominent in 2 cycles	Absent	1 – 2	Number of polyps and rows
Pocilloporidae	Solid coenosteum	Prominent in 2 cycles	Present and prominent	1	Number of polyps and rows
Poritidae	Epitheca present at < 1 month age	6 primary septa within epitheca. Prominent vertical tooth	Absent	1	Thickened septa; basal plate and primary septa beyond epitheca
Agariciidae	Epitheca form a cup	6 primary septa slowly originated from epitheca	Absent	1	Well developed primary septa
Lobophyllidae		6 prominent septa originated from the basal plate; numerous, robust and nodular spines on each septum	Rudimentary	1	2 or more septal cycles

3.2.5 Statistical analysis

All the statistical analysis was performed using the R software (R Core Team 2015). Descriptive statistics were calculated first. Normality of the data was determined using a Shapiro-Wallis test and homogeneity of the variance was calculated using Levene's test. In this study, no transformation was needed. Significance or not of difference in means was determined using one-way ANOVA and t-test, with a level of 5%.

3.3 Results

3.3.1 Variation of physico-chemical parameters of the water

The extreme values for the visibility recorded with the Secchi disks were of 1.4 m and 13.5 m. Results showed that the visibility was significantly lower during the wet warm season (6.3 ± 1.8 m) compared to the dry cold season (7.7 ± 2.4 m) ($p = 0.001$). The highest values of water visibility were observed from September to December, during which it reached > 8 m (Figure 18). The highest annual mean visibility was observed at Grande Vasque (7.6 ± 2.5 m) and the lowest at Rose Garden (6.1 ± 1.3 m) with significant difference observed between both stations ($p = 0.007$). The annual mean visibility of 6.9 ± 2.1 m at Nosy Tafara was lower than Grande Vasque and higher than Rose Garden, but no significant difference was observed.

The extreme recorded temperatures of the sea bottom varied from 21.8°C in the dry cold season to 32.4°C in the wet warm season. The average temperature measured was of 24.1 ± 1.4 °C and 27.9 ± 1.6 °C, respectively for these two seasons. During the wet warm season, the temperature was at its highest value in January and February, and at its lowest value in July and August during the dry cold season (Figure 19). No significant difference was observed between the 3 stations at which the annual mean temperature was about 25.5 ± 2.3° C.

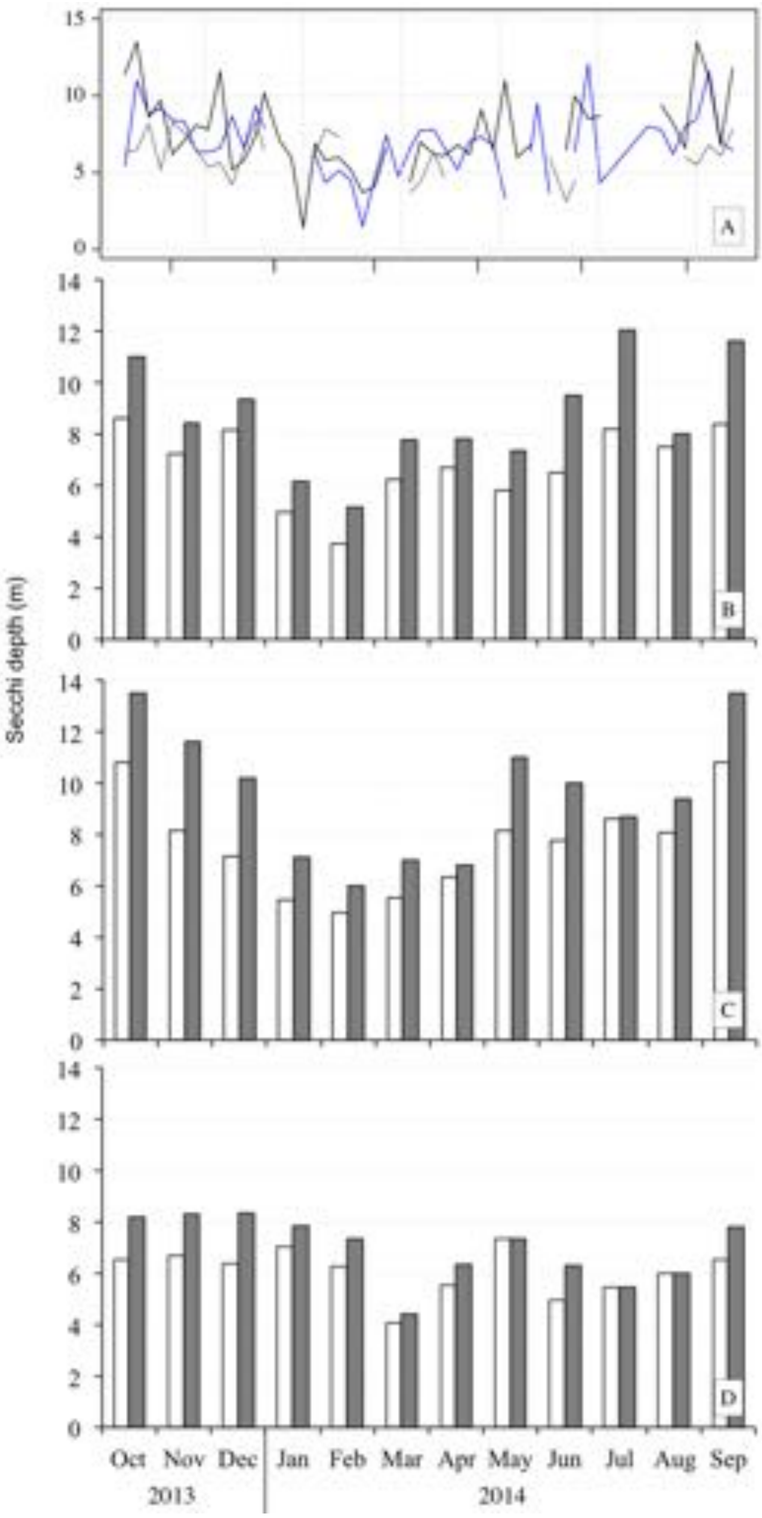


Figure 18: Visibility (Secchi depth, in meter) in the water. A. Weekly variation of the visibility. Blue line: Nosy Tafara; Black line: Grande Vasque; Grey line: Rose Garden. B, C and D: Average (white bars) and maximum (grey bars) visibility per month, at respectively Nosy Tafara, Grande Vasque and Rose Garden.

The extreme recorded values of salinity were of 30 psu and 36.5 psu with an average of 33 ± 1.3 psu in the wet warm season and 34 ± 0.8 psu in the dry cold season. The average value integrating all the values of one year was significantly lower at Nosy Tafara compared to the other stations ($p = 0.0005$): the global annual average value was of 31.9 ± 1.2 psu at Nosy Tafara against 33.4 ± 1 psu and 33.6 ± 0.9 psu respectively at Grande Vasque and Rose Garden. The lowest salinity occurred in the wet warm season.

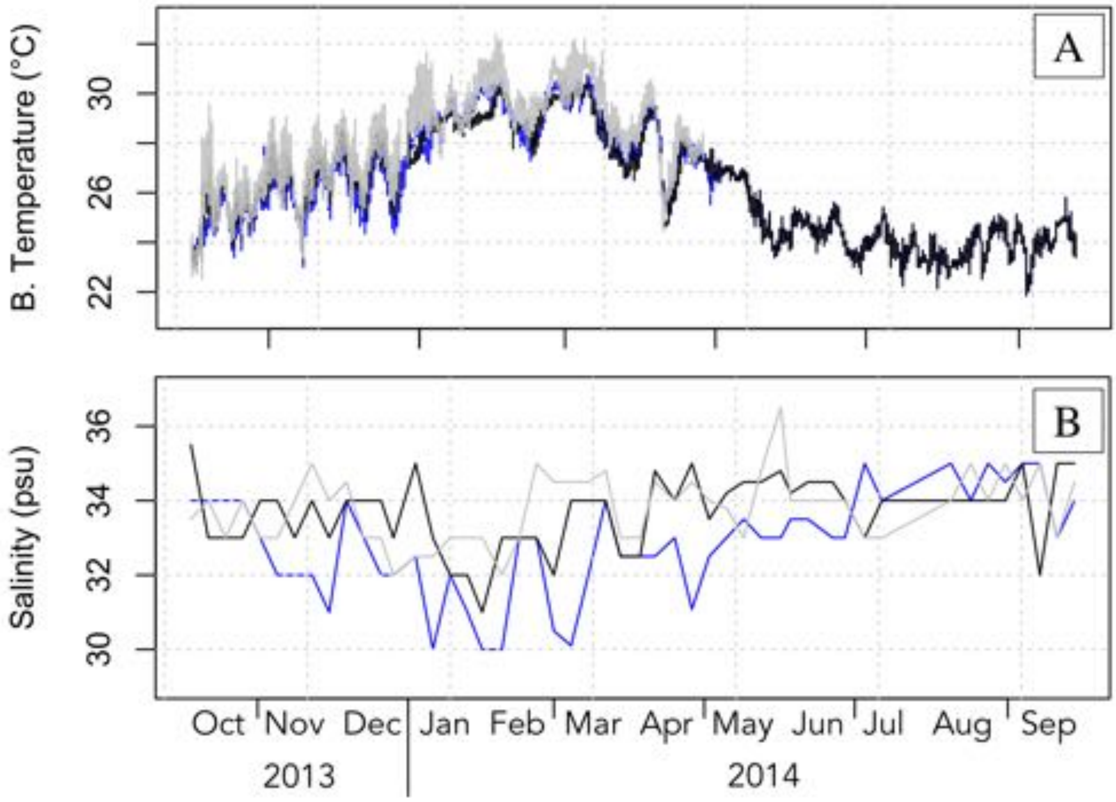


Figure 19: Variation of temperature and salinity at the studied stations. A. Temperature at the bottom; B. Salinity. Blue line: Nosy Tafara, Black line: Grande Vasque, Grey line: Rose Garden.

3.3.2 Planula records

We observed occurrence of planula 9 months over the 12, from August to December and from February to May. During 7 weeks, between December and February, sampling was interrupted because of bad weather (Table 12). The highest density of planula was observed the last week of November and the first week of December (all size confounded, Table 12). Nosy Tafara presented a higher total density of planula (3.23 larvae per m^3) compared to the other stations, with respectively 0.43 larvae per m^3 and 1.30 larvae per m^3 for Grande Vasque and Rose Garden. On the other hand, planula occurred much often at Nosy Tafara (9 months) compared to Grande Vasque and Rose Garden where we could observe planula respectively 8 and 3 months over the year.

Table 12: Annual occurrence and density of planula. Dark grey cases correspond to occurrence but when we could not count the number due to very little density. Red cases correspond to weeks during which we could not sample due to bad weather.

	13 - Oct	13-Nov	13 - Dec	14-Jan	14-Feb	14-Mar	14-Apr	14 - May	14 - Jun	14 - Jul	14 - Aug	14-Sep
Nosy Tafara		13.4				0.37	0.26	0.34				1.80
Grande Vasque		0.43				0.24	0.02	0.34				1.10
Rose Garden		1.30										

3.3.3 Recruits records

Seasonal distribution of coral recruitment was different between the stations. New settled corals were observed at Nosy Tafara every month during the survey, while they were observed only during 3 months at Grande Vasque and during 5 months at Rose Garden (Figure 20). The total abundance of recruits was significantly higher at Nosy Tafara with 1138.9 recruits per m^2 compared to Grande Vasque and Rose Garden with respectively 225 recruits per m^2 and 138.9 recruits per m^2. Highest number of recruits was observed for all the stations during the period of October to December (Figure 20). High numbers of recruits were also observed in March at Nosy Tafara and in May at the three stations.

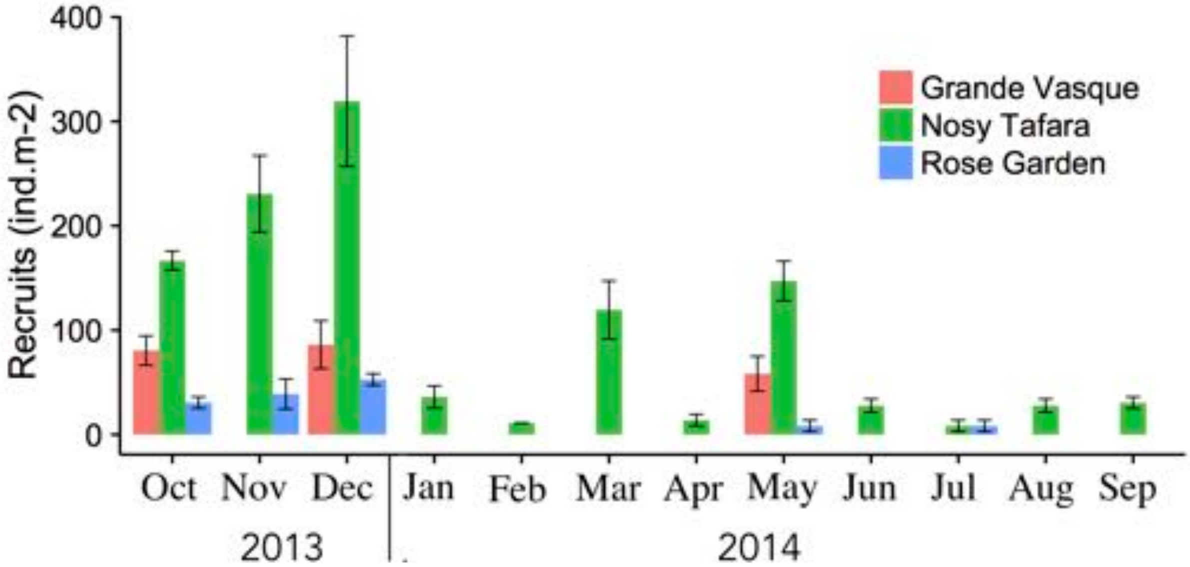


Figure 20: Total abundance of recruits per stations per month. Bars represent the mean; segments represent the standard deviation (SD); n=4.

The high number of recruits at Nosy Tafara was due to the abundance of Pocilloporidae (Figure 21) that represented 51.7% of the total recruits. A peak of Pocilloporidae recruits was observed in December, but high rates were also recorded in October and November (Figure 22A). Recruits belonging to the family Poritidae were also abundant at this station with a peak observed in March (Figure 22A). Recruits of the other families were distributed with approximately the same values. At Grande Vasque, recruits of Acroporidae were the most abundant, representing 33.3% of the total recruitment rate with a peak recorded in October (Figure 22B), followed by the Pocilloporids that represented 16%. The other families were distributed approximately with the same abundance (Figure 21) at this station. At Rose Garden, we recorded a slight dominance Pocilloporidae recruits (30%) compared to Acroporidae (26%) and Poritidae (14%) that was only recorded in December. At this station, we did not observed recruits belonging to Agariciidae and Lobophyllidae. Except for unidentified recruits that were recorded in May and July, the recruitment at Rose Garden was only observed between October and December (Figure 22C).

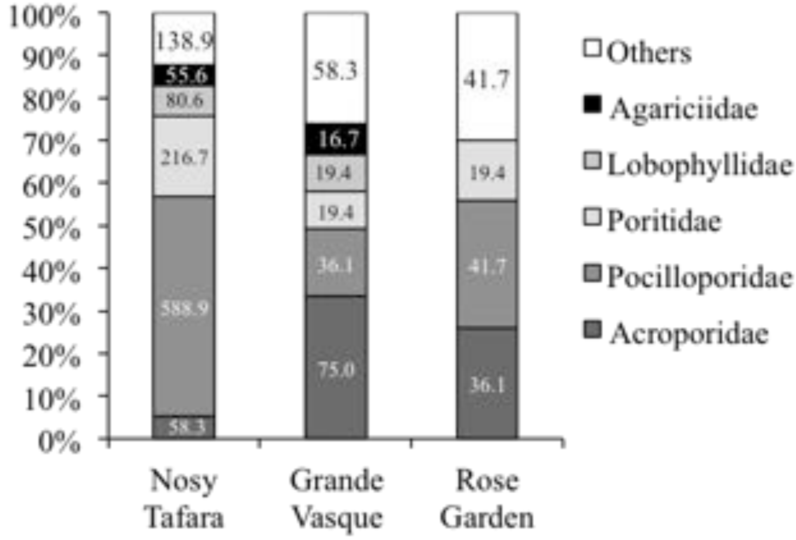


Figure 21: Proportion of the total abundance of recruit families (all months confounded).

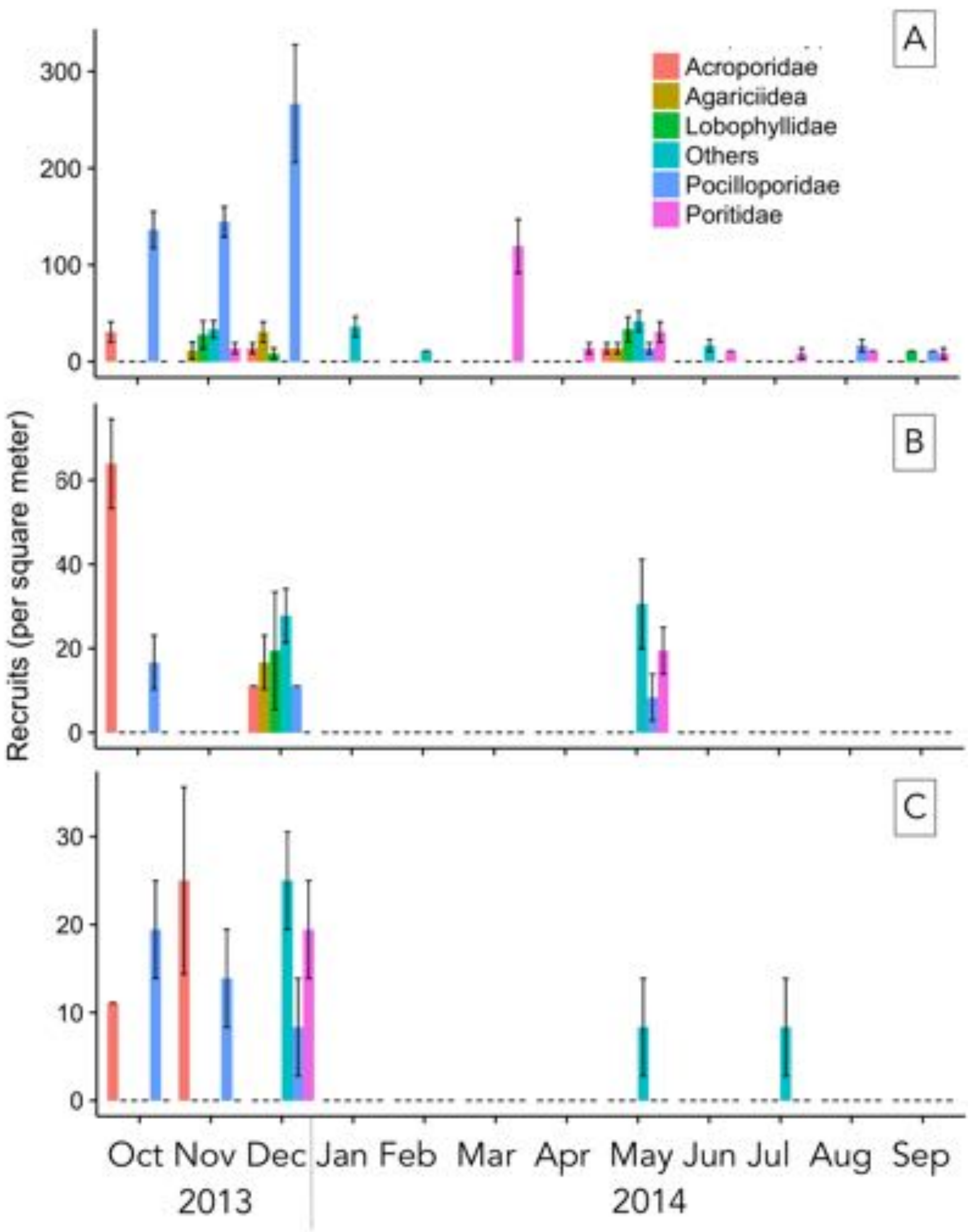


Figure 22: Monthly distribution of recruit families. A. Nosy Tafara; B. Grande Vasque; C. Rose Garden. Bars represent the mean; segments represent the standard deviation (SD); n=4.

Records from Nosy Tafara and Grande Vasque showed that Pocilloporidae juveniles of < 2 cm in diameter dominated the recorded juveniles respectively with 56.1% and 38.3% of the total abundance (all months confounded) (Figure 23). The relative abundance of Pocilloporidae juveniles of 2 to 5 cm in diameter was lower with 41.3% at Nosy Tafara and only 27.8% at Grande Vasque. Obviously, at both stations juveniles of Pocilloporidae and Acroporidae dominated more than the half of the total rate (Figure 24).

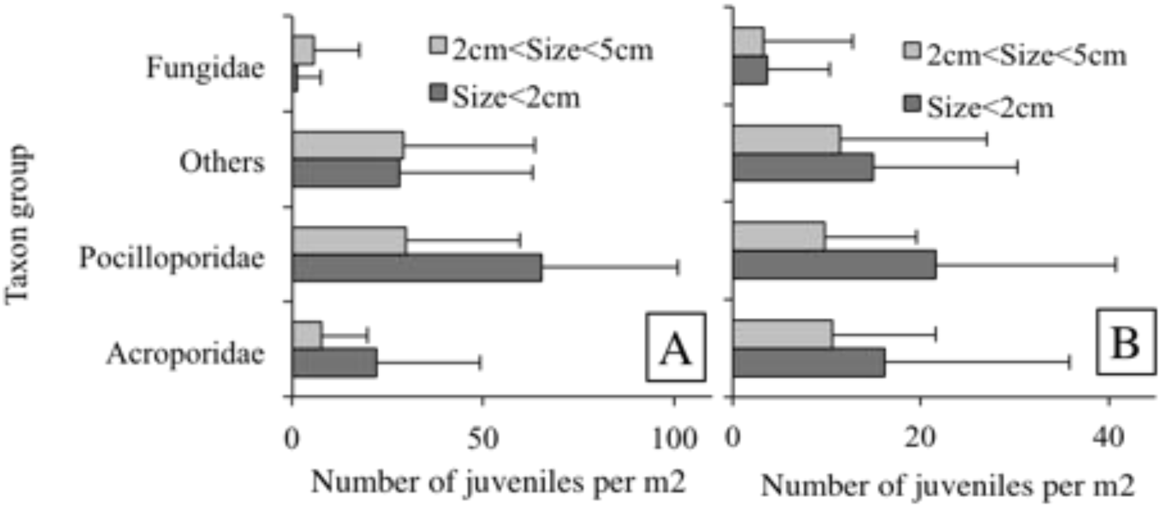


Figure 23: Coral juveniles records at Nosy Tafara (A) and Grande Vasque (B). Bars represent the mean; segments represent the standard deviation (SD); n=80.

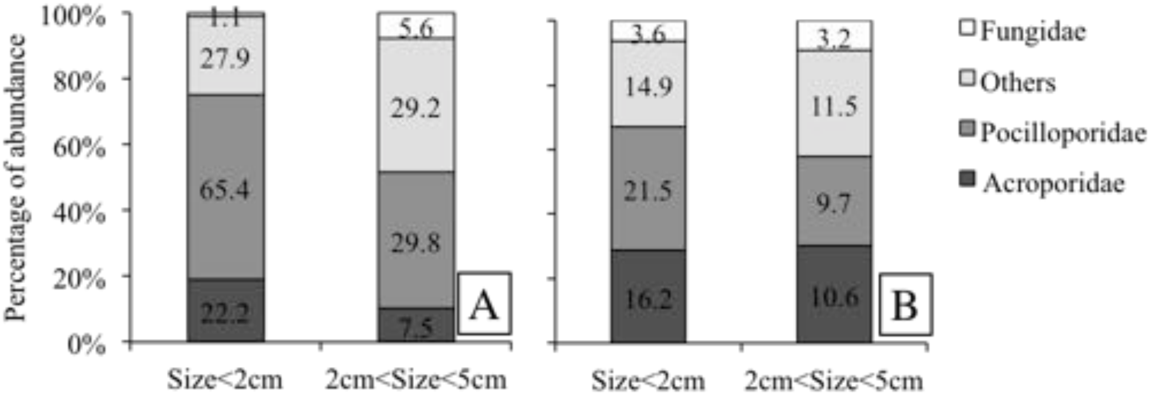


Figure 24: Proportion of the total abundance of juveniles: comparison between families. A: Nosy Tafara; B: Grande Vasque

The post-settlement mortalities can be estimated in comparing the recorded abundance (records m^{-2}) of juveniles with the recorded abundance of the recruits

(Figure 25). The results show that recruits had higher mortality than juveniles. At Nosy Tafara, abundance of early juveniles (< 2 cm) represented 10.2% of the abundance of recruits and the abundance of larger juveniles (2 – 5 cm in diameter) represented 6.3% of the abundance of recruits. At Grande Vasque, abundance of early juveniles (< 2 cm) represented 25% of the abundance of recruits and the abundance of larger juveniles (2 – 5 cm in diameter) represented 15.6% of the abundance of recruits. At both stations the abundance of larger juveniles represented respectively 61.9% and 62.2% of abundance of early juvenile.

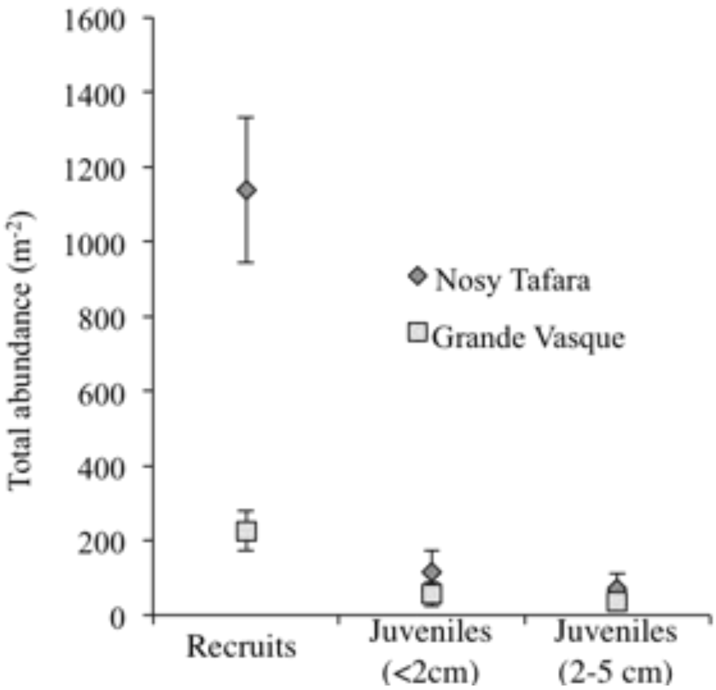


Figure 25: Total abundance (± SD) of recruits, early juveniles (< 2 cm size) and aged juveniles (2 – 5 cm).

3.4 Discussion

The present study is the first that analyses the recruitments and early development of corals in Madagascar. It covers a period of one year and includes larval records and cover estimations of coral recruits and juveniles. The only record of coral spawning in Madagascar (Gress et al. 2015) indicates a spawning event that occurred the 9th and 24th September 2015 on the coral reefs of Andavadoaka located at 50 km from the northern coral reefs studied in the present work. It happened 4 to 6 nights after the new and the full moon and concerned only *Acropora* species. In the present paper, the observation of high planula densities the last week of November and the first week of December combined with the increasing densities of recruits from October to December suggests the occurrence of massive coral spawnings in these three months.. Also, the extended presence of planula coupled with that of recruits in many months outside November/December indicates that punctual spawnings occur regularly, especially in February, March, April, August, September and October. This phenomenon is not an isolated case but has been observed in several regions where scleractinian reproduction and spawning were observed several months over year with the occurrence of a mass spawning period following the full moons from September to March (*e.g.,* Babcock et al. 1994, Guest et al. 2002, Carroll et al. 2006, Rosser and Baird 2008, Massé 2014).

The peaks of recruitment recorded from October to December in the SW of Madagascar results from the planula observed in September and/or in October, knowing that planula can survive several weeks before settlement (Baird et al, 2012). The weak recruitment in January/February suggests the end of massive spawnings in December.

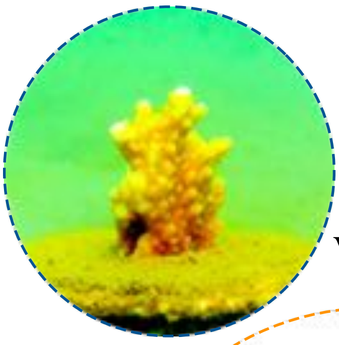
We also observed a huge difference of recruit records and juvenile records between the stations and especially between Nosy Tafara and the two other stations, Grande Vasque and Rose Garden. Nosy Tafara shows much more recruits and the recruitment occurs all the year. In Grande Vasque and Rose Garden, the massive recruitment occurs in October to November and is followed by a small recruitment in May (Grande Vasque) to July (Rose Garden). Nosy Tafara is much more exposed to the open sea than the two other stations, Grande Vasque being a basin in a reef flat and

Rose Garden a patch reef in a protected lagoon. The recruitment rates recorded in Madagascar are comparable to the highest level observed in the tropical Pacific reefs (Hughes et al. 1999) and in the Western Indian Ocean (Massé 2014), particularly at Nosy Tafara where it reached > 1000 recruits m^{-2} $year^{-1}$. The relatively low rates observed at Grande Vasque and Rose Garden is still higher compared to most of the Indo-Pacific Islands where the recruitment rates do not exceed 100 recruits $m^{-2}year^{-1}$ (Adjeroud et al. 2016). Though, eventual differences between the used methods and materials (tile surface, depth and tile nature) may lead to error in estimating and comparing results of research form different regions. These differences should be analysed by performing recruitment monitoring with all the used methods and comparing the results from the same site and same period. The observed recruitment rates of juveniles at each station were classified as very high if we refer to the theoretical assessment scale of the scleractinian recruitment rates proposed by Engelhardt (2003). This theoretical scale considers the recruitment rate as very high if the abundance of branching corals (Acroporidae and Pocilloporidae) of 2 – 5 cm size is > 10 juveniles m^{-2}.

The temperatures and visibility of water at the three stations are not significantly different but well the salinity: salinity in Nosy Tafara is lower than in Grande Vasque and Rose Garden. This is due to the proximity of the Onilahy River at a few kilometres from Nosy Tafara. The relation between the low salinity and the high recruitment observed in Nosy Tafara is not evident but one may expect that salinity could affect some predators or parasites more than the planula and the recruits. The period of September to December corresponds in Madagascar to the transition between the dry cold season and wet warm season, during which the water temperature slowly rises to reach the highest values in January and February. During that same period, the solar light intensity reaching corals is at its highest level. Solar light cycles are amongst the main conditions that determine coral spawning (Brady et al. 2009) and though, the abundance of coral recruitment. The period of January and February 2014 was particularly rainy and strong influences of tropical cyclones were noticed at the stations affecting the salinity and the water visibility. The second period of larval occurrence and recruit record (March – May) corresponds to the transition between the warm wet season and the dry cold season during which the water temperature was decreasing. Water current is also known as being one of the main dispersal factors of planula (Adjeroud et al. 2016). The high density of larvae and the higher recruitment rate recorded at Nosy Tafara may be explained by the water current regime that is mainly South to North (Ranaivomanana, 2006). The high density of coral larvae and high rate of settlement observed at this station may originate from local spawnings but also from spawning of corals located elsewhere and especially from the coral reefs of Soalara Sud and Anakao situated south from the Onilahy mouth.

The post-settlement processes are one of the important keys to characterize the dynamics and resilience of coral reef assemblages. Results presented in the present paper relate an important mortality post-settlement but the abundance of survived juvenile still represent higher rate compared to other regions (Wending 2003; Adjeroud et al. 2016). The earlier the coral stage is, the highest is the mortality. The major sources of high mortality of early recruits are unsuitable environmental conditions, competition, and predation (Adjeroud et al. 2016). At the studied stations, environmental conditions are strongly influenced by the seasons and sedimentation. During the rainy season, upstream factors such as river flow are particularly increasing and result in the water erosion of the soil and the watershed of Fiherenana (Payet et al. 2011) and of Onilahy (Rakotondralambo 2008). Sheridan et al. (2015a, 2015b) shows that sedimentation induces coral disease and mortality on coral reefs in the SW of Madagascar. In addition, anthropic pressures due to destructive fishing techniques (Mahafina 2011, Bruggemann et al. 2012, Andréfouët et al. 2013) are particularly high on these coral reefs where coral trampling is practiced (Salimo 1997). Competition with algal assemblages is also important, especially on the degraded reef flat (Bruggemann et al. 2012).

In conclusion, the coral recruitment in the region is high and could result in good resilience of the coral reef assemblages but several post-settlement factors may induce an important mortality of coral recruits and juveniles which can be a limiting factor for an effective resilience and coral community structuration. Further studies should be performed to identify the main causes and implications of coral recruitment at GRT.



Chapitre 4

Challenges in transporting coral nubbins. Water volume, dissolved oxygen concentration and light irradiance influence the physiology of *Seriatopora hystrix* in small volume

Chapitre 5

Community-based coral aquaculture in Madagascar: a profitable economic system for a simple rearing technique?

CHAPITRE 5: Community-based coral aquaculture in Madagascar: a profitable economic system for a simple rearing technique?[7]

Abstract

Since a couple of decades, coral aquaculture has been developed in many countries to face an increasing live coral market and to support conservation of endangered natural coral reefs. To evaluate the potentiality of community-based coral aquaculture in Madagascar, we experienced suitable farming techniques using the species *Acropora nasuta* and *Seriatopora caliendrum*. Survival and growth rate of the nubbins were monitored during wet, warm and dry, cold seasons. To determine economical feasibility, the coral market was investigated and the yields were also calculated using the technical, biological and social parameters of the production. Coral nubbins were reared *in situ* at appropriate conditions. Coral nubbins reared during the wet, warm season show a final survival rate of 67±6% and 57±4% respectively for *A. nasuta* and *S. caliendrum*, while in the dry, cold season, the survival rates are respectively of 85±7% and 69±1%. *A. nasuta* has a significantly higher survival rate than *S. caliendrum* during both seasons. During the wet, warm season, growth rates are respectively 0.46±0.16%d^{-1} and 0.54±0.16%d^{-1} for *A. nasuta* and *S. caliendrum*. In the dry, cold season, *A. nasuta* has 0.63±0.18%d^{-1} of growth rate, while *S. caliendrum* grows of 0.65±0.15%d^{-1}. Significant difference was observed between both species during the wet, warm season, but not during the dry, cold season. Furthermore, both species grew faster during the dry, cold season. These results are in the range of reference values for corals. The activity is profitable from 25 coral nubbins sold per month. Profit can already be perceived from the second year and a total of more than EUR 27,000 is earned after 5 years of developing project, for an initial investment of EUR 1,978. Marine animals wholesale companies and biodiversity conservation NGOs seem to be the appropriate clients for this form of aquaculture on Madagascar.

[7] Ce chapitre est accepté pour publication au journal Aquaculture: Todinanahary, G.G.B., Andrifanilo, H., Puccini, N., Lavitra, T., Grosjean, P., Eeckhaut, I. (*Accepted*) Community-based coral aquaculture in Madagascar: a profitable economic system for a simple rearing technique?

5.1 Introduction

Coral culture also known as coral aquaculture or coral[8] farming is the rearing of corals for commercial purposes (Ellis and Sharron, 1999; Department of Fisheries of Western Australia, 2009; Albert et al. 2012), reef restoration (Ng et al. 2012) or for drug discovery (Leal et al. 2013). It could provide an effective tool to restore coral reefs (Bowden et al. 1999; Martin et al. 2005; Hernández-delgado et al. 2014) that are declining worldwide (FAO 2005-2015).

In the Southwest region (SWR) of the Indian Ocean, notably in Madagascar, several studies have reported the impacts of fisheries (Bruggemann et al. 2012), tourism activities, climate change and coral bleaching (McClanahan et al. 2007; Eriksson et al. 2012). Several conservation programs have been established in the Western Indian Ocean (WIO) Region by public research institutions and non-governmental organizations (NGOs). In Madagascar, conservation policies have focused on the creation of marine protected areas (MPAs) as a tool for fisheries management. Over 60 marine reserves have been created with fishing communities and Government, the fishery and marine science Institute and NGOs (Wildlife Conservation Society (WCS), Blue Ventures, Reef Doctor and Conservation International) (Todinanahary et al. 2013). In 2008, the concept of community-based aquaculture was introduced to the traditional fishermen in Madagascar who previously had no alternative livelihood to fishing. Community-based aquaculture started with the launch of sea cucumber (*Holothuria scabra)* farming through a newly created company "Madagascar Holothurie SA" (MHSA) with the aim of reducing fishing pressure on wild communities (Laroche and Ramananarivo 1995; Rasolofonirina and

[8] The term "coral" in this work refers to the scleractinians also known as hard corals.

Conand 1998 ; Rasolofonirina, 2004; Lavitra 2008; Lavitra et al. 2009). Seaweed farming (*Kappaphyccus alvarezii*) in Madagascar began in the late 1980s, where culture tests demonstrated the feasibility of algae farming. Since few years, at least 7 private operators interested in seaweed farming have tried, with varying success, to develop commercial productions. In the SWR, the "COopérative de PEche FRIgorique de Toliara" (COPEFRITO – www.copefrito.com) Company, in partnership with Blue Ventures and the fishery and marine science institute (IH.SM) of the University of Toliara involved over 400 seaweed farmers living over 200 km off the SWR shores and the company currently exports products to Europe (Eeckhaut, pers. com.; Tsiresy et al. 2015).

Since 2008, community-based sea cucumber farming and seaweed culture have increased in both size and production volumes as a result of research and development projects involving fishermen communities, private companies, NGOs and public institutions. These stakeholders continue to work together within a working platform of community-based polyaquaculture that they constitute. In 2012, the Polyaquaculture Research Unit (PRU - http://www.polyaquaculture.mg) project was initiated (Tsiresy et al. 2013) to develop polyaquaculture in the coastal villages of Madagascar, as alternative financial resources to fishing and gathering of wild organisms (Pascal et al. 2013). The researches focused on improving sea cucumber and seaweed farming, as well as investigating the feasibility of other aquaculture initiatives such as coral aquaculture their integration into communities.

Coral aquaculture has been practiced since the 90s (Department of Fisheries of Australia 2013) at different scales in France, the Netherlands, Germany, China, Dominica, Fiji, Indonesia, Israel, Marshall Islands, Philippines, Singapore, United Republic of Tanzania, United States of America (USA), Puerto Rico, Palau, Solomon Islands and Japan and Australia (CITES 2002). Techniques vary in function of latitude and farming scale but in tropical and subtropical countries, corals are generally cultivated in the field (Ellis and Sharron 1997; Albert et al. 2012). In temperate countries coral aquaculture is often land-based (Wijgerde et al. 2012; Leblud et al. 2014a) and corals are reared in aquariums (Kangas and Walter 1996; Berges et al. 2001; Atkinson 2010). In both cases, the farming method is commonly based on the cuttings technique where small branches of corals or coral nubbins (Leblud et al. 2014b) of about 5 to 10 cm are cut from mother colonies and secured on hard surfaces. The size of the nubbins depends on the goal and the final destination of the reared coral.

Corals can tolerate a wide range of environmental conditions but they usually do not appreciate sudden changes in parameters (Osinga et al. 2011). Thus in *ex-situ* culture, it is essential to maintain the water conditions at the tolerated range and ideally at optimal values for the corals (Leblud et al. 2014a). In addition, the operational costs for *ex-situ* coral culture are very high and the cost of the production of a coral can reach over €30 (Osinga et al. 2011). The advantage of *in-situ* coral farming is that it is not necessary to control the water parameters when it is performed in the appropriate site. Therefore, the cost of the production of a coral remain less than €1 (Lal and Kinch 2005).

Since 1990, coral aquaculture continued developing but about 24 years later, farmed corals (including captive bred and captive born specimens) represent less than 20% of the global live coral trade (CITES 2016). In 2014, the total trade volume exceeded 120,000 specimens that were farmed both in aquariums and in the field (CITES 2016). The market for farmed corals remains important in volume knowing that more that 80% of the traded corals are collected from the wild. The growing coral market is essentially dominated by the USA but is also present in Canada and mostly in Europe (Green et Shirley 1999; CITES 2016).

There is very little information about community-based coral aquaculture practice. Villagers maintain most of the coral farms in the Salomon Islands (Albert et al. 2012), in Indonesia (Raymakers 2001), in the Marshall Islands, in Palau or in Fiji

(Delbeek, 2008). Then, the farmed corals are bought and exported by privates that perform the coral preparation in land-based aquariums (Lal and Kinch 2005). These countries constitute the principal producers and exporters of live corals (CITES 2016). In the Indian Ocean, coral farming is modestly developing (*e.g.,* in Mauritius, Nazurally and Rinkevich 2013). In Madagascar, *in-situ* coral farming was started in 2008 by the private society IBIS Madagascar but their production stopped few years later due to logistical problems (pers. obs.). Another private, the Marine Aquaculture of Nosy Be performs coral aquaculture both *in*- and *ex-situ* but they are limited to the production of soft corals (Menzel, pers. com.).

In this paper we analyse the potential of coral aquaculture for fishermen in villages of Madagascar. The main objective of the study is to identify a simple coral rearing technique, which is appropriate and accessible to fishermen and farmers in the coastal villages of the country. This paper also assesses the economic feasibility of the livelihood based on a business model.

5.2 Materials and methods

5.2.1 Analysis of biological, ecological and technical feasibility

5.2.1.1 Studied species

Acropora nasuta (Dana 1846), and *Seriatopora caliendrum* (Dana 1846) were used for all the experiments (Figure 35). Species were initially identified using the *in-situ* Coral finder identification guide (Kelley 2011), followed by an in-lab skeletal morphology analysis using the 3 volumes of "The corals of the worlds" (Veron 2000). Finally, DNA sequencing was performed to confirm and correctly identify these species (unpublished data). The gene Cytochrome oxydase subunit 1 (COI) of each species was sequenced and compared to Genbank (http://www.ncbi.nlm.nih.gov/genbank/) published sequences using Basic Local Alignment Search Tool (BLAST) to find out the nearest taxa.

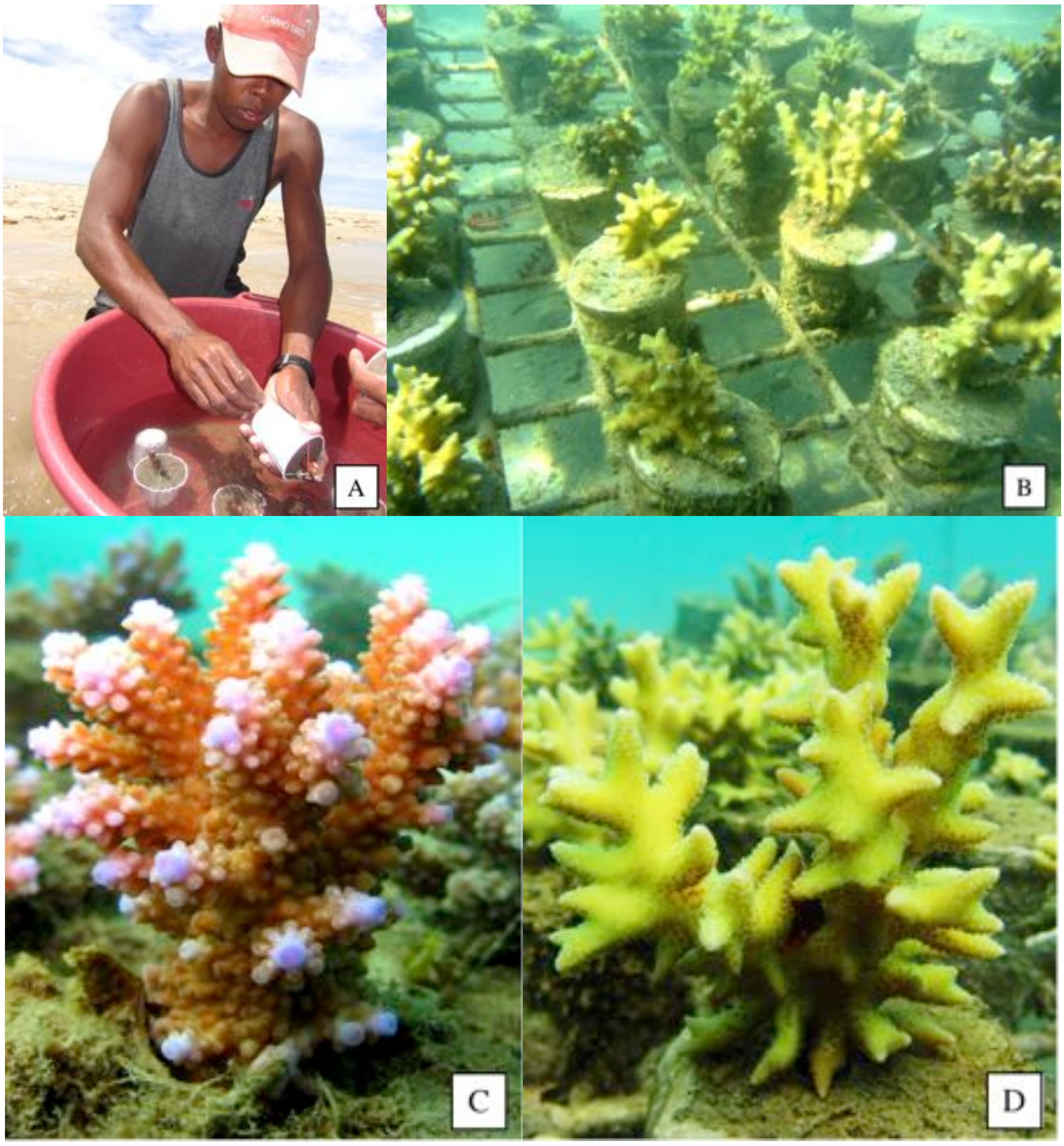


Figure 35: A: Fixation of the nubbin to the cement support prior to immersion. B: Installed coral farming table. C and D: *Acropora nasuta* and *Seriatopora caliendrum* from the experimental coral aquaculture at Sarodrano.

5.2.1.2 Selection of the farming site

Experiments were performed at the village of Sarodrano (S23°30'35", E43°44'4") (Figure 36) which is a fishing village located at the tip of an arrow-shaped dune of sand at the southern boundary of the lagoon of Toliara. This village is surrounded by a complex of coastal and marine ecosystems: at the south by the dunes and mangroves of Ambanilia, and the fringing reef of Sarodrano that runs along the arrow and separates the village from the estuary of the Onilahy river; at the east by a large area of seagrass and channels that opens on the higher limit of the intertidal zone with some mangrove species; at the North by internal reefs (Belaza, Dimadimatsy, Mareana among others) and the lagoon of the Bay of Toliara; and at the west by the southern tip of the Great Reef of Toliara and the reef complex of Nosy Tafara. These coral reefs are of diverse typology: barrier reef, inner reef, outer reef, fringing reef, and reef patch (Clausade et al. 1971).

To choose the best farming site, we first performed rearing tests at 3 stations of different depth measured at low tide of full moon: the stations A (0.4 m), B (0.6 m), C (1 m) (Figure 36). The station D corresponds to natural coral reef where mother colonies were collected. Four coral tables containing forty coral nubbins (~5 grams dry weight) of the species *A. nasuta* per station were installed. The rearing test was performed during January/February where the highest water temperatures were observed and where the heavy rains occurred, leading to the largest changes in salinity. Coral survival was weekly determined during 4 weeks after nubbins installation.

Amongst the tested stations, station C appeared to be the most appropriate for coral aquaculture. Survival rates of 57%, 63% and 96% were observed on stations A, B and C, respectively, one week after coral nubbins installation. The water motion on the station C explained this result. The current regime at this station is more similar to the site where mother colonies originate (station D on Figure 36; Pichon 1978). The depth is too low during low tides at the stations A and B. This exposed the coral nubbins at high temperature (> 30° C) during 1 to 3 hours, once or twice a day and negatively affected their growth rate, induce bleaching and at worst the death (Forsman et al. 2011). Only station C was taken forward and all subsequent results refer only to this station. It is located 5 minutes by pirogue from the village of Sarodrano. The station was at the outer limit of the degraded reef flat of patch reef of Belaza, by 1 m depth (measured during the low tide of full moon). Located on an intertidal zone, the water current regime is mainly tidal, with 4 daily movements during ebb tide (2) and rising tide (2) (Pichon 1978). The current is particularly intense during 1h prior and after the low tide of full and new moons.

At station C, temperature were hourly measured using Hobo data loggers from which data were downloaded and calculated using the ONSET HOBOware Pro version 3.7.0 (Onset Computer Corporation, 2002-2014); salinity, pH and total alkalinity were daily measured using refractometer, pH meter (sensION+, precision = 0.01) and YSI-9300 Direct-Read Photometer (precision = 20 µmol L^{-1}). Sedimentation rate was also measured during 10 days per season. Four sediment traps were installed using the method suggested by Rogers et al. (1994). Accumulated sediment was collected and dried at 60°C during 24 hours. Weight measurements were performed with an electronic balance (Sartorius BP221S, precision = 0.1 mg). The measurement of sediment rate was repeated twice during one season.

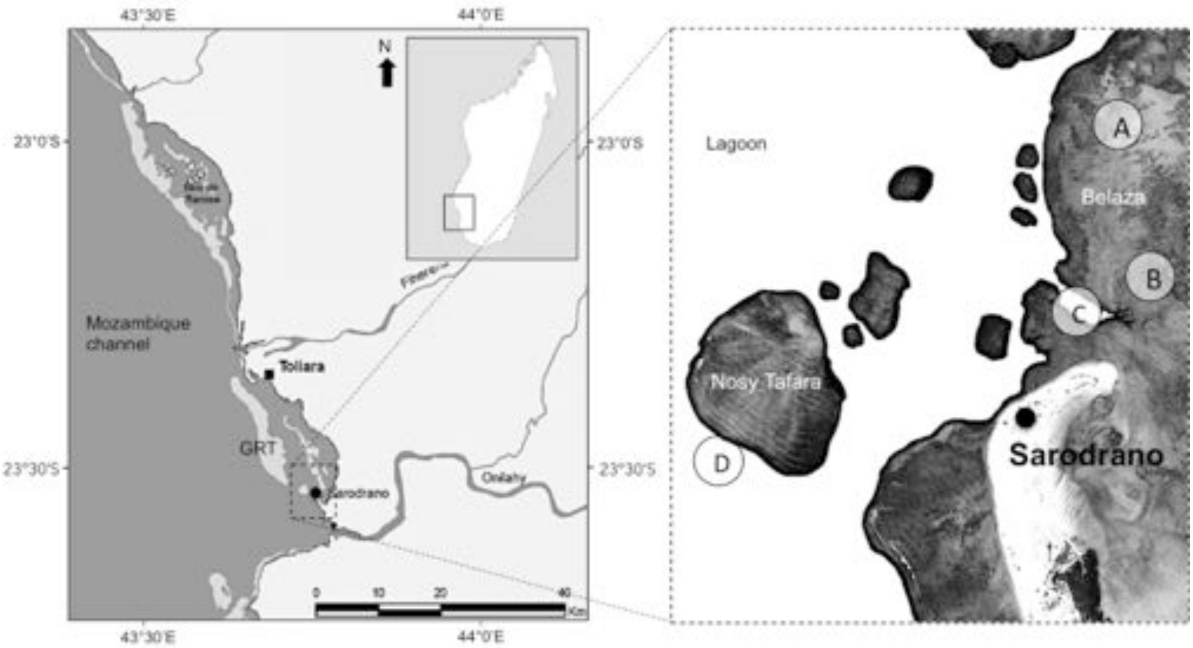


Figure 36: Location of Sarodrano village and experimentation sites. Farming tests were performed at stations A, B and C. D is the station where mother colonies were collected. White background on the right figure represents the open sea, while, dark backgrounds the coral reefs.

5.2.1.3 Coral aquaculture technique

5.2.1.3.1 Experimental design

Four coral tables 80 cm long and 40 cm wide were used to rear each species. The plates of the tables were hard iron mesh of a mesh size of 10 cm, and painted with rustproof paint. Each table of 40 cm in height was placed on the sandy bottom, at 1 m depth (measured at full moon). Were cut coral nubbins of *ca.* 5 grams dry weight (see growth measurement and skeletal calculation below) from mother colony using cutting pliers and fixed them on a cement support using elastic thread. Each cement support was placed tightly on the table mesh. A total of 40 nubbins per table produced from 15 – 20 cm colony collected in the station D (Figure 36) were installed. One different mother colony was used for each table. The rearing experiment was performed during 6 months and was repeated during the wet, warm season (November – April) and the dry, cold season (May – October). The whole experiments were performed with 4 farmers from the village of Sarodrano. The farmers performed the installation of the tables, the collection of the mother-colonies, the preparation and the installation of the coral nubbins, with a logistic and scientific support from the researchers. During the experiments, the farmers undertook the maintenance of the aquaculture facilities, while the researchers were in charge of scientific monitoring and observations. This form of organization is typical to the community-based aquaculture (Pascal et al. 2013).

5.2.1.3.2 Survival and growth measurements

The number of lost and dead coral nubbins was assessed every month. Untied nubbin was counted as dead unless it could be retied on the support and did present no physical damage or bleaching. Growth was measured monthly on 10 nubbins of each species using the buoyant weight method. Each measured nubbin was fixed on a plastic tube that is detachable from the cement support to allow measurement and easy reattachment on the cement support after measurement. Weighing was performed by suspending the nubbin, which was immersed in seawater, to a hook connected to an electronic balance (Sartorius LE623P, precision = 1 mg). Salinity and temperature of the seawater where the nubbin is immersed during the measurement were measured in order to calculate the density. The buoyant weight was converted into skeletal weight the formula detailed by Jokiel et al. (1978) that consider the density of the waters and of the skeleton (Davies 1989). Growth rate over the experimentation periods was calculated using the exponential growth formula described in Osinga et al. (2011).

5.2.2 Analysis of the economical potential

5.2.2.1 Analysis of the market

In order to identify the main accessible and potential clients for Madagascar coral farming, a survey of 20 questions was performed using the survey monkey online tool (http://www.surveymonkey.com). It consisted mainly of quantitative and qualitative economical investigation (corals demand and selling: quantity, composition, origin, size and prices), but also considered the biological aspects (species and colour, bio-ecological constraints in transport and conditioning) (See details of the questions in Annexe 3). Twelve coral farming/trade stakeholders were targeted. The present analysis is based on the answer of 3 main categories of stakeholders, from which an overview of the coral market and coral prices could be determined: A – coral farming and wholesale company, B –public zoo and botanic park and C – aquarium shop (coral retailer). Complementary information was obtained from aquariums, aquarium shops web portal, personal communications with aquarium shop and public aquarium responsible and from the literature. Obtained data was classified and calculations performed throughout the value chain of coral production and market. We also collected information from few coral reef conservation NGOs to define their interests and their activities respecting coral and coral aquaculture. Finally, detailed data on the global market of corals was downloaded from the CITES trade data dashboards in order to identify the main characteristics of the farmed corals trade including the trade volume, the list of species, the list of the importing and exporting countries and the source of traded corals. The analysis of these characteristics allowed discussing and arguing the effectiveness of the coral farming and the accessibility of the global coral market. All this information was used to discuss in details about the viability and to identify the potential clients of the community-based coral aquaculture.

5.2.2.2 Calculation of the yields[9]

Each level of the value chain (Figure 37) was evaluated financially. The cost of materials, services and human resource were identified. The following parameters obtained from our biological analyses were used for the yield calculations. They were based on 57% of survival rate during rearing (the lowest observed during the tests) and 90% after transportation to the

[9] See details of the costs analysis in Annexe 6

client. They also consider practical aspects and the used methods. The first percentage was estimated according to the experiments with farmers and the second on a real assay where coral nubbins produced by the farm where packed and sent by airmail. The total duration of the transport, from collection of coral nubbins to unpacking was 27 hours). The community-based aspect and the scale of the farming were also considered.

5.2.2.2.1 Production parameters

- We selected 8 farmers; each maintaining 6 coral tables containing 40 nubbins each. We take into account 6 tables per farmer to consider the practical aspect of the farming. We consider 8 farmers in the calculations as it fits to the range of pilot farmers starting new community-based aquaculture in the villages of Southwest Madagascar.
- A coral nubbin reaches a valuable size after 8 months of rearing. Here we prudently consider getting the L size after 8 months even if the experiment duration was 6 months and that the L size was obtained after 6 months.
- A production of 240 coral nubbins per month per farmer is reached from the 8th month. At the beginning of a coral production, it should be considered that only 6 coral tables of 1 farmer per month are installed by all of them to promote their training and increase the ability in preparing and installing coral nubbins.

25% of the production is reintroduced to the natural coral reef and ~ 10% are used as a source of new nubbins.

5.2.2.2.2 Exportation parameters

- A packed coral nubbin weights 820±20 g. The volume of seawater in the transportation bag is approximately 800 ml.
- A transportation container can contain a maximum of 30 nubbins with a total weight of 24.6 kg.

- 84 coral nubbins per month are exported and the client pays 76 survived nubbins. These numbers are estimated from the production parameters and from the stated survival rates in the literature (Delbeek 2008).

5.2.2.2.3 The human resource

The human resource parameters are based on the effective salary and income of the concerned people in 2015 and in considering coral farming only as complementary activity. All people involved in this form of aquaculture already work in one of the community-based working platform members (Pascal et al. 2013).

- 8 farmers maintain the above production of corals. Each farmer is paid MGA 50,000 per month (~15 EUR).
- 1 technician for exportation technical tasks is paid 100,000 MGA (~ 30 EUR).
- 1 secretary in charge of the relation with clients and the administrative aspect of the production is paid 600,000 MGA (~170 EUR).

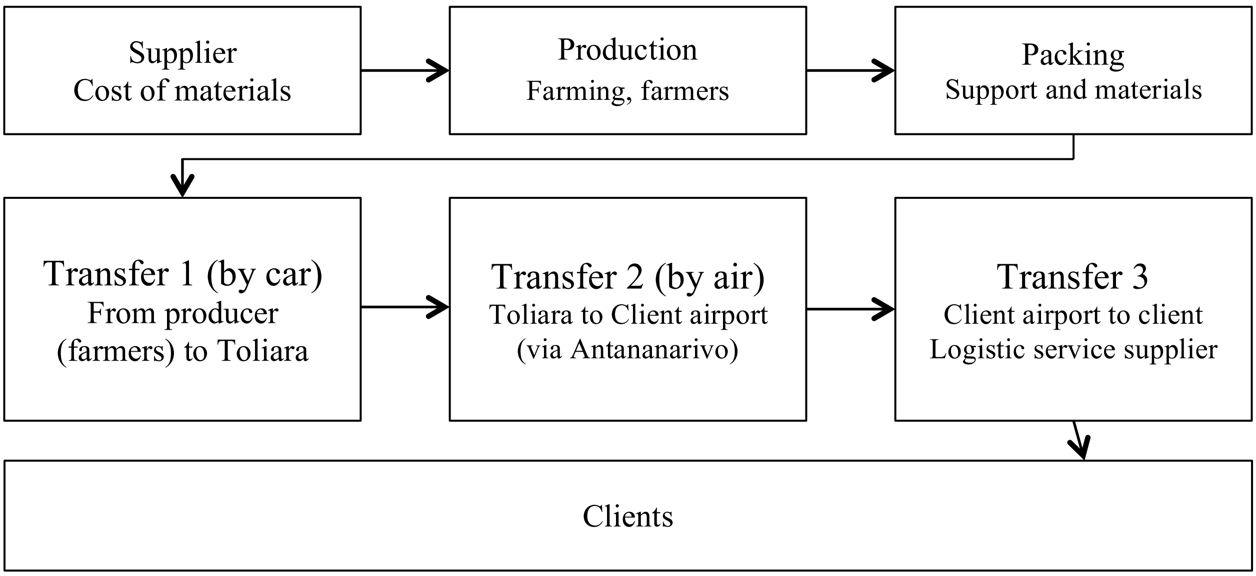


Figure 37: Value chain of the coral production from Madagascar

5.2.3 Statistical analysis

All the statistical analysis was performed using the R software (R Core Team 2015). Descriptive statistics were calculated first. Normality of the data was determined using a Shapiro-Wallis test and homogeneity of the variance was calculated using Levene's test. In this study, no transformation was needed. Significance or not of difference in means was determined using one-way ANOVA or t-test, with a level of 5%.

5.3 Results

5.3.1 Biological, ecological and technical feasibility

The measured sedimentation rate at station C was 0.55 ± 0.28 mg cm^{-2} d^{-1} (mean ± SD). The average values for temperature, salinity and pH of the water were significantly different between the wet, warm season, and the dry, cold season (Table 15). In wet, warm season the salinity was lower while total alkalinity and pH showed higher values compared to the dry, cold season (Table 13). The annual variation of these parameters is presented in the figure 36.

Table 13: Seasonal mean temperature, salinity, total alkalinity and pH of the water at the station C (4 measurements per month)

	Temperature (°C)	Salinity (psu)	Total alkalinity (µmol L^{-1})	pH (nbs scale)
Wet, warm season	27.8±1.1	32.0±0.7	1915±223	8.13±0.15
Dry, cold season	24.7±1.5	33.4±1.2	1582±652	8.03±0.13
Annual average	26.3±2.1	32.7±1.2	1748±496	8.08±0.15
Difference between seasons (p value)	<0.001	<0.001	0.26	0.018

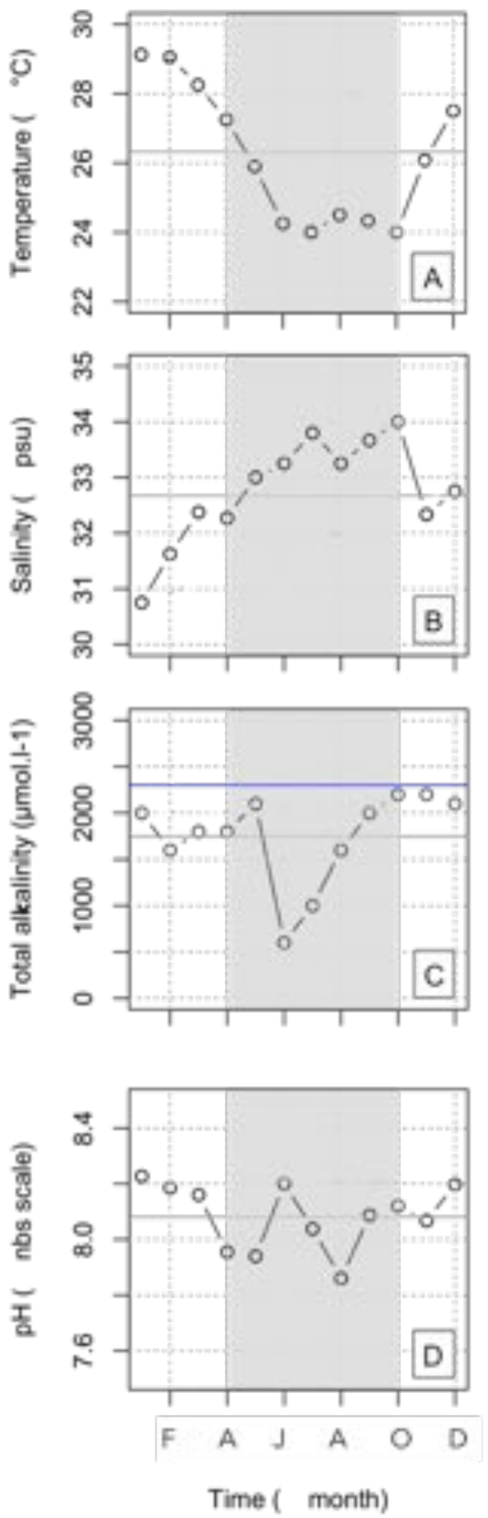


Figure 38: Annual distribution of temperature (A), salinity (B), total alkalinity (C) and pH (D) of the water during rearing experiments (mean of 4 measured values per month). Additional measurements were performed during the monitoring of survival and growth of the coral

nubbins. The grey areas correspond to the dry, cold season of Madagascar (May to October). Grey lines define the annual average value of each parameter. Blue line in C shows the reference value of total alkalinity of seawater in coral reef ecosystem (2300 µmol L^{-1}, Leblud et al., 2014).

Coral nubbins reared during wet, warm season showed a final survival rate of 67±6% and 57±4% respectively for *A. nasuta* and *S. caliendrum*, while during the dry, cold season, the survival rates were respectively of 85±7% and 69±1% (Figure 39). *A. nasuta* had a significantly higher survival rate than *S. caliendrum* during both seasons ($p= 0.029$ and $p= 0.003$ respectively). The survival rates of both species were significantly lower in the wet, warm season ($p= 0.006$ and $p= 0.002$ for *A. nasuta* and *S. caliendrum* respectively). In addition, more than 80% of the observed mortality was represented by untied coral nubbins. This implies the lower survival rates mentioned above. Recalculated survival rates (excluding untied nubbins) were 92±3% and 86±4%, respectively for *A. nasuta* and *S. caliendrum* in wet, warm season, and 97±2% and 91±7% in dry and cold season. Nevertheless, the differences between species and between seasons were conserved.

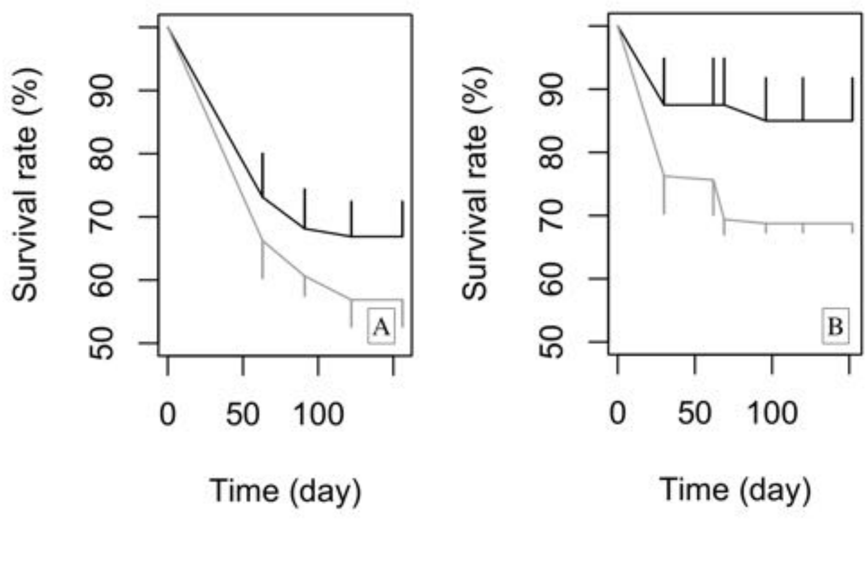


Figure 39: Evolution of survival rates of *A. nasuta* (black lines) and *S. caliendrum* (grey lines) during farming. A: wet, warm season; B: dry, cold season.

During the wet, warm season, growth rates were respectively 0.46 ± 0.16% d^{-1} and 0.54 ± 0.16% d^{-1} for *A. nasuta* and *S. caliendrum*. In the dry, cold season, *A. nasuta* had 0.63 ± 0.18% d^{-1} of growth rate, while *S. caliendrum* grew at 0.65 ± 0.15% d^{-1} (Figure 40). Significant differences were observed between both species during the wet, warm season (p = 0.030), but not during the dry, cold season (p = 0.51). Furthermore, both species grew faster during the dry, cold season. Significant differences were observed both in *A. nasuta* ($p<0.001$) and *S. caliendrum* (p = 0.001).

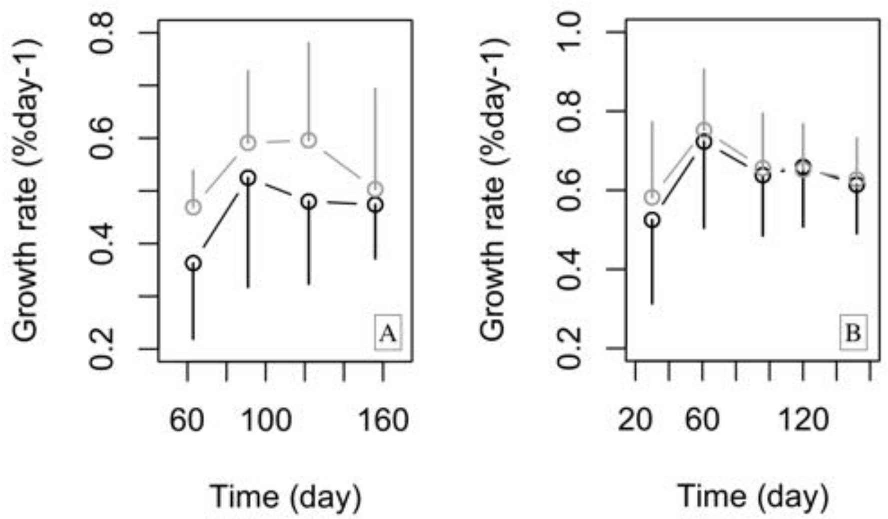


Figure 40: Average growth rate (±SD, n=10) of cultivated coral nubbin: (A) wet, warm season, (B) dry, cold season. The growth rates were based on 10 measurements for *A. nasuta* (black lines) and *S. caliendrum* (grey lines), during both seasons.

5.3.2 Economical potential

5.3.2.1 Investment and profitability

Here we propose a business that requires an initial investment of € 1,978 and an annual charge of € 15,246 including variable and non-variable costs. Based on 76 coral nubbins sold per month, the total cost per nubbin is € 21.56, including a non-variable cost of € 12.61 and a variable cost of € 8.95 (Table 14). An amortization of € 836 per annum is estimated. We suggest € 25 as the minimum price in this project but in this case we prudently consider a selling price of € 30. Thus, the project gets € 8.44 of margin per coral nubbin. That determines the minimum selling price to € 21.56, which correspond to the total costs per nubbin. The selling price to exportation of € 30 is 25% less expensive than the cheapest price of the experimented species. Reference prices were from the major coral wholesalers in Europe and were considered at the exchange rate of July 2015 (Table 15).

Table 14: Summary of costs analysis of the value chain (€).

	Total cost per coral nubbin	Initial investment	Annual charges	Annual amortization
Materials and equipment	0.22	352	476.24	71.62
Coral aquaculture staff and administration	11.12	1000	4527.42	200
Packing	0.45	625.71	309.07	146.29
Transportation (exportation)	9.77	0	9932.96	0
Total	21.56	1977.71	15245.69	835.93

Table 15: Example of price range (€) of *Acropora*, *Pocillopora* and *Seriatopora* species according to size and colour of the coral nubbin.

Genus	Color	XL size (10 – 15 cm and more)	L size (7 – 10 cm)	M size (4 – 7 cm)	S size (3 – 4 cm)
Acropora	Blue, green and bright colored	120-150	90-120	40-90	
Acropora	Violet		40-90		
Pocillopora	Rose	80-150	40-80		
Pocillopora	Green and yellow		40-80		
Seriatopora	Rose	80-150	40-80	30-40	20-30
Seriatopora	Yellow		40-80		

Provisional result accounts per year estimated in Table 16 considers that during the first year, exportation is only performed after 8 months, after which the production of 240 nubbins per month can be easily reached. In this case study, the Earning Before Interests and Taxes (EBIT) is of – € 6,938 the first year and € 11,350 from year 2 and each following year. Thus, the net result (reduced of 30% of taxes) reaches € 7,945 during cruising rhythm of the coral aquaculture project (Table 16). Table 17 proposes the financial flux of the project during 5 years from its implementation. It takes into account the initial investment and includes the annual amortization, as it is not a disbursed amount. Profit can already be perceivable from the second year. The project can make more than € 27,000 of total earn after 5 years, considering the hypothesis that the inflation is 0% and the price of the products does not change (Table 17)[10].

Table 16: Result accounts of the yield calculations

	Year 1 (€)	From year 2 (€)
Sales turnover	9,144	27,360
Exploitation charges	16,082	16,082
- Annual charges of production	15,246	15,246
- Annual amortization	836	836
Earning Before Interests and Taxes (EBIT)	-6,938	11,350
Taxes (30%)	0	3,405
Net result	-6,938	7,945

Table 17: Financial flux of the proposed coral aquaculture project (€)

Year	Gain	Cumulative gain
0	-1,978	-1,978
1	-6,102	-8,079
2	8,781	702

[10] The hypothesis of 0% inflation is the limit of our calculation. The real inflation situation depends to the global financial exchange and may induce increase or decrease of the yields.

3	8,781	9,483
4	8,781	18,264
5	8,781	27,045

In addition, calculations of profitability showed that the activity is profitable from 25 coral nubbins sold per month (Figure 41). According to the appropriate and adopted business model, a projection can be performed. With 25% of safety margin, we suggest that at least 30 coral nubbins per month should be sold to ensure a viable activity. For a production of more than 100 corals per month, profit reaches € 1,600 (per month). That is constantly increasing according to the efficiency of the coral aquaculture technique and the adopted business management[11].

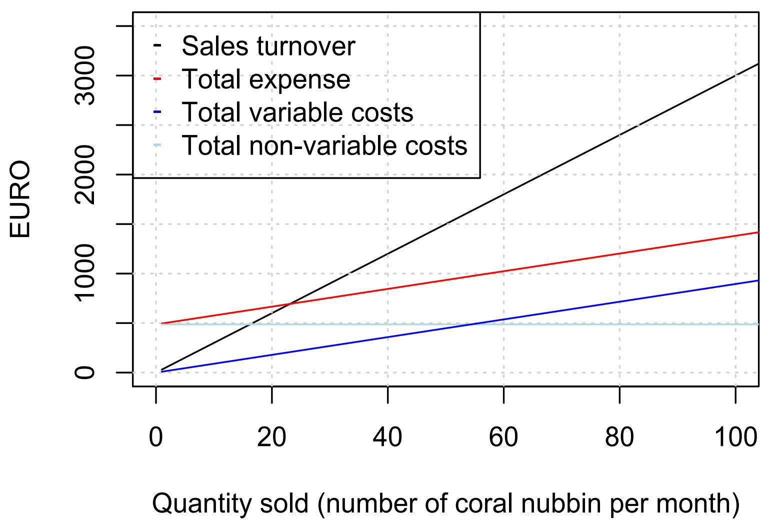


Figure 41: Break-even point of the proposed coral aquaculture project. Profit is represented by the difference between sales turnover (black line) and total expenses (red line).

[11] The results presented here consider approximative costs that may change when calculations are made with higher coral quantity produced and with inflation.

5.3.2.2 Analysis of the potential clients

Even if the coral market seems to be evident and open (Raymakers 2001; Reksodihardjo-Lilley and Lilley 2007), the main obstacle in community-based coral farming in Madagascar are finding and reaching clients. Very little information on the coral market exists and contacting main potential clients is not easy. The profitability depends on to which client to sell the farmed corals. Therefore, few scenarios could be proposed for selling corals, especially from Madagascar (Table 18).

The first scenario consists in selling the farmed corals to the European leader distributor (wholesaler) that we could contact. The European leader in importation, acclimation and distribution of fishes, invertebrates and aquarium plants from around the world is based in France. The company distributes common, rare, tropical or Mediterranean species both from aquaculture and wild species, to professionals such as resellers, wholesalers, and public aquariums. Indeed, its trans-shipping and acclimating activities are well established and certified ISO 9001.

Aquarium shops (retailers) can be considered as potential clients. They buy the corals either to the European leader distributor or directly from exporters in the major producing countries at varying price. For the *S. caliendrum*, they buy ~ € 30 a coral of L size (Osinga et al. 2011; investigations performed by authors). We identified 14 potential retailers in three European countries, Belgium, France and The Netherlands. Each contacted company showed their interest in receiving corals. These companies indicated that they could only receive small quantity of corals per month. Hence, a niche market is suggested in this second scenario, by considering two main parameters: selling expensive but uncommon coral species and promote the equity in the production system.

Selling the farmed corals to Luxury hotels and Touristic aquaria also constitute a scenario that can be considered. This scenario suggests that luxury hotels to create their own marine or land-based aquaria. However, as stated above, the challenges concern not only the cost of the implementation but also the effective management of a private installation, especially when it is installed in open water. The equitable coral aquaculture system of the project shall improve the status and prestige of the hotels. This advantage is essential to some hotels, which are currently criticized for their colossal infrastructure constructions considered as non-ecological and non-respectful of the human right. Hotels near the production site and the neighbouring countries have, by the little distance, the advantage of low transportation costs. The adoption of system of niche market can be advantage in this case as a pioneering system on the market.

Biodiversity conservation by NGOs constitutes the 4th scenario that relates the possibility of financial support on behalf of natural coral reef restoration. Three international NGOs and 2 local NGOs aimed at the protection of coral reefs have been identified and contacted for the case study. The correspondence of their activities have been analysed if either they can constitute or not a potential client or partner. The American NGO, Coral Reef Alliance (Coral Reef Alliance 2015) targets to support local population to socially, culturally and economically beneficiate from coral reef conservation. Their actions essentially focus on the education and sensitizing, and limited on coral reef repopulation. The Global Coral Reef Alliance (GCRA) works for coral reef management through coral aquaculture. The third international NGO, Reef Check acts also for coral reef conservation. Its activities make this NGO a potential client to the coral aquaculture of Madagascar. The program of these NGOs associates the local communities to government authority, Universities and private company to efficiently manage coral reefs. They already permitted creation of new MPAs and improvement of existing ones essentially in Asia an Oceania (Reef Check Foundation 2014). It permitted to conciliate the coral reef conservation to a sustainable management of the fishery, including the participation of the local communities to decision making about fisheries. The approach of the program of this NGO is based on 4 elements: low cost of the corals, involvement of local communities, long-term monitoring and scientific research implication. This last option places the Reef Check programs as suggested client in this 4th scenario. The two last NGOs suggested in this scenario are local NGOs in Madagascar: Reef Doctor and Blue Ventures, 2 English NGOs aimed at marine conservation and located respectively in Ifaty and Andavadoaka, in the SWR. These NGOs work for a responsible management of marine areas and fisheries. Their activities include education and sensitizing of the local communities on behalf of fishery management, but also social aspects such as health, conflict and family planning.

Table 18: comparative summary of advantages and disadvantages of each scenario.

	Advantages	Inconveniences
Scenario 1: European leader distributor	Experience improvement and services Use of well-established systems	Loss of community-based character Loss of independence and scientific research aspect Expensive
Scenario 2: Aquarium shops (Pet shops)	Difference of the ethic (new approach from Madagascar) New provenance of the corals	Oligopolistic offer and pure concurrence Coral replanting feasible by the clients Limited offer
Scenario 3: Luxury hotels	Participation to reef protection Innovative target for the sector Improve the image of the clients Low transportation fees for nearing hotels	Target difficult to reach Too much requested quantity Reticence
Scenario 4: Biodiversity conservation NGOs	Conservation of the ethic Experience improvement	Dependence not secured

5.4 Discussion

Madagascar has more than 2,400 km^2 of coral reefs along 1,400 km of coast (Cook et al. 2000). Most reefs in the SWR of the country have the same geomorphological structure as those close to where the present work was performed, including the presence of barrier reefs, fringing reef and patch reef in shallow water (Clausade et al. 1971). In addition, optimal sites for sea cucumber aquaculture and marine red algae were conditioned by the presence of a reef protection allowing the formation of a lagoon and calm water in intertidal zone. Accordingly, villages in the SWR and the North regions of Madagascar, where holothuriculture and algoculture are implemented might present ideal characteristics for coral aquaculture.

The observed growth rates in the present study were in the range of the similarly calculated average growth rate of the studied species (0.4 to 1% d^{-1}, Grosjean, pers. com.; Leblud et al. 2014). *S. caliendrum* grew faster than *A. nasuta* but it presented lower survival rate due to the fragility of its branches. These parameters can be considered in controlling the production rhythm by, for example, adopting bigger or smaller coral branch to bred. They should also be considered when significant loss of coral nubbins or simply slower growth may occur for many reasons such as cyclones, and sudden change brought by fluvial water flow, with extreme sedimentation (Sheridan et al. 2014), temperature rise or salinity decrease. Alternatively, anthropogenic activities constitute an important risk of coral loss: fishing using gear net, trampling by fishermen during low tide fishing, or obvious intense and spontaneous pollution from neighbouring big cities, such as Toliara in the case of Sarodrano and other villages around. Theft and wilful destruction of the coral aquaculture infrastructures are also significant risks in community-based aquaculture.

Acropora is the most demanded both by wholesalers and retailers. For wholesalers, the most prized species belong to the genus *Montipora, Seriatopora,* *Turbinaria* and *Caulastraea* while for retailers, the most requested species are *Porites, Euphylia, Plerogyra, Cataphyllia, Fungia* and *Helofungia*. Colour and size of the coral nubbin is also decisive for price. The most brightly coloured the coral. the more expensive it is. The most valuable group includes the green and blue colour morphs while violet and rose corals of the same size are less expensive. Table 16 shows example of the prices for *Acropora*, *Pocillopora* and *Seriatopora* of different sizes and colours. Investigations by the clients and coral sellers suggest that the brightness and fullness of the colour is most influencing parameter, instead of the colour itself: two coral of the same species, same size and same colour may have different price according to the intensity of their colour. Trade registrations of CITES (2016) correspond to the species list given by the investigated coral importers. The top twenty most traded genera recorded by CITES include, in descending order of quantity, *Acropora, Euphyllia, Montipora, Caryophyllia, Goniopora, Hydnophora, Pocillopora, Turbinaria, Caulastraea, Seriatopora, Plerogyra, Stylophora, Trachyphyllia, Porites, Agaricia, Lobophyllia, Fungia, Tubastraea, Dendrophyllia, Heliofungia*. This list represents the corals exclusively from aquaculture. The high coral species diversity in Madagascar constitutes an advantage (Pichon 1978; Obura 2012; Veron et al. 2015). Madagascar has also some endemic species (Veron 2000; Maharavo, pers. com.) that might be an additional value to the offer from a coral farm in the country.

The activities of the European leader distributor (scenario 1) request highly controlled aquarium facilities and well-established logistic services. Such facilities and services are very expensive and the operational costs can reach more than € 11 m^{-2} day^{-1} (1 m^{-2} aquarium can host up to 100 colonies of ~ 100 g that correspond to the size of a fist and the L size presented in the present paper, Osinga et al. 2011). Consequently, the production cost of the species *S. caliendrum* for example, can reach € 25 to more than € 30, which are close to other wholesale value of similarly sized aquarium (Osinga et al. 2011). This means that they must buy corals from the exporter countries for less than € 25 and limit their importation to maintain a profitable activity. Besides, this company own an *in situ* farm implemented in the Pacific islands and have its own logistic services, which allow them to maintain their activities competitive and viable. It also performs several extra-coral activities. The suggested selling price of the coral farming project from Madagascar is too expensive to be attractive to this company and such kind of distributor.

Selling the corals directly to aquarium shops is a solution (scenario 2). An ethic community-based coral aquaculture as it is in Madagascar should be an influencing parameter for these clients. Yet, as they have the appropriate facilities, they can easily replant the imported coral species in their aquaria and thus a small production of the same species may induce a decreasing demand. Secondly, the supply side of the market is oligopolistic *versus* the perfect competition of the demand side, meaning that there are few big providers to satisfy large demand of companies of similar range. Then, little offer shall barely penetrate this custom made market. Suggested solutions are respectively to diversify the production and the exported species and to be a privileged partner to few companies with low price of the proposed coral species.

In the scenario 3, the main obstacle consists to the difficulty of reaching clients. In addition, very high quantities of corals will be demanded in a relatively short period of time and the production of the community might not be sufficient in early-established project. On the other hand, the profitability of such kind of project is extremely delicate for the hotels. A big investment is needed in creating the reserve or the aquaria, yet the economical advantage ought be perceivable far after.

The advantage of the scenario 4 is importantly the conservation of the ethic and community-based aspects of the proposed coral aquaculture project. However, the dependence on only these NGOs is not sustainable. Furthermore, NGOs essentially involve volunteers for their activities and financial supports are not secured. With more than 60 coral reef reserves, which are similarly managed in Managed in Madagascar, especially in the SWR (56 reserves after Todinanahary et al. 2013), the correspondent activities of the NGOs can fit with the coral aquaculture program proposed in the present paper. Financial support is the main obstacle in this scenario as it suggests that 100% of the produced corals are transplanted to the natural coral reef. This can imply a limitation of the price of each coral nubbins and consequently the income.

For all the scenarios, the geographical location of the client determines the efficiency of the coral shipping. It is known that to get more than 90% of post-transportation survival. The duration of the coral transport including the preparation and transit time should not exceed 30 hours (Delbeek 2008). To sell corals from Madagascar, buyers from the Indian Ocean region (South Africa, Swaziland, Sri Lanka) and Europe (France, Denmark, Greece, Netherlands, Sweden, Germany, Ireland, Switzerland) are suggested. These countries belong to the registered importers of live corals (CITES 2016) and are less than 15 hours flight from Madagascar. The USA, Japan, Mexico, Brazil and Canada in descending order also belong to the top 10 importers of live corals before Singapore, Hong Kong, New Zeland, China and Costa Rica. These countries do not constitute interesting destination for farmed corals from Madagascar as the flight duration usually exceed 20 hours from the country and they are much closer than the experimented coral producers and exporters such as the top five Marshall Islands, Indonesia, Taiwan, Solomon Islands and Tonga.

The European leader distributor is the only scenario that does not fit to the objectives and the adopted philosophy of the coral aquaculture presented in the present paper. Scenario 3 is difficult to establish due to the high quantity required, but it is to be considered for long-term purposes when the project is well-established. Combination of scenario 2 and 4, with Aquarium shops and biodiversity conservation NGOs seem to be the appropriate clients for the community-based coral aquaculture from Madagascar. They can buy the corals at the suggested price and their rhythm of importation fits with the small-scale production.

In Madagascar, community-based coral aquaculture is technically and bio-ecologically feasible. The worldwide most used farming techniques of coral are adaptable to the coastal villages of the country, using locally available materials for coral aquaculture tables and hard supports to fix coral nubbins. The activity can be fully profitable at a small-scale production if partnership with appropriate clients or partners such as aquarium shops and coral reef conservation NGOs is adopted. Relatively low initial investment is needed and amortization of the invested found could be quick. The integration of the coral aquaculture within an existing production structure like the polyaquaculture work platform is suggested (Pascal et al. 2013). It allows the small-scale production to be economically profitable and to be viable at long-term with its social and environmental benefits.

Chapitre 6

Discussion générale

CHAPITRE 6 : Discussion générale

Cette thèse a eu pour but général d'estimer le potentiel de la coralliculture villageoise à Madagascar, en particulier dans la région sud-ouest de l'île. Dans ce contexte, nous avons identifié les scléractiniaires les plus communs, évalué leur potentiel de recrutement et choisi certains candidats pour la coralliculture. Nous avons aussi analysé la croissance de ces scléractiniaires sur sites villageois, étudié la méthode de transport la plus adéquate et évalué avec l'ensemble des paramètres que nous possédions le potentiel économique de la coralliculture villageoise. La thèse a donc fait appel à des méthodes d'analyse biologique couplées à d'autres, économiques, en intégrant certains paramètres sociaux et je propose d'en faire une analyse critique dans cette discussion générale à la lueur de ce qui se fait dans d'autres parties du monde.

6.1 Biodiversité, reproduction et recrutement : trois paramètres importants à connaître dans les sites à coralliculture villageoise

Chez les scléractiniaires, l'identification des espèces n'est pas aisée. Les clés d'identification sont basées sur la morphologie du squelette et la structuration des polypes en colonie (*e.g.,* Nishihira 1988 ; Veron et Marsh 1988 ; Wallace 1999 ; Veron 2000). Beaucoup de décisions taxonomiques prises lors des identifications sont difficiles sachant qu'il existe des différences morphologiques pour une même espèce d'une région géographique à une autre, même parfois d'un biotope à l'autre au sein d'un même récif corallien (Veron 2000). Les récentes avancées moléculaires ont suggéré l'utilisation du « DNA barcoding » comme identité universelle de chaque espèce animale (Hebert et al. 2003) et la cytochrome oxydase 1 (CO1) est le marqueur moléculaire le plus communément utilisé. Cependant chez les scléractiniaires, ce marqueur s'avère trop peu évolutif : malgré quelques analyses qui utilisent ce gène (*e.g.* Fukami et Knowlton 2005 ; Kitahara et al. 2010 ; Gittenberger et al. 2011), d'autres démontrent qu'il est limité par une très faible divergence interspécifique (van Oppen et al. 1999; Shearer et Coffroth 2008). D'autres marqueurs moléculaires comme l'« Internal transcribed spacer » (ITS) et l'ADN de la petite sous-unité ribosomale (18S) sont également largement utilisés jusqu'à l'heure actuelle, mais aucune ne présente les caractéristiques adéquates pour permettre une délimitation spécifique non ambiguë soit à cause de la très faible divergence interspécifique que montrent les séquences des taxons sous étude (Chapitre 2), soit, à l'inverse, à cause de l'existence de divergences intraspécifiques (Takabayashi et al. 2006).

A l'échelle mondiale, Veron et al. (2015) donne un aperçu de la distribution spécifique des coraux hermatypiques en se basant sur des observations qui couvrent 845 espèces de scléractiniaires sur 4941 sites dans 85 écorégions coralliennes sur les 150 estimés dans le monde. Les auteurs ont clairement noté la difficulté de l'identification des espèces et de l'incongruence de certaines données d'une région à l'autre. L'épicentre de la diversité spécifique des scléractiniaires se situe dans le triangle corallien (traduit de « Coral triangle ») qui définit la région tropicale incluant l'Indonésie, la Malaisie, la Papouasie Nouvelle-Guinée, les Philippines et les îles Salomon (Hoegh-Guldberg et al. 2009). Des sanctuaires secondaires de la diversité des scléractiniaires ont été identifiés dans la Mer Rouge et dans la région Nord de Madagascar (Veron et al. 2015). Contrairement aux régions Pacifique et aux Caraïbes, l'Océan Indien ne présente pas de division latitudinale bien distincte, mais plutôt une bande de diversité élevée sur toute la région (Sheppard 1998). Une étude récente rapporte trois cent soixante-neuf espèces réparties dans l'ouest de l'Océan Indien, avec un maximum de diversité spécifique de 297 rencontré à Nacala, Mozambique et un minimum de 174 à Farquhar, Seychelles (Obura 2012). En outre, cette même étude classe les sites suivants, dans l'ordre décroissant, selon la richesse spécifique observée : Pemba (Mozambique), Mafia et Mnazi (Tanzanie), Mayotte (France), Vamizi (Mozambique), Songo (Tanzanie), KenyaS (Kenya), Nosy Hara (Madagascar), Chagos (Royaume – Unis), les Comores, Amirantes et Aldabra (Seychelles), Glorieuse et La Réunion (France), Lamu (Kenya), Djibouti, Saint Brandon (Maurice) et Kiunga (Kenya). Toutefois, outre la difficulté d'identification, la différence de couverture des sites investigués explique également l'inégalité et la divergence de la diversité d'une région à l'autre ou d'un pays à l'autre.

Dans le sud-ouest de Madagascar, les seules études sur la biodiversité font état de 112 espèces (Pichon 1978, reviewed by Sheppard 1998). L'étude que nous avons réalisée dans cette même région et sur les mêmes sites relate la présente de plusieurs espèces qui n'ont pas été observées 40 ans auparavant (Chapitre 2). Ceci montre également l'importance du facteur « période d'investigation », étant donné que les peuplements de scléractiniaires ne sont pas seulement difficiles à caractériser extemporanément, mais changent constamment de structure en fonction des paramètres climatiques et des paramètres de circulation des masses d'eau.

A l'instar des peuplements adultes, l'identification et la caractérisation du potentiel de recrutement des scléractiniaires sont des aspects encore très difficilement maîtrisés. Ils constituent toutefois aussi un élément important dans la compréhension de la répartition des espèces de scléractiniaires et pour la résilience des récifs coralliens (Lindén et al. 2002 ; Adjeroud et al. 2016). Les méthodes d'investigation pour l'identification des stades jeunes sont de faible résolution et plus difficile à réaliser en fonction du bas âge et du faible stade de développement des coraux. Les larves ne s'observent en général qu'*in situ* et leur identification est encore limitée au niveau de l'ordre, ce qui limite l'évaluation de leur répartition spatiale et temporelle aussi bien au niveau d'un site récifal qu'au niveau d'une région géographique. Nous avons effectué la première investigation sur les planula à Madagascar et cela a permis d'évaluer leur densité aux abords du Grand Récif de Toliara par des prélèvements hebdomadaires. Il a été mis en évidence que les larves s'observent pendant 9 mois avec des densités élevées entre septembre et décembre (Chapitre 3). Bien qu'ils n'aient pas permis une identification taxonomique des planula, les résultats de cette étude correspondent à ce que nous avons observé avec les recrues étudiées au niveau du même récif. L'étude sur les recrues montre par ailleurs que certains sites sont plus facilement colonisés que d'autres (Chapitre 3). Ces deux types de résultats combinés ont également montré un pic de la reproduction sexuée (ponte et fixation des larves) des scléractiniaires sur le GRT entre octobre et décembre. En outre, les résultats ont également évalué la mortalité des coraux au début de leur vie : l'abondance des juvéniles observée représente moins de 10% de l'abondance des recrues. Ces résultats sont probablement sous-évalués car certaines espèces ne se fixent probablement pas sur les substrats artificiels utilisés (Adjeroud et al. 2016). Comparé à d'autres sites de l'Océan Indien, le GRT présente un taux de recrutement (juvéniles) très élevé (Engelhardt 2003). Ce taux très élevé est particulièrement représenté par les espèces branchues appartenant aux familles Acroporidae et Pocilloporidae, qui dominent largement les peuplements des recrues et des juvéniles (Chapitre 3).

Sachant que le recrutement est un facteur déterminant pour la dynamique et la capacité de résilience des peuplements coralliens, les résultats présentés dans cette étude permettent de considérer que les récifs coralliens de la région sud-ouest de Madagascar, en particulier le GRT a une dynamique naturel évolutif et un potentiel de recrutement assez élevé qui pourront offrir une capacité adéquate de restauration des assemblages récifaux. Ceci pourrait aussi ouvrir une porte aux besoins d'une coralliculture villageoise à des fins purement commerciales (satisfaction des besoins du marché de coraux) et à des fins de conservation.

La convention sur le commerce internationale des espèces de faune et de flore menacées d'extinction (Convention on International Trade in Endangered Species of Wild Fauna and Flora – CITES) exige l'utilisation du nom d'espèce dans le processus de commerce. La difficulté d'identifier les coraux implique que des erreurs de classification se produisent dans la compilation des permis CITES (Green et Shirley 1999). Cette situation est préoccupante d'autant plus que les acteurs de la coralliculture et du commerce des coraux ne sont pas forcément des experts en taxonomie des scléractiniaires. Bien que la CITES soit l'unique source de données fiable (Wells et Barzdo 1991), la situation rend très difficile la compilation des données commerciales et leur comparaison avec les informations scientifiques sur la biodiversité et la répartition des scléractiniaires dans chaque écorégion et chaque pays. En 2013, après de multiple discussions sur la standardisation de la nomenclature des classes (dont la classe des Anthozoa entre autres) la CITES a adopté une liste regroupant les espèces pour lesquelles une identification jusqu'au niveau genre est acceptée. Toutefois, les informations enregistrées par la CITES montrent que sur 275 taxons de scléractiniaires enregistrés depuis 1990 (exclusivement des produits aquacoles et vivants), 81.5% ont été enregistrés sous leur nom d'espèce et 18.5% ont été identifiés sous leur nom de genre seulement dont environ 0.4% identifiés comme « *Scleractinia spp.* » (Tableau 19). Depuis les premières investigations et avec notre étude, 126 espèces ont été observées sur le GRT (Pichon 1978 ; Sheppard 1998 ; présente étude), soit 46% du nombre de taxons enregistrés par la CITES. Trente-deux de ces espèces ne figurent pas dans la liste des échanges commerciaux, même pas sous le nom du genre.

Tableau 19: Liste des taxons (espèces) de scléractiniaires commercialisés dans le monde entre 1975 et 2014 (source : CITES 2016). Les noms en gras représentent les espèces (ou groupes taxonomiques) rencontrées sur le GRT. Les noms d'espèce ou de genre inconnus sont enregistrés sous le nom *Scleractinia spp.* QC = Quantité commercialisée (nombre d'individus); PT = Pourcentage par rapport au total

Genre / Espèce	QC	PT	Genre / Espèce	QC	PT	Genre / Espèce	QC	PT
Scleractinia spp.	39614	25.4	***Pocillopora damicornis***	350	0.2	*Acropora spathulata*	150	0.1
Acropora millepora	15723	10.1	*Acropora maryae*	348	0.2	*Euphyllia fimbriata*	150	0.1
Acropora spp.	14293	9.1	***Stylophora pistillata***	347	0.2	*Porites harrisoni*	150	0.1
Montipora spp.	6681	4.3	*Tubastraea spp.*	339	0.2	*Seriatopora spp.*	150	0.1
Acropora microclados	5588	3.6	*Astrocoeniidae spp.*	330	0.2	*Turbinaria frondens*	150	0.1
Acropora formosa	4633	3.0	***Stylophora spp.***	325	0.2	*Echinophyllia spp.*	146	0.1
Euphyllia ancora	4448	2.8	*Acropora austera*	320	0.2	*Acropora hoeksemai*	145	0.1
Acropora latistella	3700	2.4	*Montipora digitata*	315	0.2	***Dendrophyllia spp.***	138	0.1
Euphyllia glabrescens	3465	2.2	*Acropora desalwii*	314	0.2	*Acropora gemmifera*	137	0.1
Acropora tenuis	3199	2.0	*Acropora yongei*	272	0.2	*Hydnophora spp.*	135	0.1
Acropora aculeus	3198	2.0	*Acropora abrolhosensis*	259	0.2	*Acropora aspera*	130	0.1
Goniopora spp.	2668	1.7	*Euphyllia paraancora*	252	0.2	***Echinopora lamellosa***	128	0.1
Acropora echinata	1660	1.1	*Fungia spp.*	251	0.2	***Favites spp.***	127	0.1
Acropora loripes	1647	1.1	*Heliofungia actiniformis*	249	0.2	***Acropora abrotanoides***	126	0.1
Acropora granulosa	1598	1.0	***Pocillopora verrucosa***	249	0.2	*Acropora selago*	126	0.1
Hydnophora rigida	1585	1.0	*Acropora caroliniana*	232	0.1	*Acropora suharsonoi*	126	0.1
Acropora divaricata	1584	1.0	*Acropora papillare*	227	0.1	*Acropora pulchra*	124	0.1
Caryophyllia corrugata	1523	1.0	*Caulastraea furcata*	225	0.1	*Acropora chesterfieldensis*	117	0.1
Caryophyllia capensis	1516	1.0	***Acropora nobilis***	217	0.1	*Montipora danae*	116	0.1
Acropora insignis	1511	1.0	*Acropora plana*	216	0.1	*Caulastraea curvata*	115	0.1
Acropora humilis	1313	0.8	*Acropora carduus*	215	0.1	***Plerogyra spp.***	115	0.1
Acropora secale	1287	0.8	***Porites spp.***	215	0.1	***Goniastrea spp.***	114	0.1
Acropora cerealis	1245	0.8	*Dendrophyllia robusta*	200	0.1	***Porites nigrescens***	105	0.1
Acropora subulata	1223	0.8	*Trachyphyllia spp.*	199	0.1	*Acropora cylindrica*	100	0.1
Acropora polystoma	1152	0.7	***Acropora robusta***	197	0.1	*Euphyllia paradivisa*	99	0.1
Acropora nasuta	965	0.6	*Montipora aequituberculata*	190	0.1	***Acropora digitifera***	95	0.1
Acropora valida	916	0.6	***Merulina ampliata***	187	0.1	***Echinopora spp.***	95	0.1
Turbinaria spp.	861	0.6	*Plerogyra simplex*	185	0.1	*Goniopora lobata*	91	0.1
Acropora rosaria	815	0.5	*Acropora florida*	179	0.1	***Turbinaria peltata***	91	0.1
Acropora horrida	811	0.5	***Goniopora stokesi***	179	0.1	*Galaxea spp.*	90	0.1
Acropora parilis	732	0.5	*Acropora hemprichii*	178	0.1	***Montipora verrucosa***	89	0.1
Plerogyra sinuosa	667	0.4	*Blastomussa wellsi*	177	0.1	*Acropora prostrata*	87	0.1
Seriatopora hystrix	662	0.4	*Acropora palmerae*	173	0.1	*Acropora gomezi*	85	0.1
Caulastraea spp.	660	0.4	*Catalaphyllia jardinei*	172	0.1	*Acropora palifera*	85	0.1
Pocillopora spp.	660	0.4	*Acropora turaki*	169	0.1	*Montipora spongodes*	84	0.1
Acropora efflorescens	609	0.4	***Seriatopora caliendrum***	169	0.1	*Catalaphyllia spp.*	81	0.1
Acropora microphthalma	561	0.4	*Acropora grandis*	168	0.1	***Platygyra spp.***	81	0.1
Agaricia agaricites	541	0.3	*Acropora kimbeensis*	162	0.1	*Acropora navini*	80	0.1
Lobophyllia spp.	441	0.3	*Acropora roseni*	162	0.1	*Montipora hispida*	80	0.1
Acropora hyacinthus	401	0.3	*Favia spp.*	161.5	0.1	*Scolymia spp.*	79	0.1
Montipora foliosa	396	0.3	***Galaxea fascicularis***	158	0.1	*Balanophyllia floridana*	75	0.0
Trachyphyllia geoffroyi	387	0.2	***Pavona cactus***	157	0.1	*Montipora tuberculosa*	74	0.0
Euphyllia spp.	383	0.2	*Duncanopsammia axifuga*	156	0.1	*Acropora cophodactyla*	70	0.0
Acropora nana	377	0.2	*Acanthastrea amakusensis*	150	0.1	*Montipora mollis*	70	0.0
Euphyllia cristata	371	0.2	*Acanthophyllia deshayesiana*	150	0.1	*Turbinaria reniformis*	69	0.0
Acropora anthocercis	363	0.2	*Acropora downingi*	150	0.1	***Turbinaria mesenterina***	66	0.0

Tableau 19 (suite)

Genre / Espèce	QC	PT	Genre / Espèce	QC	PT	Genre / Espèce	QC	PT
Acropora jacquelineae	64	0.0	*Favia pallida*	21	0.0	***Montipora informis***	8	0.0
Fungia fungites	61	0.0	*Montipora venosa*	20	0.0	*Acropora glauca*	7	0.0
Acropora fenneri	60	0.0	*Mycedium robokaki*	20	0.0	*Acropora sarmentosa*	7	0.0
Porites cylindrica	58	0.0	*Favites chinensis*	19	0.0	*Pachyseris spp.*	7	0.0
Trematotrochus corbicula	58	0.0	*Montastrea cavernosa*	19	0.0	*Acropora elegantula*	6	0.0
Goniopora minor	56	0.0	*Acropora valenciennesi*	18	0.0	***Acropora pharaonis***	6	0.0
Caulastraea tumida	55	0.0	*Acropora vaughani*	18	0.0	*Acropora simplex*	6	0.0
Acropora loisetteae	54	0.0	*Hydnophora grandis*	18	0.0	*Acropora tenella*	6	0.0
Fungia paumotensis	51	0.0	***Lobophyllia hemprichii***	18	0.0	***Blastomussa spp.***	6	0.0
Acropora solitaryensis	50	0.0	*Paraclavarina triangularis*	18	0.0	*Cynarina spp.*	6	0.0
Euphyllia yaeyamaensis	50	0.0	*Montipora peltiformis*	17	0.0	*Montipora capitata*	6	0.0
Acanthastrea spp.	47	0.0	***Tubastraea coccinea***	17	0.0	*Pavona venosa*	6	0.0
Acropora tortuosa	46	0.0	*Acropora awi*	16	0.0	*Pectinia paeonia*	6	0.0
Pectinia spp.	46	0.0	***Astreopora spp.***	16	0.0	*Acropora danai*	5	0.0
Acropora branchi	43	0.0	***Hydnophora exesa***	16	0.0	*Acropora intermedia*	5	0.0
Acropora parahemprichii	40	0.0	*Polyphyllia talpina*	16	0.0	*Acropora paniculata*	5	0.0
Heliofungia spp.	38	0.0	***Echinophyllia aspera***	15	0.0	***Acropora retusa***	5	0.0
Mycedium spp.	37	0.0	*Acropora schmitti*	14	0.0	*Acropora striata*	5	0.0
Blastomussa merleti	35	0.0	*Montastrea annularis*	14	0.0	*Acropora vermiculata*	5	0.0
Acropora subglabra	34	0.0	***Acropora samoensis***	13	0.0	*Montipora hirsuta*	5	0.0
Merulina spp.	33	0.0	***Alveopora spp.***	13	0.0	*Plerogyra turbida*	5	0.0
Polyphyllia spp.	33	0.0	*Fungia moluccensis*	13	0.0	*Porites astreoides*	5	0.0
Pocillopora meandrina	32	0.0	***Galaxea astreata***	13	0.0	*Acropora listeri*	4	0.0
Australogyra spp.	31	0.0	***Montipora undata***	13	0.0	*Acropora monticulosa*	4	0.0
Euphyllia divisa	31	0.0	*Porites porites*	13	0.0	*Dendrophyllia ramea*	4	0.0
Montipora samarensis	31	0.0	*Acropora elegans*	12	0.0	***Hydnophora microconos***	4	0.0
Stephanocyathus spp.	30	0.0	*Acropora verweyi*	12	0.0	***Leptastrea spp.***	4	0.0
Cynarina lacrymalis	29	0.0	*Montipora spumosa*	12	0.0	*Notocyathus conicus*	4	0.0
Acropora variolosa	28	0.0	*Acropora kosurini*	11	0.0	***Tubastraea micranthus***	4	0.0
Caulastraea echinulata	28	0.0	*Acropora lokani*	11	0.0	*Acropora exquisita*	3	0.0
Pavona spp.	28	0.0	*Acropora multiacuta*	11	0.0	*Montastrea spp.*	3	0.0
Acropora longicyathus	27	0.0	***Symphyllia spp.***	11	0.0	*Acropora rudis*	2	0.0
Acropora walindii	27	0.0	*Acropora copiosa*	10	0.0	*Acropora tizardi*	2	0.0
Eguchipsammia fistula	27	0.0	*Acropora globiceps*	10	0.0	***Heterocyathus spp.***	2	0.0
Physogyra lichtensteini	27	0.0	*Alveopora spongiosa*	10	0.0	*Montastrea annuligera*	2	0.0
Lobophyllia corymbosa	26	0.0	*Deltocyathoides orientalis*	10	0.0	*Montipora stellata*	2	0.0
Oxypora spp.	26	0.0	***Favites abdita***	10	0.0	*Montipora turgescens*	2	0.0
Acropora natalensis	24	0.0	***Leptoseris spp.***	10	0.0	***Pachyseris rugosa***	2	0.0
Montipora monasteriata	24	0.0	*Montastrea valenciennesi*	10	0.0	***Pachyseris speciosa***	2	0.0
Mycedium elephantotus	24	0.0	*Montipora confusa*	10	0.0	*Acropora pichoni*	1	0.0
Acropora acuminata	23	0.0	*Platytrochus spp.*	10	0.0	*Goniopora djiboutiensis*	1	0.0
Acropora speciosa	23	0.0	*Acropora macrostoma*	9	0.0	*Merulina scabricula*	1	0.0
Montipora capricornis	23	0.0	*Australomussa rowleyensis*	9	0.0	*Montipora saudii*	1	0.0
Acrhelia spp.	22	0.0	***Physogyra spp.***	9	0.0	*Montipora solanderi*	1	0.0
Pavona maldivensis	22	0.0	*Acropora batunai*	8	0.0	*Oxypora glabra*	1	0.0
Acropora donei	21	0.0	*Acropora elseyi*	8	0.0			

Tableau 20: Liste des espèces rencontrées sur le GRT qui ne figurent pas sur la liste des taxons commercialisés

Astrea curta	*Gyrosmilia interrupta*	*Plesiastrea versipora*
Culicia cuticulata	*Halomitra pileus*	*Pleuractis paumotensis*
Cycloseris cyclolites	*Herpolitha limax*	*Podabacia crustacea*
Cycloseris distorta	*Horastrea indica*	*Polycyathus sp.*
Cycloseris somervillei	*Isopora palifera*	*Psammocora contigua*
Cyphastrea chalcidicum	*Leptoria phrygia*	*Psammocora haimiana*
Cyphastrea microphthalma	*Lithophyllon repanda*	*Psammocora verrilli*
Danafungia horrida	*Oulophyllia sp.*	*Siderastrea radians*
Diploastrea heliopora	*Oulophyllia crispa*	*Sphenotrochus sp.*
Dipsastraea favus	*Paracyathus sp.*	*Stylocoeniella guentheri*
Dipsastraea pallida	*Parascolymia vitiensis*	

6.2 Coralliculture villageoise, une aquaculture socio-écologique au potentiel économique réel mais limité

Il est clair qu'une diversité corallienne élevée et un potentiel de recrutement important sont des paramètres favorables pour développer dans un endroit une coralliculture villageoise. La sélection des sites d'aquaculture propices est aussi un paramètre primordial et doit être couplé par l'utilisation de techniques de culture simples, peu coûteuses et accessibles aux principaux exploitants des récifs coralliens, dans notre cas, les communautés de pêcheurs traditionnels.

La plupart des premiers pays producteurs de coraux d'aquaculture pratiquent cette activité dans des sites à faible profondeur. A Palau Serangan (Bali, Indonésie), la ferme entretenue par une trentaine de villageois se situe dans une baie de surface d'environ 150000 m^2 et couvre une zone de 30000 m^2, soit environ 3 hectares. A marée basse, les boutures de coraux sont à 10 – 30 cm en dessous de la surface de l'eau. Sable, débris coralliens, herbiers et algues dominent le fond marin dans cette baie. Ces caractéristiques sont similaires aux principaux sites d'aquaculture de coraux impliquant la participation des villageois (*e.g.,* aux îles Salomon, Albert et al. 2012 ; Hawaï, Delbeek 2001) et sont suggérés pour des projets de coralliculture dans le sud-ouest de Océan Indien, particulièrement à Maurice (Nazurally et Rinkevich 2013).

A Madagascar, plusieurs sites répondent à ces conditions et au moins un a déjà montré la faisabilité de la coralliculture (site de Nosy Ankao, près d'Antsiranana, 12°48'S – 49°49'E). Dans la Région sud-ouest de l'île, la baie de Ranobe et la baie de Tuléar présentent des caractéristiques favorables à cette activité. Les sites favorables dans la baie de Tuléar, particulièrement au niveau du village de Sarodrano couvrent une zone très large de plus de 100 hectares (Figure 42). Les sites proposés ici se situent à moins de 5 minutes en pirogue du village de Sarodrano et moins de 20 minutes des autres villages autours. La profondeur de l'eau varie entre 3 et 5 m à marée haute (~1 m à marrée basse) ce qui facilite le travail des villageois sur les installations à marée basse et ce qui permet d'éviter une surexposition des boutures à l'intensité de la lumière solaire et à une chaleur excessive pendant les marées basses de vives eaux.

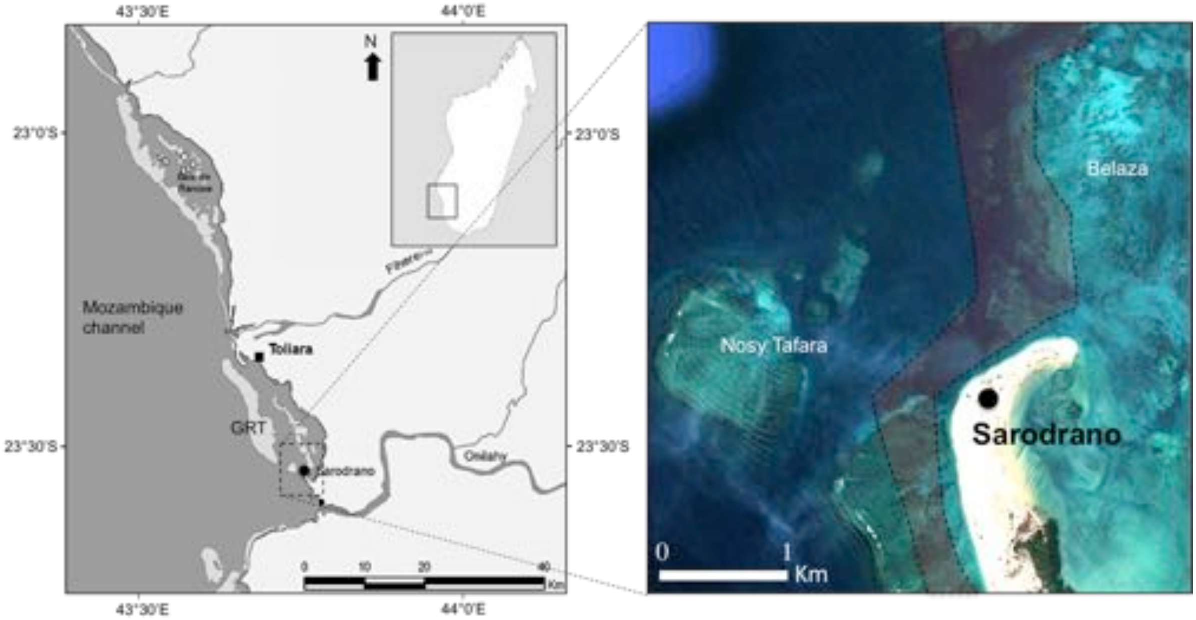


Figure 42: Sites propices à la coralliculture villageoise près du village de Sarodrano, Madagascar. La zone comprise dans la bande rouge est à la fois propice à la coralliculture et facilement accessible aux villageois.

Le bouturage est la technique la plus utilisée en coralliculture. Il consiste à replanter un fragment de corail de 1 cm à 10 cm préalablement extrait d'une colonie mère, sur un support de nature variable. Les supports en ciment (Albert et al. 2012) ou en morceaux de squelette de coraux morts (Ellis et Ellis 2002, Main et al. 2006) sont les plus communément utilisés. Il existe plusieurs façons de fixer les boutures sur leur support mais les plus utilisés sont la résine époxy bi-composant, la colle cyanoacrylate (super glue), le ciment prompt avec du mastic époxy (Ellis et Ellis 2002 ; Shafir et al. 2006) et des élastiques. Les supports avec les boutures fixées sont ensuite fermement arrimés à une table métallique dont la forme et la taille dépendent de l'ampleur de la ferme, de la circulation de l'eau sur le site et de la forme des supports des boutures.

Le choix des matériaux utilisés est fonction de l'ampleur et de la taille de la production. En coralliculture villageoise, notamment celle de Madagascar, afin d'être le plus économique possible, les matériels et surtout les consommables doivent être disponible sur le marché local. La confection des tables de coralliculture est assez facile, sachant qu'une table d'environ 1 m^2, haute de 1 m et qui peut supporter 100 boutures coute environ € 15. En ajoutant les coûts des supports de bouture, les systèmes de fixation et les accessoires nécessaires au bouturage et à la maintenance des installations, le coût des fournitures par bouture s'élève à € 0,22. Cela représente moins de 5% du coût de production unitaire d'une bouture qui s'élève à € 25 pour une vente d'un peu moins de 100 boutures par mois, et qui serait profitable pour un investisseur à partir de la troisième année (Chapitre 5). Ce coût de production est similaire au coût calculé pour les producteurs villageois aux Îles Salomon entre 2000 et 2004 (Lal et Kinch 2005). La coralliculture dans ce pays a été estimé non viable avec une production et vente en faible quantité (~1500 boutures en 2 ans). Elle devient profitable aux villageois seulement lorsque la taille de la production est doublée. Dans ce système, les villageois gagnent moins de € 1 par bouture. Cela représente 1 à 5% du prix final des boutures aux détaillants. Les exportateurs qui s'occupent de la préparation des boutures et de leur envoi aux grossistes perçoivent 5 à 10%. Le reste revient aux grossistes qui en retireront les coûts investis dans le fonctionnement de leur aquarium. Ce coût peut s'élever jusqu'à plus de € 30 par bouture, investissement compris (*e.g.,* pour *Seriatopora caliendrum*, Osinga et al. 2011).

La coralliculture villageoise est viable à petite échelle si chaque partie prenante du commerce, notamment les villageois (producteurs), les exportateurs et les vendeurs (grossistes et détaillants) gagne un profit à la hauteur du temps de travail et des investissements. Le passage par un grossiste qui doit investir beaucoup dans les installations *ex situ* augmente considérablement le coût de production par bouture. L'idée adoptée ici est d'exporter directement les coraux aux détaillants ou simplement au prix du détaillant ce qui éliminerait les coûts colossaux des aquariums et augmenterait le profit des exportateurs. Le profit serait plus marqué en considérant que l'activité soit une alternative au lieu d'être une activité principale (Figure 43). A Madagascar, l'idée est d'intégrer la coralliculture en tant qu'activité additionnelle à l'holothuriculture et l'algoculture. Ce système, commencé en 2008, a comme objectif de développer la polyaquaculture villageoise impliquant les communautés de pêcheurs, les autorités administratives, les institutions de recherche publique (Universités), les entreprises privées et les organisations non-gouvernementales (ONGs) qui sont regroupés dans une plateforme de travail (Pascal et al. 2013). Au départ, la première installation du matériel et le bouturage d'un grand nombre de coraux peuvent nécessiter plus de 2 heures de travail pendant 2 à 3 jours. Ensuite, l'entretien d'une dizaine d'installations aquacoles (tables de coralliculture) ne nécessite pour un fermier qu'un travail d'environ 1 heure par jour pendant 2 ou 3 jours pendant les périodes de vives eaux (toutes les deux semaines), soit moins de 6 heures par mois. Ce système permet également de réduire considérablement les coûts liés aux installations nécessaires à la préparation des boutures pour l'exportation et les frais du personnel sachant que chaque partie prenante en dispose déjà en grande partie à travers leurs autres activités de production (entreprises privés) ou de recherches (Universités).

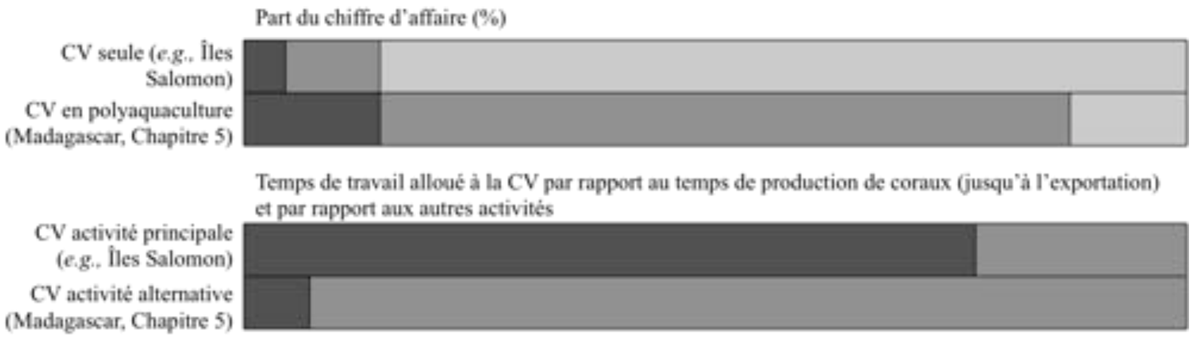


Figure 43: Différence de profit entre la coralliculture villageoise (CV) seule comme activité principale et la coralliculture villageoise en polyaquaculture (activité alternative). Gris foncé : Villageois ; Gris : Exportateurs (plateforme de travail dans le cas de la polyaquaculture) ; Gris clair : Grossistes.

6.3 Coralliculture villageoise : une place sur un marché international ?

L'accès au marché est un des plus grands défis pour une coralliculture villageoise à petite échelle. Le marché de coraux vivant existe, mais elle reste assez restreint à cause des exigences techniques liées à la biologie des ces animaux très sensibles. Le plus grand exportateur de coraux sont les Îles Marshall (Figure 44) mais la plupart des pays exportateurs appartiennent au triangle corallien (« Coral Triangle »). Vingt et un pays importent des scléractiniaires vivants en provenance d'aquaculture (Figure 45). Les Etats-Unis d'Amériques (USA) sont les premiers importateurs avec un total de 116 845 pièces importées entre 1990 et 2014 (Données CITES 2016). Les données entre 2009 et 2013 classent dans un ordre décroissant d'importance après les USA, le Brésil, le Canada, le Danemark, Singapour, les Pays-bas, l'Afrique du Sud, Hong Kong, la Chine et l'Irlande.

L'aquaculture de coraux est une filière en développement depuis les années 1990 (Figure 46). Toutefois, elle représente encore moins de 20% du volume total de commerce de coraux vivants (incluant les coraux élevés en captivités et les coraux nés en captivités). La coralliculture villageoise est une forme d'aquaculture qui a commencée à se développer depuis moins de 20 ans dans les principaux pays exportateurs tels que les îles Salomon et Palau (Green et Shirley 1999, Albert et al. 2012). Dans l'Océan Indien, cette pratique est seulement en phase d'expérimentation (*e.g.,* à Maurice ; Nazurally et Rinkevich 2013 ; à Madagascar, présent travail). A Madagascar, la coralliculture est profitable en tant qu'activité additionnelle par rapport aux autres activités alternatives à la pêche telles que l'holothuriculture et l'algoculture (Pascal et al. 2013). Pour se développer, elle doit se présenter comme un élément de la polyaquaculture villageoise qui est en essai dans certains villages. Par ailleurs, la coralliculture villageoise est une forme d'aquaculture éthique et elle est un nouvel outil de sensibilisation pour la protection des récifs coralliens. Les résultats des enquêtes de perception au niveau du village pilote de Sarodrano ont montré que les coraux ont toujours été considérés par les pêcheurs comme des pierres mais pas des organismes vivants jusqu'à ce que la présente recherche y ait été introduite et que les expérimentations leur ont prouvés la croissance des scléractiniaires sur les tables de coralliculture.

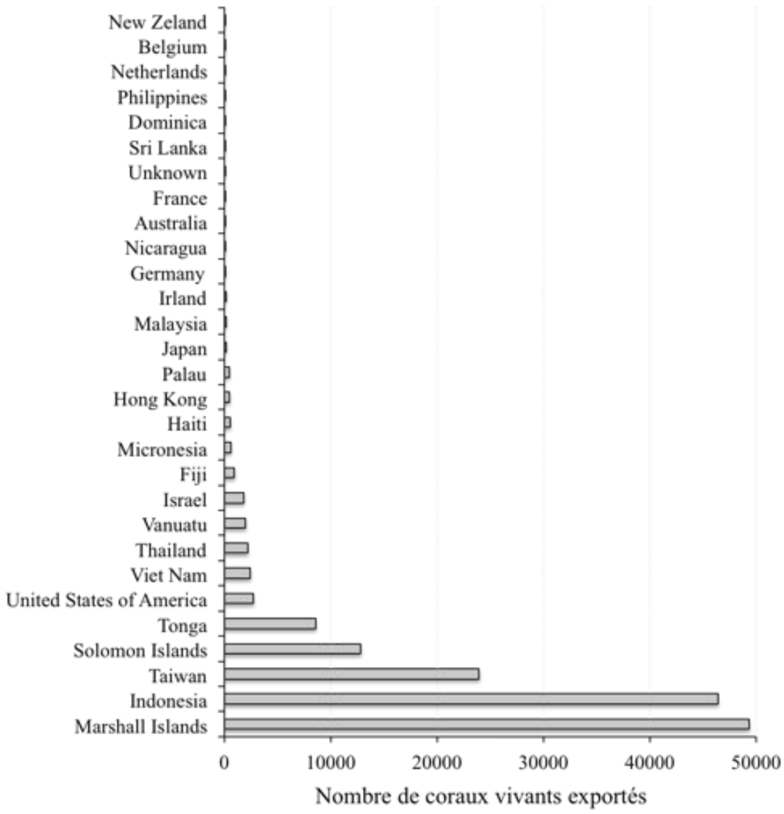


Figure 44: Nombre de scléractiniaires d'origine aquacole exportés par pays producteurs entre 1975 et 2014 (source : CITES 2016).

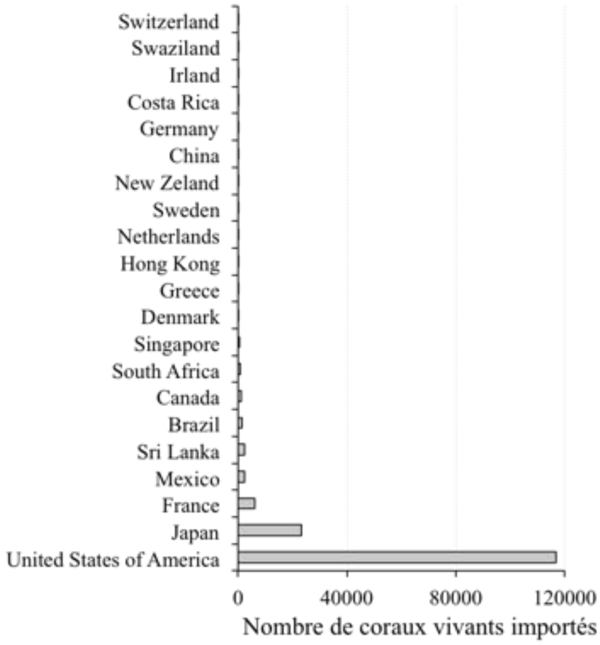


Figure 45: Les pays importateurs de coraux scléractiniaires vivant en provenance d'aquaculture (Source : CITES 2016).

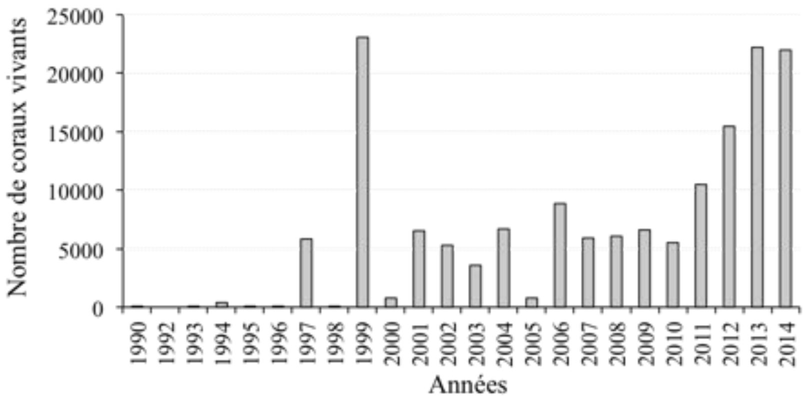


Figure 46: Volume du commerce de coraux provenant de l'aquaculture au fil du temps (Source : CITES 2016)

A quelques exceptions près, tous les pays importateurs ont une économie florissante. Bien que les données concernant l'utilisation finale de ces coraux soient manquantes, l'existence et le dynamisme de centaines de sites internet et de forums d'aquariophiles nous renseignent sur l'importance de la part de l'aquariophilie dans ce marché. Avec le développement de la recherche et l'avènement des multiples actions pour lutter contre le changement climatique, d'autres débouchés pourraient voir le jour et engager aussi bien les pays développés que les pays en voie de développement parmi lesquels figurent la plupart des pays insulaires bordés de plusieurs centaines de milliers d'hectares de récifs coralliens. Les débouchés économiques alternatifs à l'aquariophilie sont le repeuplement des récifs naturels à travers la transplantation de la même manière que les reboisements forestiers (Lindahl 1998 ; Cros et McClanahan 2003) ou la recherche médicale (Tableau 21). La création de jardin récifaux artificiels avec des coraux vivants est également une pratique en gestation et prometteuse pour le développement du tourisme écologique (écotourisme). Actuellement, les programmes de repeuplement coralliens sont beaucoup moins développés et financés que le reboisement forestier. Par ailleurs, les ONGs constituent les plus proches interlocuteurs au niveau des communautés et l'existence de plateformes de travail avec les autres acteurs tels que les Universités, les entreprises privées et les autorités administratives publiques devrait constituer un avantage pour le développement de la coralliculture villageoise.

Tableau 21: Principaux débouchés potentiels de la coralliculture

Utilisations des coraux	Etat de développement de l'activité	Principaux acheteurs	Références
Aquarium domestique (coraux vivant et morts)	En développement constant dans les pays développés	Magasins d'aquarium, particuliers	Delbeek 2001
Aquariums publics, hôtels	En développement discret	Aquariums publics, Hôtels	Shafir et Rinkevich 2008
Jardin corallien (tourisme)	A développer	ONGs	Symes 2010
Transplantation, conservation	En développement discret	ONGs	Spurgeon et Lindahl 2003, Hernández-Delgado et al. 2014
Molécules bioactives (recherche)	Naissante et prometteuse	Universités, centre de recherche pharmaceutiques	Shafir et al. 2006, Leal et al. 2013

Quel que soit le débouché et le pays concernés, les procédures administratives, bien que nécessaires pour lutter contre une exploitation non raisonnée, forment un frein au commerce de coraux d'aquaculture. Etant donné que ces animaux sont inscrits en Annexe 2 de la CITES, une autorisation de la part de celle-ci et plusieurs autres documents délivrés par les autorités compétentes de chaque pays exportateurs et importateurs sont indispensables (Delbeek 2008). Par ailleurs, l'obtention des autorisations requises ne suffit pas pour assurer une exportation/importation de coraux vivants. Des règles internationales sur le transport d'animaux vivants sont à respecter et chaque compagnie de transport dispose de ses propres exigences techniques ou administratives. Ainsi, avant de lancer une exportation, ou même avant de lancer une coralliculture, il est primordial de se renseigner et de se conformer à toutes les procédures requises.

Les contraintes techniques et biologique liées au transport des coraux sont également importantes et constituent aussi un frein au développement de la coralliculture surtout si le transport nécessite un envoi vers un pays lointain. A l'heure actuelle, la durée maximale du transport de coraux vivants ne dépasse pas 30 heures ; au-delà de ce temps, la mortalité post-transport est très élevée, voire totale. Malgré quelques différences sur les détails en fonction de la taille des colonies transportées, les types de transport restent similaires pour toutes les espèces, en utilisant la méthode sèche ou immergée avec de l'oxygène 100% et de l'eau de mer filtrée dont le volume et la concentration diffèrent selon la durée estimée du transport (Delbeek 2008). Cet aspect de la filière constitue également une grande partie des coûts de production. L'obtention d'un taux de mortalité post-transport de 0% est souvent la clé de la viabilité économique d'une coralliculture.

Les résultats de nos études sur l'effet du volume d'eau, de la concentration en oxygène et de l'intensité de la lumière sur la physiologie des boutures de *Seriatopora hystrix* ont démontré qu'il était possible d'améliorer la résistance des boutures au transport et d'augmenter le temps de transport jusqu'à 72 heures sans utiliser de l'oxygène concentré (Chapitre 4).

Par ailleurs, la technique élimine complètement le coût de l'utilisation de l'oxygène 100% qui rend le transport coûteux. Elle constitue une marge de sécurité pour les transports classiques sachant que le retard ou l'annulation de vol arrive parfois. En outre, elle peut être très pratique pour les pays très éloignés des importateurs, notamment la plupart des îles de l'Indo-Pacifique. La durée des vols depuis les principaux pays exportateurs du Pacifique vers l'importateur majoritaire, les Etats-Unis d'Amérique varie entre 13 et 20 heures, tandis que celle des vols vers l'Europe peut atteindre 25 heures (*e.g.,* : de Vanuatu vers la France). Sachant que la durée du transport est un élément crucial dans le commerce de coraux vivant, cela peut expliquer le relativement faible volume de transaction entre ces exportateurs du Pacifique et les pays de l'Europe par rapport aux pays de l'Amérique et du Japon (Figure 45). Un transport aérien de plus de 20 heures implique que la durée totale du transport des coraux incluant la préparation et les temps d'attente aux aéroports, peut atteindre 30 heures. Par ailleurs, les îles de l'Océan Indien sont beaucoup plus proches des importateurs européens que des autres importateurs ce qui représente un débouché potentiel pour ces îles.

6.4 Conclusion et perspectives

En conclusion, nous avons analysé les forces et les faiblesses de la coralliculture villageoise pour son développement dans le sud-ouest de Madagascar.

Biologiquement, la croissance des coraux est telle que des villageois aquaculteurs peuvent obtenir un revenu tout les mois ou tous les 5 à 8 mois selon le système de gestion adopté par la plateforme de travail, selon le rythme et la quantité de boutures prises en charge (Chapitre 5). Par ailleurs, leurs exigences vitales sont telles que des conditions environnementales particulières sont nécessaires pour une croissance adéquate ce qui limite leur exploitation au niveau des côtes. Ces exigences impliquent aussi à l'heure actuelle des limites aux temps d'exportation et donc à la distance à laquelle ces coraux peuvent être exportés. Socialement, la coralliculture est tout d'abord un moyen éducatif grâce auquel les villageois peuvent se rendre compte de la nature vivante du corail et de l'importance économique que le récif corallien joue. La coralliculture villageoise ne pourra par ailleurs se développer que si les villageois y voient un intérêt financier : comme pour l'algoculture et l'holothuriculture, une diminution du rendement économique est souvent accompagnée d'un abandon de l'aquaculture et d'un retour vers les activités de pêche traditionnelle. Economiquement, notre étude démontre la faisabilité d'une coralliculture villageoise à petite échelle qui s'intègre très bien dans le schéma global du développement de la polyaquaculture villageoise.

Dans l'absolu, et peut être de manière un peu utopique, il faut espérer pouvoir renverser la tendance générale qui concerne la dégradation généralisée des récifs coralliens à la manière de ce qui est illustré sur la Figure 47. Depuis plus de 40 ans, les pressions anthropiques et les changements climatiques ont perturbé l'écosystème que forment les récifs coralliens en affectant leur surface vivante et leur biodiversité et en diminuant les possibilités de recrutement des coraux. Les pêcheurs villageois participent malheureusement grandement à cette pression anthropique, directement par la pêche effectuée à pied ou indirectement par la diminution des poissons brouteurs d'algues en utilisant des filets de senne. Changer les habitudes des pêcheurs villageois en leur proposant des moyens alternatifs à la pêche traditionnelle diminuerait ces pressions si ces pratiques se généralisaient. En particulier, dans le cas où on pourrait voir se développer la coralliculture villageoise grâce au développement de divers débouchés économiques (programme de repeuplement, développement de produits utilisés en médecine), le marché de la vente des coraux pourrait se développer de manière éthique et favoriser le repeuplement des récifs.

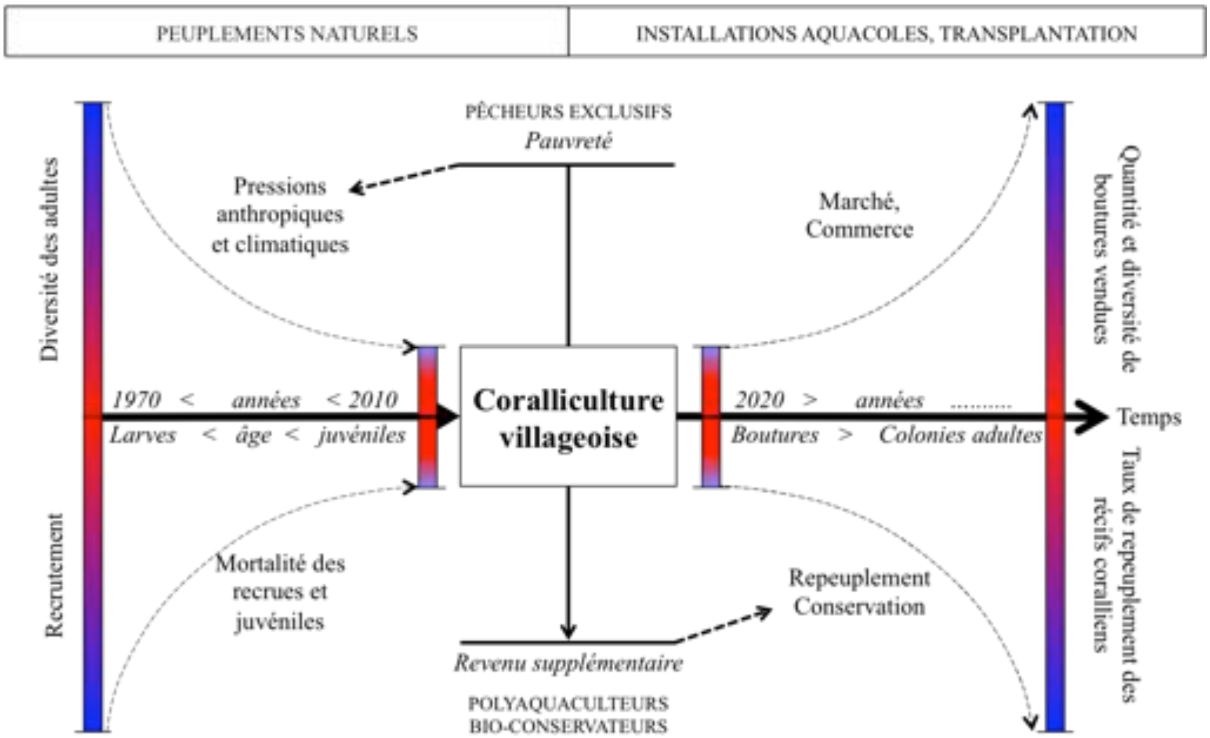


Figure 47: Intérêts bio-écologique et socio-économique de la coralliculture villageoise. Bleu : niveau élevé, Rouge : niveau critique

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Terrana L, Caulier G, **Todinanahary** G. Lepoint G, Eeckhaut I (2016) Characteristics of the infestation of Seriatopora corals by the coral gall crab Hapalocarcinus marsupialis Stimpson, 1859 on the Great Reef of Toliara, Madagascar. Symbiosis [DOI: 10.1007/s13199-016-0391-1]

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Conférences scientifiques et workshops

Décembre 2015 : Symposium International sur la « Dynamics of Indian Ocean, Perspective and Retrospective », Goa, Inde

Octobre 2015 : 9ème Symposium scientifique international de WIOMSA, Port Edward, Afrique du Sud. Présentation poster et Organisation d'un Atelier sur « Coral reef : a common heritage ? »

Août 2015 : Conférence International Aquaculture 2015, Montpellier, France. Présentation orale

Octobre 2015 : 8ème Symposium scientifique international de WIOMSA, Port Edward, Afrique du Sud. Posters

Novembre 2014: Advanced course on Basics of Taxonomy, describing, illustrating and writing biodiversity. WIOMSA/CEPAM, Pemba Mozambique

Octobre 2014: Ecole d'Eté Australe sur la Vulnérabilité du Patrimoine Récifal. IRD/IH.SM, Université de Toliara, Madagascar

Juillet 2012: Ecole internationale d'été des jeunes créateurs de coopératives. Campus coopératives, Université de Poitiers, France

Mars 2012: Marine GIS application using ArcGIS, avec IODE/IOC-UNESCO, Ostende, Belgique

Octobre – Novembre 2011 : Outreach and communication Tools, avec IODE/IOC-UNESCO, Ostende, Belgique

Juillet 2011: International Water Association, PUB - Singapore International Water Week: Water Convention. Singapour

Novembre 2010: IUCN - Scientific and Capacity-Building Workshop, The South African Institute of Aquatic Biodiversity (SAIAB), Grahamstown, South Africa

Liste des annexes

Annexe 1:

Todinanahary GGB, Terrana L, Tsiresy G, Eeckhault I, Lavitra T (2016) First records of illegal harvesting and trading of black corals (Antipatharia) in Madagascar. Journal of Madagascar Conservation and Developpement, 11: 1 [DOI: 10.4314/mcd.v11i1.5]

Annexe 2: Les reserves marines de la région sud-ouest de Madagascar (Todinanahary et al. 2013)

Annexe 3: Supplementary material for “Chapitre 3”: Photographs of scleractinian at the different development stage

Annexe 4: Supplementary material for “Chapitre 5”: Questions asked during the survey for the analysis of the coral market

Annexe 5:

Terrana L, Caulier G, **Todinanahary** G. Lepoint G, Eeckhaut G (2016) Characteristics of the infestation of Seriatopora corals by the coral gall crab Hapalocarcinus marsupialis Stimpson, 1859 on the Great Reef of Toliara, Madagascar. Symbiosis [DOI: 10.1007/s13199-016-0391-1]

Annexe 6: Summary of the costs of the value chain for coral aquaculture

Annexe 7: Analysis of Variance Tables corresponding to statistical tests in Chapitre

Annexe 1

Todinanahary GGB, Terrana L, Lavitra T, Eeckhault I (2016) First records of illegal harvesting and trading of black corals (Antipatharia) in Madagascar. Journal of Madagascar Conservation and Developpement, 11: 1 [DOI: 10.4314/mcd.v11i1.5]

ARTICLE

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First records of illegal harvesting and trading of black corals (Antipatharia) in Madagascar

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ABSTRACT

Black corals (Cnidaria: Antipatharia) have been used all around the world for a long time, whether as money or for medicinal purposes and jewellery manufacturing. Except in Hawaii where these fisheries are well known, black coral harvests are usually made without any control or any management. This is the case in many tropical islands and particularly in Madagascar, where the illegal trade is continually expanding. Since 2011, an illegal traffic of black corals has been occurring in the main cities of the southern and coastal regions of Ambovombe and Tolagnaro. In 2014 and 2015, hundreds of kilograms of black coral skeletons and a lot of diving material were seized by the authorities in the Anosy and Androy regions. Despite this and the continual harvesting of these natural resources, there has been no study of the excessive exploitation in this region. This paper is the first to talk about this new threat and to analyse and discuss the benefits of these fisheries. The first seizures and the efforts carried out on the island to stop the trade are explained. This paper highlights the urgency of studying these corals before making an appropriate conservation and management plan.

RÉSUMÉ

Le corail noir (Cnidaria : Antipatharia) est exploité dans le monde entier depuis très longtemps. Bien qu'inscrit à l'Annexe II de la convention sur le commerce international des espèces menacées d'extinction (CITES), le squelette du corail noir est utilisé sous forme de monnaie d'échange, à des fins médicinales ou pour être transformé en bijoux.Excepté à Hawaii où s'est développé une pêcherie durable, leur collecte s'effectue depuis toujours sans le moindre contrôle ni la moindre gestion. C'est le cas dans de nombreuses îles tropicales, et plus particulièrement à Madagascar où le commerce illégal se développe de plus en plus. Depuis 2011, un trafic se déroule dans les principales villes côtières du sud, Ambovombe et Tolagnaro. En 2014 et 2015, des centaines de kilos de squelettes de coraux noirs et une grande quantité de matériel de plongée furent saisis par les autorités dans les régions d'Anosy et Androy. Malgré cela, et pendant que les ressources naturelles s'épuisent continuellement, il n'existe aucune étude sur le déroulement d'une telle exploitation. Cette étude est la première à analyser et discuter des collectes ayant lieu à Madagascar. Les premières saisies ainsi que les efforts mis en place sur l'île pour stopper les collectes sont expliqués. L'étude met également en exergue l'importance et l'urgence d'accroître les connaissances sur les coraux noirs avant de pouvoir développer un programme de conservation durable de ces ressources.

INTRODUCTION

Antipatharians, called black corals, are marine organisms that have attracted people for a long time. Historically, they were used by religious people and for medicinal purposes (Bruckner et al. 2008). During the Paleolithic, some populations used them as money to trade (Tescione 1968) and from antiquity to the present, they have been used worldwide mainly for jewellery. Small black coral fisheries have always existed all around the world, but it increased with the development of scuba diving equipment and techniques until it became an important source of income in several regions and countries, such as Cayman Islands, Cuba, Mexico, Taiwan, the Philippines and the Dominican Republic (Castorena and Metaca 1979). The latter three were responsible for the trade and export of 72 metric tons and 7,400,000 pieces of black coral between 1982 and 1998. In 1996, 473,000 black coral pieces imported into the United States were reported to be worth $447,000 (Guitart et al. 1997).

At the moment, these fisheries are best known, managed and controlled in the Hawaiian Islands. Grigg (1993) explains in detail the precious coral fisheries in the region. The black coral meadows located around them were discovered in 1958 at between 30 and 75 meters depth and 14 species were found within it, with 3 being harvested and exploited: *Antipathes dichotoma*, *A. grandis*, and *Myriopathes ulex*. The others are found at over 100 meters depth and their diameter is not sufficient to be profitable to fishermen (Grigg and Opresko 1977). In 1969, black coral fisheries and precious coral exports to Asia were worth $2 million in Hawaii. Quickly, population and stock management problems appeared and academic studies started in 1970 led to the development of a selective harvesting system utilizing a manned submersible

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CITATION Todinanahary, G., Terrana, L., Lavitra, T. and Eeckhaut, I. 2016. First records of illegal harvesting and trading of black corals (Antipatharia) in Madagascar. Madagascar Conservation & Development 11, 1: http://dx.doi.org/10.4314/mcd.v11i1.5 **Early view**

(Grigg et al. 1973), allowing the development of the sustainable management of these resources. These selective fisheries and coral management are based on coral growth rates and reproductive cycles, which are supported and approved by the Western Pacific Regional Fisheries Management Council (Grigg 1976). Fishermen also need a license and an authorization to collect black corals around the Hawaiian islands (Bruckner et al. 2008). The Hawaiian islands make $50 million with the precious coral fisheries, with $30 million for black corals (Grigg 2010). These fishery industries employ about 1,000 people: the current wholesale value of unworked black coral being about $US 35 per pound, and the retail prices for manufactured black coral jewellery range from around $US 35 to $300 for earrings to over $US 3,000 for more ornate necklaces and bracelets (Grigg 1993, Kahng and Grigg 2005).

Elsewhere in the world, very little is known about black coral fisheries and management. At this time, the United States is the main importer, followed by Japan, but the USA is importing less than 1,000 pieces per year, which is a very small quantity of corals. The biggest provider of black corals is Taiwan, with more than 90 percent of the total of black coral legally sold, while the most harvested region is the Philippines. There is no official report of black coral trade in Africa nor in Madagascar but it is notorious that the illegal trade occurs without exportation control and management. In Madagascar this illegal trade involves fishermen, small collectors in villages, foreign scuba divers and exporters in big cities where a kilogram of black coral is bought for €50 from fishermen.

The global conservation status of black coral has not been evaluated, but they are protected by international treaties restricting their exploitation and exportation/importation. According to the CITES (Convention on International Trade in Endangered Species of wild fauna and flora), the main threats are harvesting and invasive alien species such as the octocoral *Carijoa riisei* (Kahng and Grigg 2005). Black coral exploitation generally occurs in different steps: seabed exploration, discovery of black coral meadows, exploitation and depletion (Grigg 1989). Their stocks gradually run out, and fishermen continually search for new meadows to maintain sales. Overexploitation of black coral quickly leads to local population extinctions causing a great loss of biodiversity without a proper management plan. Conservation plans for black coral are, however, difficult to establish because these organisms are characterized by a slow growth, a delayed first reproduction (after about 10 years), a long life, an annual release of gametes, a high colony fecundity, a low recruitment of larvae and a slow rate of recovery when individuals are damaged (Parker et al. 1997). Mortality often results from sediment covering and substrate erosion (Grigg 1993). At the moment, there is no integrative biological data on shallow-water black coral populations from the Indian Ocean and it is consequently not possible to properly manage their populations in this region.

BLACK CORALS: UNKNOWN RESOURCES IN MADAGASCAR

Research on coral reefs began in Madagascar in 1961 with the establishment of the first marine station of Toliara. French researchers from the marine station of Endoume in France studied the southwestern region of Madagascar, including the Great Reef of Toliara (GRT) (E043° 20', S23° 30'), and the coral reefs of the Bay of Ranobe (E042° 58', S23° 18'). The first published results describe the location and the physiography of these reefs (Clausade et al. 1971, Thomassin 1971, Battistini et al. 1975). Since this time, several research programs have been carried out on the coral reefs of the region (Pichon 1978, Laroche and Ramananarivo 1995, Salimo 1997, Vasseur 1997, Laroche et al. 1997, Gabrié et al. 2000, Bruggemann et al. 2012, Andréfouët et al. 2013), but none of these included black corals.

No scientific study on black corals has been made in Madagascar until now: their communities remain completely unknown. Moreover, there is no data available from the main fishery and marine science research centres of Madagascar (Fishery and Marine Science Institute - IH.SM and the National Centre for Oceanographic Research - CNRO), or from the National Environmental Research Centre (CNRE). This publication is the first to exclusively talk about antipatharians from Madagascar and the problems related to their illegal exploitation, with the lack of management.

THE FIRST OFFICIAL SEIZURE OF BLACK CORALS. In 2014, a total of 178 kg of illegally-harvested black coral was seized by the Fisheries Control Centre (Centre de Surveillance des Pêches - CSP, based in the capital Antananarivo), in the southern regions of Anosy and Androy (Figures 1 and 2). Samples of the seizure were sent to the authors. The diameter of the base of the samples and their length were recorded with their origin (Table 1). Most of the black coral samples were fragments with a branch diameter higher than 36 mm (Figure 2). The harvested corals seized in Tolagnaro were first branched corals with a bush-like shape before being cut into fragments. Our investigations have confirmed that the bigger the branches are, the more expensive the price is. Furthermore, during the 31st May 2015, a new official seizure of

Figure 1. Southern coast of Madagascar. The two main regions concerned by the illegal harvesting of black corals, Androy and Anosy, are highlighted in red. Their capitals are respectively Ambovombe and Tolagnaro.

Figure 2. (a) Large bags containing dried black coral skeletons in Ambovombe, Androy. (b,d) Details of black coral skeletons collected. (c,f) Pictures of diving tanks used by poachers seized by the authorities in Kotsala, in the Ambazoa municipality of Ambovombe. (e) A branching black coral belonging to the Myriopathidae family photographed off the southwestern coast of Madagascar at approximately 20 meters deep. This coral has the same shape and belongs to the same family as the corals harvested in Tolagnaro. (g) Pieces of black corals collected in the Anosy region showing the scale of corals that are harvested. (scale bar: 1cm)

100 kg of black coral was made in Andranobory, in the municipality of Analapatsy (Anosy region), bringing the number of official arrests in the Malagasy territory to four.

Dry tissues from these samples were also collected and fixed in 100% ethanol for DNA analysis. The primers LCOant forward and HCOant reverse were used to flank the CO-1 barcoding region (see Wagner et al. 2013 for the PCR conditions) and the same primers were used for DNA sequencing. Sequence analyses showed a high similarity with *Myriopathes* sp. and *Tanacetipathes* sp., two branched species belonging to the Myriopathidae family (Figure 2, unpublished data).

BLACK CORAL HARVESTING: AN ILLEGAL BUT LUCRATIVE BUSINESS. From the start of the operations in 2010 to today, it is known that antipatharians are collected from two regions of Madagascar: Anosy and Androy. These neighboring regions are located in the deep south of the country. They are famous for the aridity of their climate (especially in the Androy region) and the important richness of their marine resources (Bemiasa 2009). However, it is likely that harvesting of these marine resources occurs in other regions of the country. For example, in March 2012, a private operator officially requested an authorization to the Malagasy Ministry of Fishery and Aquatic Resources to collect black corals in four regions of Madagascar. The region of Androy was not targeted.

Table 1. Description of the black corals seized by the authorities in southern Madagascar (* given as mean ± SD; ** not sampled given that the seizure happened after the sampling date)

Date of Seizure	Sample	Weight (kg)	Diameter of base (mm)*	Length (mm)*	Region
24 March 2014	10	8	19.3 ± 3.7	199.4 ± 71.7	Androy
13 May 2014	10	163	35.7 ± 8.8	395.3 ± 97.2	Anosy
13 May 2014	10	70	12.1 ± 2.8	247.3 ± 73.6	Anosy
21 May 2015**	NA	100	NA	NA	Anosy

Information from the CSP investigations were analyzed and cross-checked with interviews of local people (boat drivers, fishermen, fishing agent services and NGO staff) liable to fishing activities. Data obtained (Table 2) were used to estimate the average amount collected by each diver, each local fish trader (at the village level) and each seller (at the national level). According to all the people questioned, poachers come mainly from China with a lot of means, vehicles and diving materials (Supplementary Material, Table S1). It is estimated that a collection of 4-5 months could lead to the production of more than 5000 kilograms of black coral. At the same time, a few farmers and managers from different regions of Madagascar made contact with universities and local authorities to obtain either authorization or license to legally collect black corals (Supplementary Material, Table S2).

In Madagascar, black corals are so lucrative that local people have named them the "rosewoods of the sea". Fishermen claim that the value of unworked black coral sold from the villages is between 10,000 to 15,000 Ariary per kilogram from scuba divers/fishermen to local collectors and 15,000 to 20,000 Ariary from local collectors to national collectors. The price per kilo from the capital Antananarivo for international exportation, mainly headed to Asia, ranges between 500,000 to 700,000 Ariary. In a country where a worker earns an average of 120,000 Ariary per month, black coral harvesting represents an assured money supply. According to Table 2, a scuba-diver harvesting black corals can earn 750,000 Ariary per day, his monthly salary reaching more or less

Table 2. Estimations of the amount of black coral collected and sold by people involved in these fisheries. (*: scuba divers are professionals external to the villages)

Source of information	Scuba divers*	Fishermen	Local fishery service	NGO people
Role in the harvesting	Dive, collect, sale	Dive, collect, boat driver, sale	Should control trade	Interactions with people
Estimation of black coral collected per day (kg)	30 ± 10	[illegible]	> 100	± 40
Working day per week	4 ± 2	4 ± 1	5 ± 1	NA
Duration of a harvest season	25 weeks	84 weeks	12 weeks	NA
Estimation of total black coral collected (kg)	3,200			
Region	Anosy	Androy, Anosy	Anosy	Anosy

12 million Ariary. This is higher than the salary of a government official even when all costs related to the collection of corals are deducted. This income is a thousand times higher than the monthly revenue received by a traditional fisherman in Madagascar.

ALERTS, PETITIONS AND LOBBYING. People in Madagascar have became more and more interested in the harvest and sale of black corals, which are very lucrative. Fishermen and collectors from different regions of the country have tried to gather information about the geographical distribution and the available stock of black corals. As soon as researchers and students became aware of the fisher interest, alerts and lobbying have been launched with local authorities to inform them of the illegality of these banned fisheries.

A few months later, an alert about the illegal trade of black corals in Madagascar was launched by some students who took the initiative to start a petition. The purpose of this petition was to raise awareness and put pressure on government officials to promote the rational and sustainable management of fisheries resources. The petition, which was held in two stages, first invited the authorities to sign and publish laws prohibiting the exploitation of these resources. The second stage, which was launched after the release of a Ministerial Order, invited all administrative officials involved in the exploitation of these resources, including local authorities, the regional Director of fisheries, regions, gendarmerie and the national police, customs authorities and justice, to respect and apply the laws. The petition did not collect many signatures in three months, but the actions represented students, researchers and teachers from around the world (Madagascar, France, Norway, Belgium, United States, United Kingdom and Australia). The petition has become the forerunner of a wave of advocacy and lobbying conducted by environmental civil society organizations, such as FAMARI (*Ala Fatidihin'ny Maike sy ny Riaka*), AVG (*Alliance Voahary Gasy*) and the Regional Platform of Civil Society Organizations of Atsimo Andrefana, which includes more than 250 associations and NGOs as members. These organizations are among the largest and most influential in Madagascar. All these actions have together led to the signature and publication of regional and national bylaws preventing and prohibiting any form of black coral exploitation.

REGIONAL AND NATIONAL BYLAWS. Thanks to the willingness of leaders and managers of fisheries and marine resources service of the Region of Anosy, a regional bylaw suspending the collection of black corals in the region (Région Anosy 2013. *Arrêté n° 308-REG /ANOSY du 12/12/2013 portant suspension de collecte de corail noir ou TANGOARAKY dans la Région Anosy*) was enacted. This attitude of the Anosy regional authorities was an example for all the coastal areas authorities, for the responsible management of the marine resources of Madagascar. Indeed, a few weeks after the publication of the bylaw, the presence of about 10 scuba divers and black coral collectors was confirmed by local NGOs in the Androy Region. Immediately, a regional bylaw was enacted to ban black coral harvesting in the whole region (Région Androy 2014. *Arrêté n°021/14/REG/ANDROY/CR/Tangoharake du 5 Mars 2014 portant interdiction de collecte de corail noir ou "TANGOHARAKE" dans le littoral de la Région Androy*). However, these bylaws did not stop the illegal traffic in either regions. Scuba divers continued quietly to collect corals and civil society, including fishermen associations and NGOs, reported anonymously the arrival of professional divers in the area, with their diving materials. Nevertheless, the use of scuba is prohibited by the Article 10 of Ordinance No. 93-022 of 4 May 1993 on the regulation of fisheries and aquaculture in Madagascar. In June 2014, a ministerial decree prohibiting the exploitation of black coral at the national level was published by the ministry of aquatic resources and fisheries (bylaw No. 21816/2014 of 12 June 2014). This decree stipulates that all forms of exploitation including the extraction, collection, storage, transport, purchase and sale of black coral (Order Antipatharia) is strictly prohibited in the whole country. The CSP and the competent fisheries authorities are empowered to note and pursue infringements.

APPLICATION OF THE LAWS: FRAGILITY AND CONSTRAINTS. The laws preventing the harvest of black coral in the natural environment constitute a tool for the government to better manage these resources. They allow local authorities and police to directly question any people whatever their role in the traffic: diver, collector, transporter or exporter. However, the traffic has not yet been affected by the publication of these laws. Indeed, anonymous informants from the Anosy and Androy regions were reporting the presence of black coral poachers. Every interviewed person refused to provide information on poachers for fear of being blackmailed or even condemned instead of them. These people included traditional fishermen, farmers, boat drivers, police, heads of regional or municipal services and researchers. Since the beginning of the traffic until June 2015, only four arrests and seizures were performed by the CSP. The most important seizure included 49 dive tanks, additional scuba equipment and an outboard engine for a speedboat (Table 2). The CSP also seized camp equipment, several saw blades used to cut the branches of corals and a weighing machine. Officially, no speedboat has been seized. However, unofficial sources report that the arrest that led to the largest seizure also allowed the capture of two speedboats.

THE FUTURE OF BLACK CORALS IN MADAGASCAR

The efficient management of black coral is based on (1) the effectiveness of laws and rules that control the exploitation, (2) the protection of living stocks by the development of marine reserves, (3) the research on methods of transplantation in protected areas and reproduction in aquaria and (4) the awareness of populations especially via the education of children. The situation in the country since the beginning of the political and economic crisis in 2009 does not facilitate proper management. Black corals, among many other resources under CITES protection, have became indisputable objects of illegal harvesting and trade. At this time, the government of Madagascar cannot ensure the protection of these resources. The laws are not respected, and police and justice efforts are inefficient. The return of Madagascar to a constitutional political order in January 2013 constituted a new hope for the effective management of these natural resources. However, the situation has not improved. Indeed, several local sources, from the government, from NGOs or fishermen claim to be aware of several cases of law violation including the harvest, collection, sale and exportation of the resources mentioned above. Information about coral harvesting is growing over time. Corruption is one of the sources of the non-resolution of these problems of natural resource looting. Protection of black corals depends on the stability, independence and transparency of each concerned government entity, either directly or indirectly by the management of these natural resources, which are more and more in danger.

In Madagascar, the Decree No. 97-1455 of 18 December 1997, establishing general organization of maritime fishing, defines and clarifies the principles and guidelines set by Ordinance No. 93-022 of 4 May 1993 on the General regulation of fisheries and aquaculture. Figure 3 illustrates all the parts involved in the exploitation of the – unknown – natural stocks of natural resources, including black corals in Madagascar. Collection activities include purchase within a collection area, processing, storage, conditioning and/or transportation of fishery products, in order to sell them on the market, but they do not include fishing or direct capture in any form; or collection of animals from the aquatic environment. Any collecting authorization entitles the holder to the issuing of up to five collecting permits and is valid only in one zone as mentioned in the authorization. Furthermore, fishing activities are subject to the prior approval of the Ministry of Fisheries and Fish Resources. An industrial investment project (mining, fishing, production factory or else) that directly or indirectly affects the environment (including living natural resources) is subject to well defined rules. An environmental impact study is required for a large project, while for a small one, an environmental commitment program is enough. In any case, the decree of 'compatibility of investments with the environment' (MECIE / Decree No. 2004-167 of 3 February 2004) governs all legal clauses that an operator must respect.

At this time, not any conservation program for black coral can be established. A better knowledge of the biology and ecology of black corals is essential to ensure an effective management of these resources. The implementation of a conservation and management program is subject to major restrictions without a basis of reliable and updated scientific data.

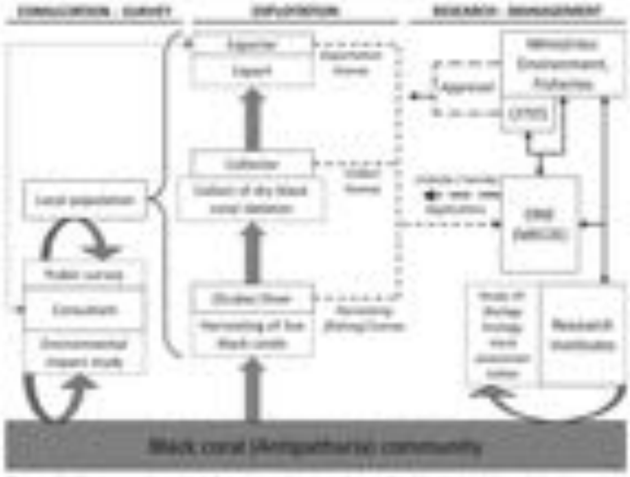

Figure 3. Diagram showing the normal procedures for black coral exploitation. The natural stock of antipatharians should be controlled through three clearly defined parts: research and management performed and ensured essentially by public centres and the government; consultation and surveys of exploitation impacts to the environment and local human societies; and exploitation itself, including harvesting, collect, transformation and exportation. Furthermore, the exploitation percentages of each part are not known yet for black corals. Meaning of the different arrows: 1- Black coral destination; 2- Application for license; 3- Approval, licensing and survey; 4- Consultancy for survey; 5- Interaction and data exchange; 6- Research and/or survey and consultation.

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SUPPLEMENTARY MATERIAL

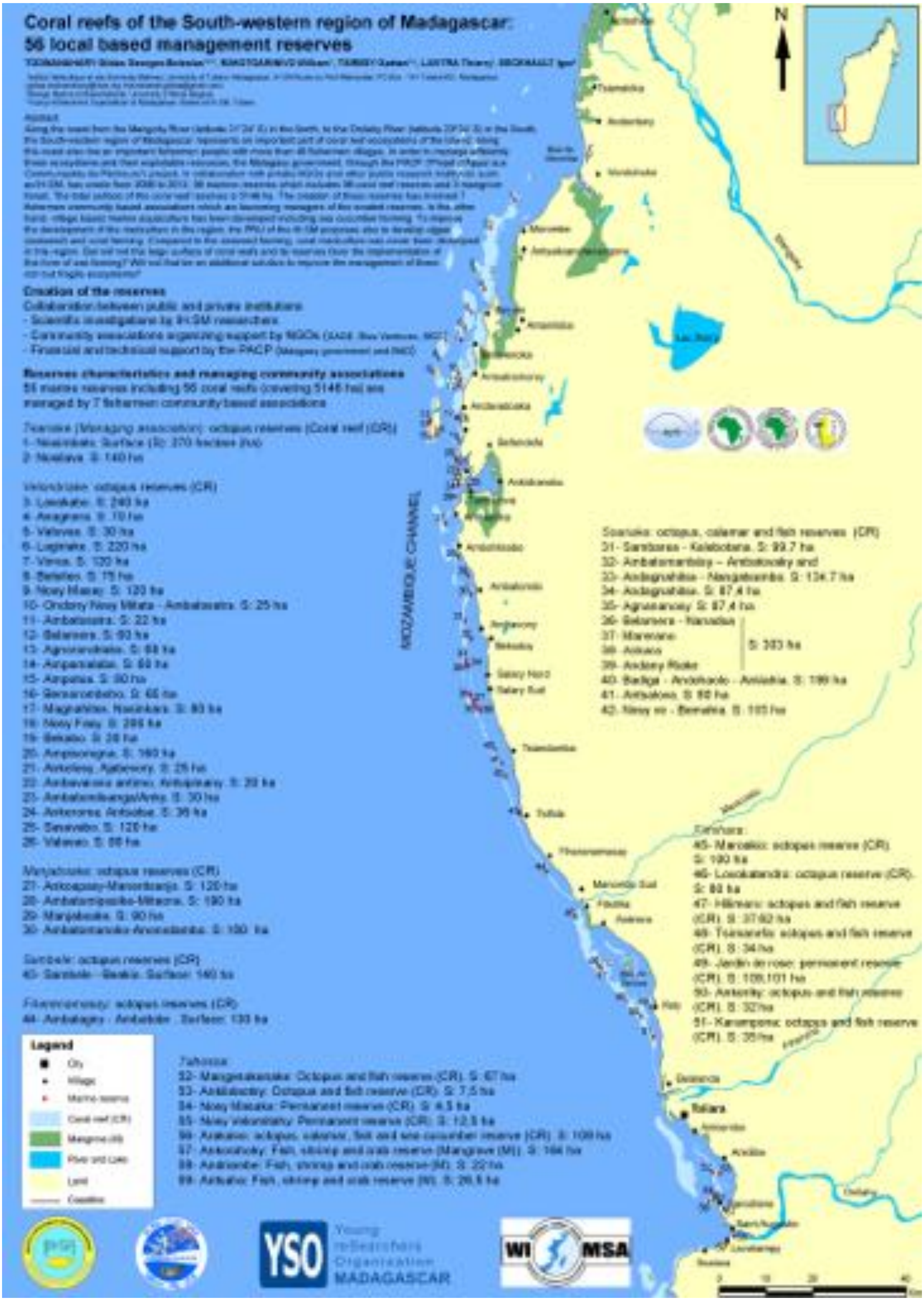
Available online only.

Table S1. Description of the material seized by the authorities that was used to collect black corals.

Table S2. Collection permits delivered by the ministry of fishery and aquatic resources in 2012.

Annexe 2:

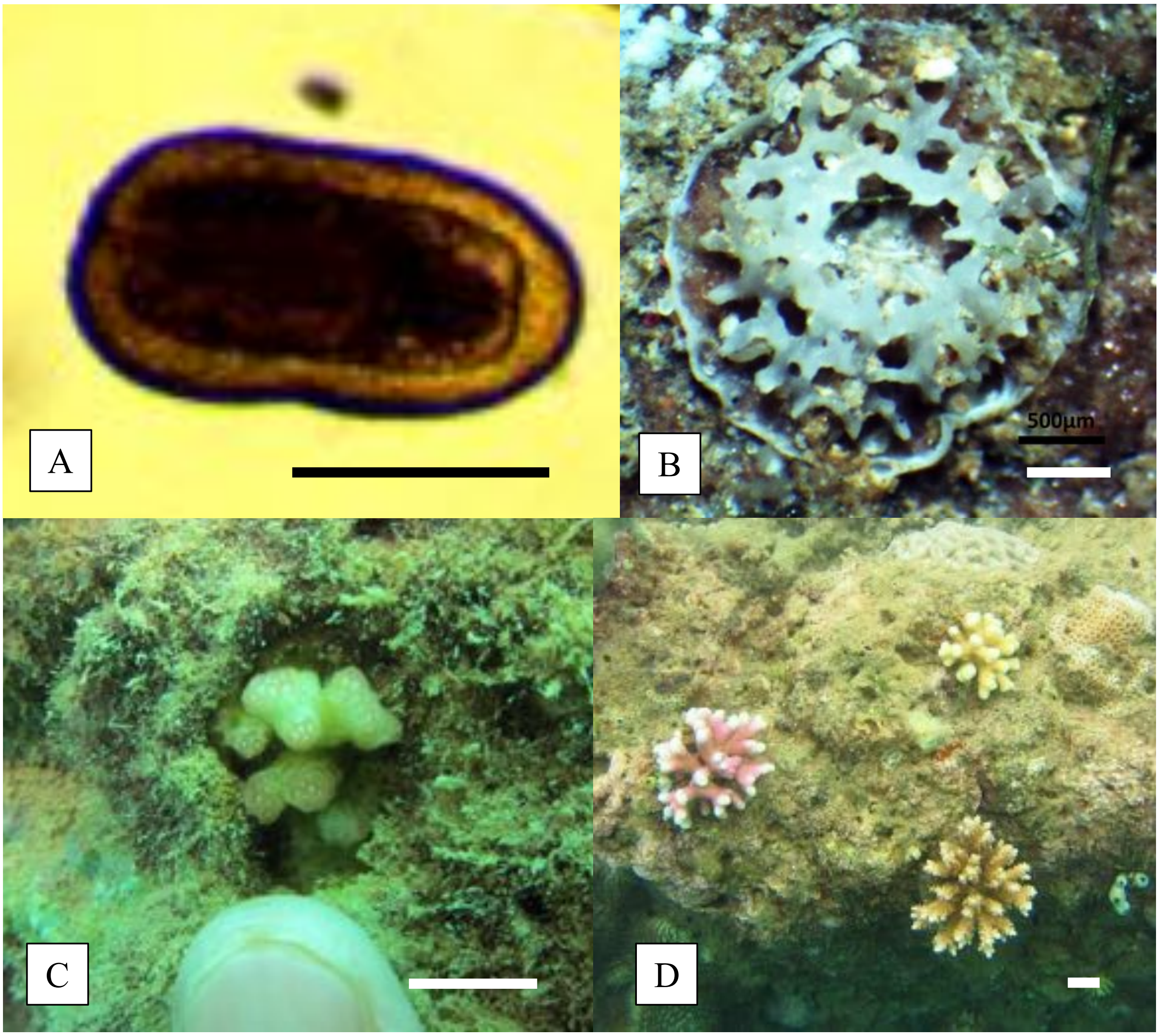
Les reserves marines de la région sud-ouest de Madagascar (Todinanahary et al. 2013)



Annexe 3:

Supplementary material for “Chapitre 3”:

Photographs of scleractinian at the different development stage: A. planula; B. Recruit (Acroporidae); C. Early juvenile of *Pocillopora* (< 2 cm); D. Juveniles of *Acropora* and *Stylophora* (2 – 5 cm). A, B and D were sampled from Nosy Tafara and C from Grande Vasque. Scale bar: A and B = 500 µm; C and D = 1 cm



Annexe 4:

Supplementary material for "Chapitre 5":

Questions asked during the survey for the analysis of the coral market

Twenty questions were asked during the survey using the survey monkey online tool (https://fr.surveymonkey.com/) and telephone interviews.

Prior to these questions, we asked general information about the interviewed people and his company.

Questions

1. How many species of corals are you selling?
2. What is the proportion of your soft corals, small polyp stony (SPS) and large polyp stony (LPS)?
3. What about the total number of coral colonies that you order a year or month?
4. Which corals providers do you work with?
5. What are their positive points?
6. What are their negative points?
7. How they deliver the corals? At what frequency?
8. What is the approximate total number of corals that you have in stock?
9. What is the approximate total number of corals that you can store in your facilities?
10. How long does it take a coral to be ready to export? At what size/age are the corals sold?
11. Are the imported corals directly marketable or should you grow them in your facilities?
12. What species do you sell the most?
13. What colours are most requested by your aquarists?
14. What determines the prices (for purchase)? Are prices and demand depending to the uniqueness of the coral, the beauty perceived by the buyer, supplier or another reason?
15. What species is the most expensive?
16. Do you wish specific species that are not available from your usual suppliers?
17. What are the main constraints for your activities? (Mortality, maintenance, risk, how to keep unsold corals and for how long?)
18. What is the mortality rate when you receive the corals? When you keep them? When you sell?
19. What importance (in additional percentage) are you ready to give to corals from an equitable coral aquaculture?
20. What are the prices of corals you buy?

Annexe 5

Terrana L, Caulier G, **Todinanahary GGB**, Lepoint G, Eeckhaut G (2016) Characteristics of the infestation of Seriatopora corals by the coral gall crab Hapalocarcinus marsupialis Stimpson, 1859 on the Great Reef of Toliara, Madagascar. Symbiosis [DOI: 10.1007/s13199-016-0391-1]

Symbiosis
DOI 10.1007/s13199-016-0391-1

Characteristics of the infestation of *Seriatopora* corals by the coral gall crab *Hapalocarcinus marsupialis* Stimpson, 1859 on the great reef of toliara, Madagascar

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Abstract This study describes the association between the obligatory symbiont coral gall crab *Hapalocarcinus marsupialis* and its stony coral hosts *Seriatopora sp.* within the Great Reef of Toliara in Madagascar and attempts to discuss their symbiotic status through comparison with previous studies. These corals are inhabited by crabs living in galls that can be categorised in four distinct morphological stages, where the first one corresponds to a small bud and the last one represents a completely closed gall surrounding the crab inside. Within the reef, 563 colonies of *Seriatopora* species were observed by scuba-diving at ten different stations: 37.8 % of them were infested by *H. marsupialis*, with a total of 763 galls, and with a majority of stage 4 galls. Galls are monopolised by females that can have different morphologies. Females store the sperm in two spermathecae and are fertilised when their morphology and size are similar to males and the gall is not closed. Histological observations coupled with scanning electronic microscopy analyses show that closed galls are made of an external living tissue, a mid skeletal layer and an internal living tissue. The internal living tissue includes polyps similar to the external tissue, some of them being sexually mature. Nitrogen and carbon isotopic signatures confirmed that these crabs are filter-feeders and do not feed on their host. This association perfectly highlights the difficulties to define the symbiotic status of a symbiont if one considers inflexible the three categories of symbiosis commonly defined.

Keywords Coral gall crab · Stony coral · Cryptochiridae · Madagascar

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1 Introduction

Coral reefs are considered to be a crucial ecosystem for the biosphere as they allow the development of thousands of different marine species. This is illustrated, for example, by the high potential of symbiotic interactions associating scleractinian corals with various symbionts (Castro 1976). Among them, the genera *Acropora*, *Pocillopora*, *Seriatopora* and *Stylophora* have the most diversified symbiotic fauna (Vytopil and Willis 2011). Symbiotic organisms take advantage of corals to shelter from predators or benefit from a food source (Stella et al. 2011). The branching shapes of these corals can also change the hydrodynamism around the colony (Helmuth et al. 1997) which leads to an increase of the available ecological niches, such as a hypoxic area, a thicker surface boundary layer or a modified flow of organic particles (Vytopil and Willis 2011).

Brachyuran decapods are particularly abundant among branching corals (Patton 1974; Castro 1976) and especially in the Acroporidae and Pocilloporidae families (Abele 1984). Obligate corals' symbiotic crabs generally belong to the families Tetraliidae, Trapeziidae, Xanthidae and Cryptochiridae (Stella et al. 2011), the latter being represented by small and cryptic coral gall crabs currently belonging to 21 genera and 52 species (Davie 2015). Coral gall crabs are

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obligate symbionts inhabiting the skeleton of scleractinian corals by forming a gall or a pit in their host's tissue (Wei et al. 2013). These crustaceans have been known for more than 150 years and many recent studies have been made into their biology and ecology (Jamieson and Tudge 2000; Carricart-Ganivet et al. 2004; Johnsson et al. 2006; Badaro et al. 2012; van der Meij 2012; Mohammed and Yassien 2013; Wei et al. 2013; Vehof et al. 2014; van der Meij 2014; Nogueira et al. 2014), their evolution and phylogeny (Wetzer et al. 2009; van der Meij and Schubart 2014; van der Meij 2015) and their taxonomy (Kropp 1990). The coral hosts act as both protection and a food source for the Cryptochirid crabs. Some species living in shallow depressions or cylindrical pits feed on coral mucus, tissue or trapped organic particles (Kropp 1986; Abelson et al. 1991; Simon-Blecher et al. 1999) while crabs living on galls are filter-feeders (Marshall and Orr 1960; Abelson et al. 1991). Free-living males may move from one colony to another to mate or share a gall with a female (Castro 1976; McCain and Coles 1979; Warner 1977; Vehof et al. 2014). Cryptochirid female crabs remain inside the cavity they inhabit for breeding their entire lives. They have an allometric growth of their abdomen that forms a brood pouch under the cephalothorax. This feature is a synapomorphic character of the Cryptochiridae family that can be also found among female pea crabs (Pinnotheridae, Becker 2010).

Although the obligate character of the symbiosis between coral gall crabs and stony corals is unquestioned, their symbiotic status is not clearly determined as the crabs may be commensals, mutualists or parasites (Kropp 1986; Abelson et al. 1991; Reed et al. 1982; Simon-Blecher et al. 1999; Carricart-Ganivet et al. 2004). While these crabs induce morphological deformations on their coral hosts, they may not have any significant negative effects on their hosts (Rotjan and Lewis 2008).

In this study, a population of the symbiotic coral gall crab *Hapalocarcinus marsupialis* on its coral hosts *Seriatopora* sp. within the Great Reef of Toliara was characterised by considering the following: (i) are the crabs abundant in these locations and (ii) what are the effects of the crabs on their host? The findings, based on histological sections and the symbiotic status of this relationship, will be discussed.

2 Material and methods

2.1 Sampling

The sampled coral hosts were identified as *Seriatopora hystrix* according to the work of Veron and Pichon (1976). However, recent molecular studies have highlighted the difficulty to properly discriminate species diversity among scleractinian corals, especially for the Pocilloporidae family (Stefani et al. 2011; Keshavmurthy et al. 2013; Pinzon et al. 2013; Warner et al. 2015). Corals from the *Seriatopora* genus have a morphological plasticity which renders difficult the definition of species boundaries based on morphological criteria (Veron and Pichon 1976). For this reason, all the *Seriatopora* individuals where coral gall crabs have been collected are cited here as *Seriatopora* sp. The samplings were done by SCUBA diving at depths of 10–15 m in the shallow reef of Toliara (south-western coast of Madagascar) in November and December 2013. A total of 88 females *Hapalocarcinus marsupialis* were collected using pliers to break off the galls without otherwise damaging the colonies, while 46 males were found free living on the coral hosts. Samples were kept in sea water during the transfer to the laboratory before being fixed in Bouin's solution for 24 h and then stored in 70 % ethanol for histological analysis.

2.2 Crab infestation and transects

Gall formations were divided into four different developmental stages as described by Kotb & Hartnoll (2002; see results). A colony of *Seriatopora* was considered infested when it showed at least one stage 1 gall. Ten stations (Fig. 1) were studied in order to determine the infestation prevalence of the coral gall crabs on their host (number of infested colonies/total number of colonies), and the infestation rate (number of galls on each infested colony). Line transects were carried out by scuba diving and consisted of a surface of 10 m long and 4 m width, in which every *Seriatopora* colony was counted. Transects were made at a constant depth between 10 and

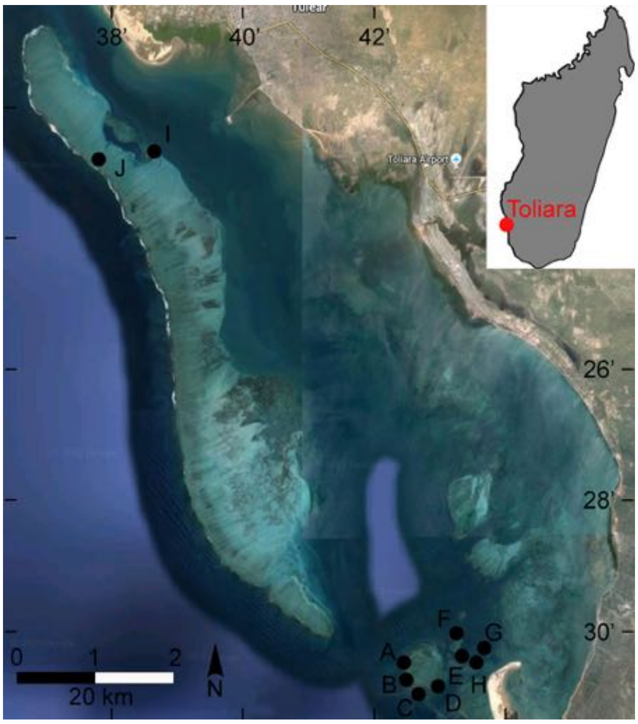

Fig. 1 Areas of the study. Transects performed on the Great Reef of Toliara, Madagascar. Satellite view from Google Maps

15 m depending on the location. (Nosy Tafara reefs including Nosy Arakaivo: station A 23°30′31.4886″S 43°42′35.4846″E, station B 23°30′36.5976″S 43°42′38.016″E, station C 23°30′46.965″S 43°42′46.9188″E and station D 23°30′47.6928″S 43°42′55.0002″E and Nosy Velomitahy: station E 23°30′14.6298″S 43°43′27.822″E and station F 23°30′0.1074″S 43°43′27.4686″E; Belaza reef: station G 23°30′20.4366″S 43°43′53.4252″E and station H 23°30′24.0156″S 43°43′49.7526″E). Stations I and J were located just behind the barrier reef in an area called "Grande Vasque" which is quite protected from tidal currents. The Nosy Tafara reefs are located in the southern channel of the Great Reef in Toliara Bay which is continually subject to tidal currents. Stations A, B, C and D are located in the outer reef of Nosy Arakaivo, and E, F, G and H in small patch reefs in the lagoon. The results were compared with Chi^2 tests and multiple comparisons using the statistical R software.

2.3 Analyses of the coral galls

The coral galls were studied through optical microscopy and scanning electron microscopy in order to see if the crab presence, inducing the gall formation, would affect the coral tissue, the skeleton structures and the gonadal development of the polyps.

Ten coral galls were fixed in 3 % glutaraldehyde buffered by 0.1 M sodium cacodylate and 1.5 % NaCl (pH adjusted to 7.8 with HCl) for 24 h then repeatedly rinsed with the same buffer and increasing ethanol baths (25–50–70). Fragments were then coated with an agarose gel before being decalcified. Agarose blocs were immersed in 10 % citric acid and 10 % formalin solution and changed every day for one week to decalcify. Coral samples were then embedded in paraffin before sectioning. Seven to 10 μm thick sections were made with a Zeiss Microm HM 340E microtome. For general tissue differentiation, coral galls were compared to coral branches without gall crabs and sections were stained with a trichromatic Masson-Goldner light green staining.

The coral skeleton was also observed by scanning electron microscopy to see if any modification was induced by the crab. The skeleton was obtained through a 24 h bath of 10 % sodium hypochlorite, to eliminate living tissues, before being metallised with a JEOL JFC-1100E Ion Sputter and observed with a JEOL JSM 6100 scanning electron microscope.

2.4 Coral gall crab development

Before being embedded and prepared for histology as explained above for coral galls, the sizes of crab cephalothoraxes were measured to determine if there was a correlation between the crab size and its maturity. Cephalothoraxes were measured with the ImageJ software (Rasband 1997) from the top of the rostrum to the cephalothorax basis for the Carapace Length (CL), and between the lateral extremities for the Carapace Width (CW) for all the females. On the 88 females, 24 of them showed a brood. All the eggs from 10 randomly chosen females were counted with a binocular magnifier and their diameter measured with the same software. Females were considered sexually mature when vitellogenic oocytes were present in their ovaries, while they were considered fertilised when sperm was observed in their spermathecae.

2.5 Coral gall crab feeding mode

The feeding habit of *Hapalocarcinus marsupialis* was investigated with the measurements of δ15N and δ13C isotopic compositions of crab tissues. For that purpose, tissues of 11 females (entire individuals) and of three potential food sources were investigated (coral tissues, suspended organic matter and incrusting algae found at the basis of coral colonies). Tissues of 10 coral colonies of *Seriatopora* sp. that inhabited the crabs, 4 filtrates (0.2 μm) of 5 l each of sea water collected in the vicinity of corals and tissues of 3 unidentified incrusting algae were collected and analysed following the method explained in details in Caulier et al. (2014). In brief, samples were oven-dried at 60 °C for 48 h before being crushed into powder and acidified with 37 % fuming HCl in a jar for 48 h in order to remove skeleton carbonates that do not come from the diet. Isotopic ratios and elemental content measurements were performed with a mass spectrometer (VG Optima, Isoprime, UK) coupled to a CNS elemental analyser (Carlo Erba, Italy) for combustion and automated analysis. Nitrogen and carbon contents are expressed in percent relative to dry weight. Isotopic ratios are presented as δ values (‰), expressed relative to the VPDB (Vienna Peedee Belemnite) standard for carbon and to atmospheric N2 for nitrogen. Reference materials were IAEA-N1 (δ15N = + ± 0.04 ‰) and IAEA CH-6 (sucrose) (δ13C = −10.95 ± 0.11 ‰). Non parametric statistical Mann-Withney and Kruskal-Wallis tests were used to compare the isotopic signatures.

3 Results

3.1 Gall structure and development

During the gall formation, four distinct stages were observed at the coral branch extremity (Fig. 2). The first one corresponds to a little bud at the top of the branch, measuring a few millimetres in size; the second one presents two little valves up to 1 cm in height with the beginning

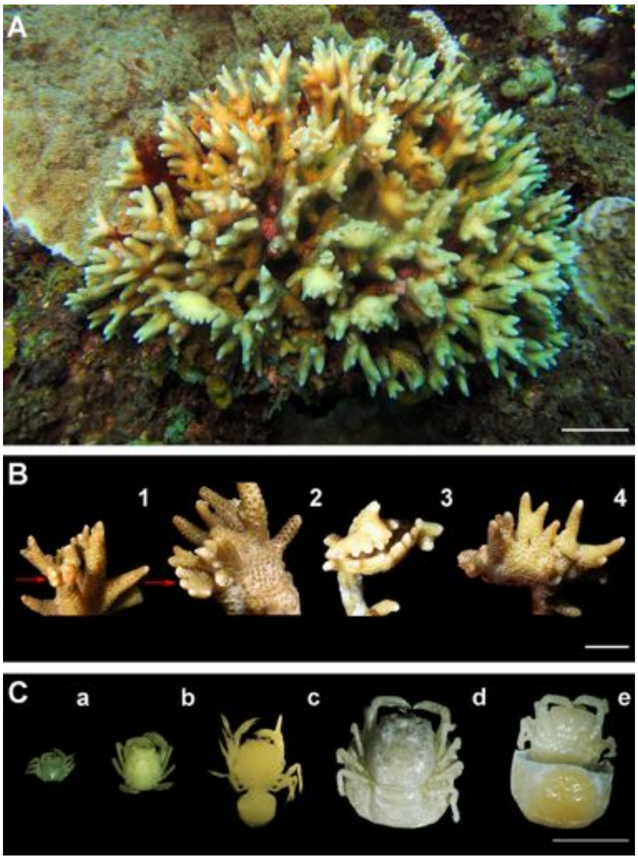

Fig. 2 The coral host and its symbiotic crabs **a** Colony of *Seriatopora* sp. showing several galls at different developmental stages (scale bar: 5 cm) **b** Developmental stages of a gall induced by the coral gall crab (scale bar: 1 cm) **c** Adult male (a) and females (b-e) at different developmental stages (b, c, d in dorsal view, e in ventral view) of the coral gall crab *H. marsupialis* (scale bar: 5 mm)

of a curving shape; the third one is higher than 1 cm and is characterised by two big valves but is not closed, forming a large cavity for the crab; and the fourth stage represents the completely closed gall confining the symbiotic crab inside and measuring more than 3 cm. When the gall is closed, there are always small holes all around the gall closure, opening to the outside.

Scanning electron microscopy images show no difference between the skeleton of a branch belonging to an uninhabited coral and the one of the gall valves (Fig. 3). However, different shapes of the polyp columella can be seen on the coral valves: it can either be smooth and cylindrical or shapeless (Fig. 3).

No modifications of the polyp tissues were observed on the coral sections. There were polyps located on the inner surface of the galls as well as the outer surfaces (Fig. 4). In Fig. 4a, the two valves (lv and rv) are visible and polyps are present on the outer surface. The empty space between the two valves represents the location where the female crab lived. Polyps are also present at the base of the gall, and both the valve polyps and the base can be mature, showing well-developed male and female gonads (fg and mg, Fig. 4). The female gonad is clearly visible due to the presence of the vitellogenic oocyte, while the male gonad shows spermatozoids (Fig. 6).

3.2 Crab infestation

The crab *Hapalocarcinus marsupialis* was found on *Seriatopora* species and *Pocillopora sp*. Only *Seriatopora* sp. was focused on. A total of 563 colonies were observed: 213 of them were infested by at least one gall. A total of 763 galls were recorded which corresponded to an infestation rate ranging between 1 and 27 galls in a single colony. The percentage of inhabited corals was at its maximum at station B (57.10 %), which is located on the outer reef, even though here the number of colonies was the lowest. The lowest percentage of inhabited corals was at stations H and F (15.50 % and 16.70 % respectively, Fig. 5) with the lowest number of galls (23 and 5 respectively). These two stations are located in a channel between the Nosy Araikavo reef and the coast. The maximum number of coral galls was observed at station D, with 187 galls for 37 coral hosts (Table 1). Considering all the stations, the prevalence of crab infestation reached 37.8 % and the stage 4 gall was the most abundant with 319 observations. The numbers of stage 1, 2 and 3 galls were 134, 177 and 133 respectively. There is no correlation between the total number of inhabited corals on a station and the infestation rate (Pearson's correlation $r = 0.46$; p-value >0.05). The eight stations located on the Nosy Tafara reefs can be put into two groups: the West Side including stations A, B, C and D, on the outer reef Nosy Arakaivo, and the East Side, including stations E, F, G and H, in the channel between the reef and the coast. The number of colonies was nearly equal between the west side and the east side (219 and 207 colonies respectively) but the infestation rates were significantly different: 47 % of the corals were inhabited on the west side and 26.6 % on the east side (chi-squared =5.69, $p < 0.05$). Consequently, there were more galls observed on the west side ($n = 262$) than the east side ($n = 167$, chi-squared =21.04, p-value <0.05), while the stage 4 gall was the most represented with 203 galls observed for the west side and 56 for the east side. Table 1 summarises the dataset for each station. There was no linear correlation between the number of infested corals and the average number of galls on a single colony at each station (Pearson's correlation, $p = 0.46$) Table 2.

3.3 Female coral gall crabs maturity

Females with a cephalothorax measuring less than 2.575 cm long had a similar morphology to the males. Bigger females had a hypertrophied abdomen forming a

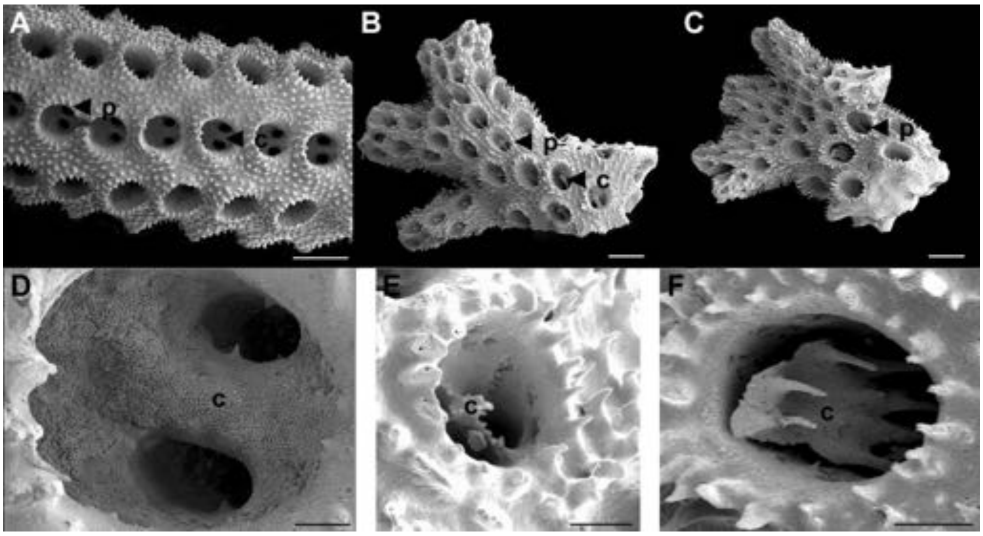

Fig. 3 Scanning electron microscopy of the coral skeleton and detailed views of the columella **a** Healthy branch of a coral colony (scale bar: 1 mm) **b** External surface of the stage 1 gall (scale bar: 1 mm) **c** Internal surface of the stage 1 gall (scale bar 1 mm) **d** Columella of a polyp located on a healthy branch (scale bar: 100 μm) **e** Columella of a polyp located on the external surface of a stage 1 gall (scale bar: 250 μm) **f** Columella of a polyp located on the internal surface of a stage 1 gall (scale bar: 250 μm). c: columellae, p: polyp

large pouch, the marsupium, under the cephalothorax (Fig. 1). A total of 59 females with a fully developed abdomen were observed, 24 of them incubated a brood in their pouch, and they were always inside completely closed galls. The other females were collected in open galls and had no brood. The number of eggs ranged between 148 and 565 in a single brood for the 10 randomly chosen females. The mean egg diameter was about 0.492 ± 0.014 mm and there was no difference between the egg sizes from either the same brood or different broods (p = 0.1; ANOVA). Histological sections showed three distinct maturity stages according to the female morphology. Immature females with a similar aspect to the males had no vitellogenic oocytes and empty spermathecae (Fig. 6). Females with a completely developed marsupium were always fertilised and had the spermathecae filled with spermatozoids, but they showed immature oocytes or vitellogenic oocytes (Fig. 6). Immature females (1.9 ± 0.5 cm length, 1.9 ± 0.6 cm width) were always smaller than females with the

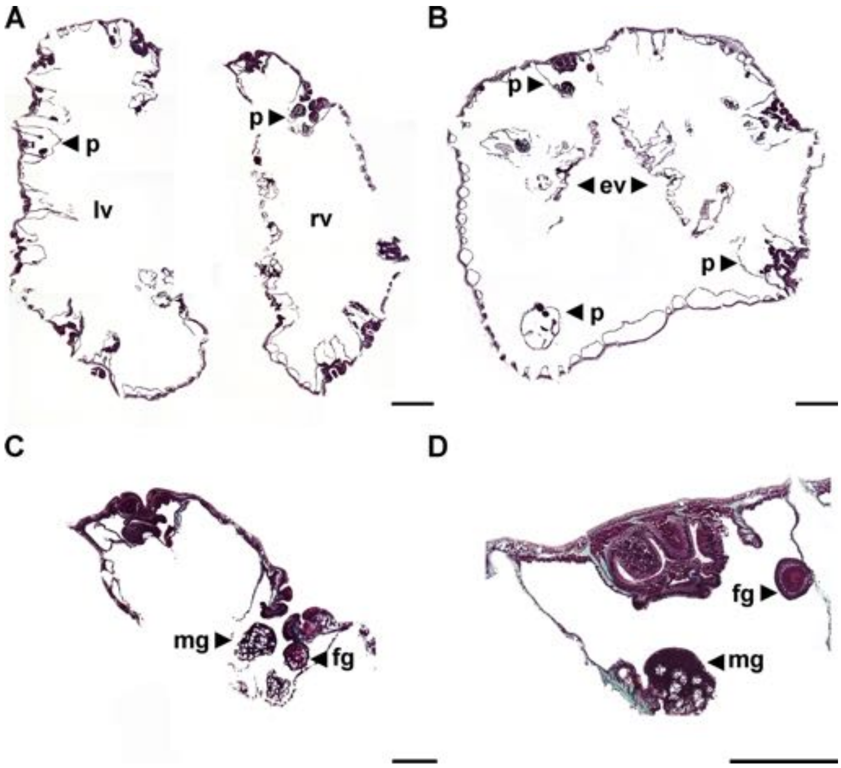

Fig. 4 Coral gall histology **a** Transverse section through the two valves of a stage 2 gall (scale bar: 500 μm) **b** Transverse section through the basis of the gall showing the end of the internal surfaces of the valves (scale bar: 500 μm) **c** Transverse section of a polyp located on the external surface of the right valve (scale bar: 100 μm) **d** Transverse section of a polyp located on the branch surface (scale bar: 100 μm) ev: end of the valves, fg: female gonad, lv: left valve, mg: male gonad, p: polyp, rv: right valve

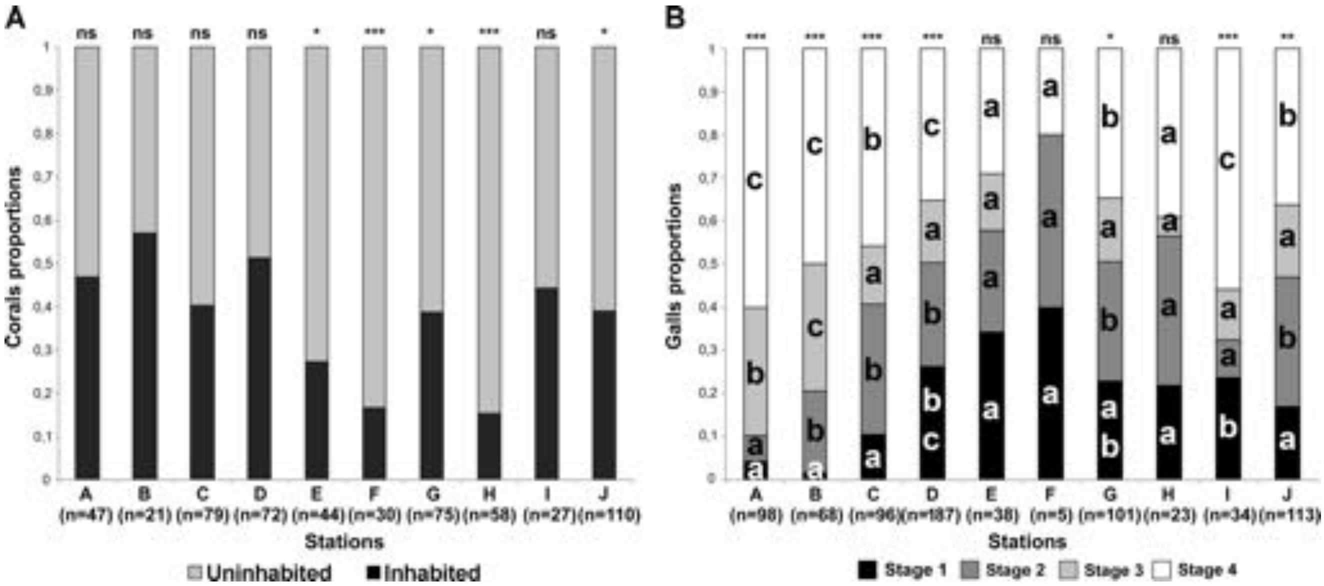

Fig. 5 Characteristics of the infestation by the coral gall crab on the Great Reef of Toliara **a** Comparison of the infestation rate between each station (uninhabited corals versus inhabited corals) **b** Comparison of the proportions of each infestation stage for each station. For both figures, the stars above the bars represent the statistical significance of the Chi-squared tests for the multiple comparisons. The letters refer to the multiple comparisons test between each developmental stage for one station (chi-square tests). ns: non-significant *: significant $p < 0.05$ **: very significant $p < 0.01$ ***: highly significant $p < 0.001$

marsupium (3.5 ± 0.4 cm length, 3.7 ± 0.4 cm width). According to these samples, females of less than 2.3 cm in length were immature and their marsupium was not fully developed. Yet, females were mature from 2.5 cm and had both spermathecae filled with spermatozoids and vitellogenic oocytes (Figs. 6 and 7).

4 Discussion

A recent molecular study demonstrates that a complex of cryptic species occurs inside the coral gall crab family Cryptochiridae (van der Meij 2015). For example, the crab *Fungicola fagei* was formerly considered as a single species until van der Meij (2015) discovered a complex of cryptic species in which the new crab *F. syzigia* share different fungiid coral hosts, and have very subtle morphological differences with *F. fagei*. Since such genetic differences are found inside cryptochirid crabs, it is not unlikely that the coral gall crab *Hapalocarcinus marsupialis*, always regarded as a single species in this study, may also refer to a complex of cryptic species.

On the Great Reef of Toliara, *H. marsupialis* was found on 37.80 % of the 563 colonies of *Seriatopora* species observed. The prevalence of the infestation on Toliara reached similar values to that observed in the Red Sea, where 37.1 % of 101

Table 1 Number of infested and healthy corals recorded on each station with the number of the different developmental stages observed St 1 to 4: stage of the galls

	Corals observed			Prevalence (%)	Galls observed					Mean galls/coral
Station	Healthy	Infested	Total		St1	St2	St3	St4	Total	
A	25	22	47	46.80	4	6	29	59	98	4.45
B	9	12	21	57.10	1	13	20	34	68	5.67
C	47	32	79	40.50	10	29	13	44	96	3.00
D	35	37	72	51.40	49	45	27	66	187	5.05
E	32	12	44	27.30	13	9	5	11	38	3.16
F	25	5	30	16.70	2	2	0	1	5	1.00
G	46	29	75	38.70	23	28	15	35	101	3.48
H	49	9	58	15.50	5	8	1	9	23	2.55
I	15	12	27	44.40	8	3	4	19	34	2.83
J	67	43	110	39.10	19	34	19	41	113	2.63
Total	350	213	563	37.80	134	177	133	319	763	3.38

Table 2 Mean values of $\delta^{15}N$ and $\delta^{13}C$ (± SD) of the coral gall crab *H. marsupialis* and its potential food sources

Specimens	Number tested	Mean isotopic ratio measurement	
		δ15N	δ13C
H. marsupialis	11	−18.05 (±0.40)	5.64 (±0.48)
S. hystrix	10	−20.08 (±0.81)	2.64 (±0.28)
Filtrates	3	−17.64 (±1.10)	3.38 (±0.94)
Algae	3	−11.39 (±3.31)	3.108 (±0.73)

colonies of *Stylophora pistillata* (Pocilloporidae) were infested with a maximum of 14 galls on a single colony (Mohammed and Yassien 2013). This is more than previous studies into pit crabs inhabiting non-branching corals (Simon-Blecher and Achituv 1997; Van der Meij and Hoeksema 2013; Nogueira et al. 2014), which is probably due to a smaller suitable surface for crabs. The host specificity of *Seriatopora* species was also found on the Queensland reefs in Australia, where *H. marsupialis* lived on every species of the Pocilloporidae family but were particularly abundant on *S. hystrix* (Patton 1966). Such selectivity has been suggested to optimize survival and reproductive success (Orians and Wittenberger 1991; Pulliam and Danielson 1991).

Our study shows that the infestation rate is different between the locations: corals from the west part of Nosy Tafara reef are more infested by crabs than the eastern part. The establishment of *H. marsupialis* on the western sites is older (i.e. has the highest proportion of closed galls) than the eastern sites. These observations are probably the result of hydrodynamic and environmental effects that could influence larval dispersion and settlement. The Nosy Tafara reefs divide the south of Toliara into two parts: the west side is strongly exposed to swells and tides while the east side is more set back and protected (Pichon 1978). Moreover, larvae do not seem to choose where to settle based on the numbers of adult crabs. This can be assumed as there is no correlation between the number of infested corals at a station and the average number of galls on a single colony. Furthermore, a maximum of 27 galls were observed per coral. In comparison, authors of other studies into pit crabs found a maximum of 4 crabs per coral with a more widespread occurrence of 1 or 2 symbionts (Simon-Blecher and Achituv 1997; Nogueira et al. 2014). While an intraspecific competition is expected in cryptochirid crabs (Nogueira et al. 2014), it is not the case for *H. marsupialis*. This could be explained by the the branching shape of the coral hosts that provide more possibilities to settle alone on the top of a branch without competing with conspecifics (Vytopil and Willis 2011). These groupings of crabs on the same coral host may also provide significant advantages for both males and females to reproduce, as males are free-living and look for sedentary females (Vehof et al. 2014).

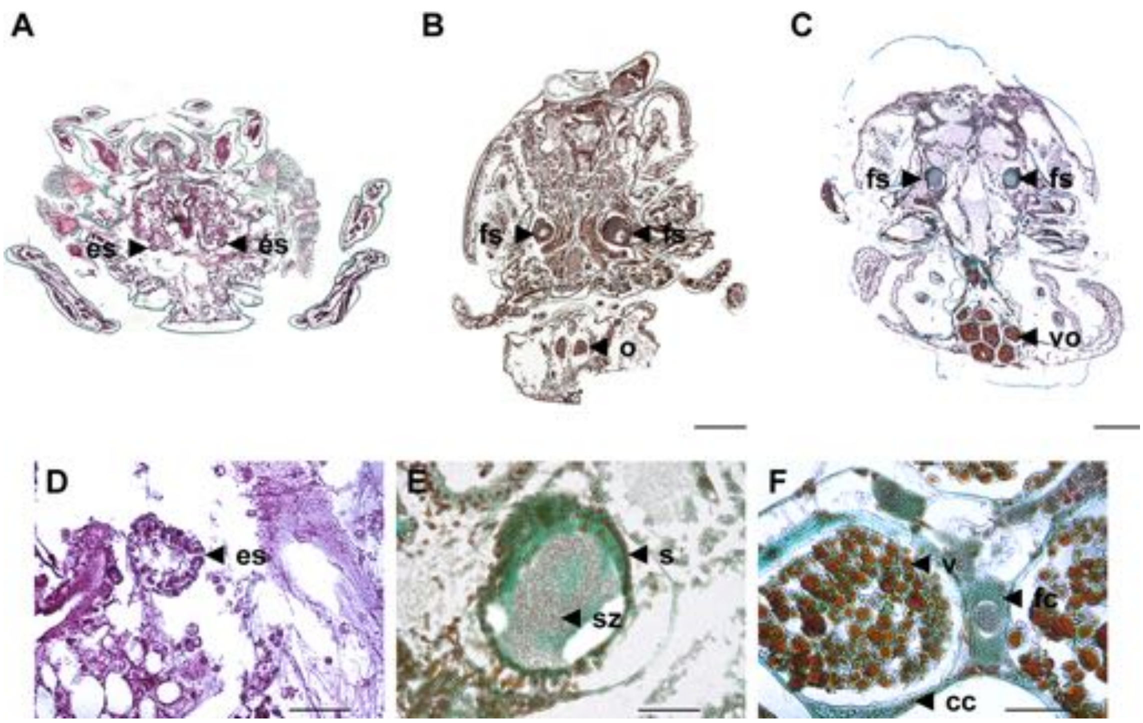

Fig. 6 Gonadal developmental stage of female crabs **a** Section through an immature female crab (scale bar: 500 μm) **b** Fertilized female crab showing its spermathecae full of spermatozoids (scale bar: 500 μm) **c** Mature and fertilized female crab showing full spermathecae and vitellogenic oocytes (scale bar: 500 μm) **d** Detailed view of an empty spermathecae (scale bar: 100 μm) **e** Detailed view of a spermathecae filled with spermatozoids (scale bar: 50 μm) **f** Detailed view of a vitellogenic oocyte (scale bar: 50 μm). cc: conjonctive capsule, es: empty spermathecae, fc: follicular cell, fs: full spermathecae, o: oocytes, s: spermathecae, sz: spermatozoids, v: vitellus, vo: vitellogenic oocytes

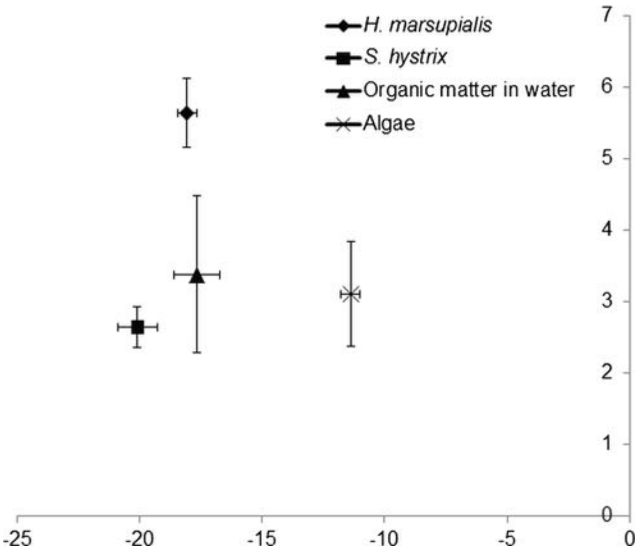

Fig. 7 Average values (±S.D.) of $\delta^{15}N$ and $\delta^{13}C$ for the crabs and their potential food sources: coral hosts, algae and organic matter in water

The diet of the coral gall crab *H. marsupialis* has been discussed many times in the past, and a lot of different feeding habits have been assigned to this species (Stimpson 1859, Henderson 1906, Potts 1915, Patton 1976, Kropp 1986). Our results based on carbon and nitrogen isotopic signatures show that *H. marsupialis* is mainly a suspension-feeder as they capture organic particles from the water flow, the morphology and hydrodynamism of the galls probably favouring particles trapping and availability (Abelson et al. 1991). Since heavier particles may settle inside galls (Abelson et al. 1991) and Kropp (1986) observed crabs gathering mucus at the coral surface, it is plausible that there are multiple feeding strategies in the Cryptochiridae family.

Histological analyses show that immature females that live in unclosed galls are fertilized when their shape is still similar to males, i.e. when they have not a marsupium. Females grow in parallel to the gall development and only females with the marsupium completely developed lie inside closed galls. After the gall closes, the female produces eight or more egg batches within the following 10 months (Kotb and Hartnoll 2002). Mating could be a stimulus accelerating the female growth and allowing the abdomen to have its final morphology. The latter forms a large marsupium under the cephalothorax where eggs are brooded. The female body size is limited by the gall cavity and this is the principal determinant of reproductive output in addition to the body cavity that limits brood size in brachyuran crabs (Hines 1982). Because the females are relatively small, the development of a marsupium allows them to brood a high number of eggs that are protected against coral cnidocytes. The mean egg size of 0.492 mm for *H. marsupialis* is relatively high related to the body size that reach up to 25 mm in carapace length. In comparison, the blue crab *Callinectes sapidus* produce eggs with a diameter of only 0.252 mm while its body size reach up to 180 mm in carapace length (Hines 1986; Hines et al. 1987). According to Hines (1982), this large size corresponds to a short larval development and a higher recruitment size increasing the settlement efficiency.

Survival of females are thus strongly dependant of their hosts, as immature females are never found inside closed galls and fertilized females are never found outside them. This spectacular synchronisation between the life cycle of the symbiont and the abnormal growth of the coral host branches brings the matter on the symbiotic status of the coral gall crab *H. marsupialis*; are they parasites, commensals or mutualists? Those three categories are defined in accordance with their effects on the hosts, which are respectively negative, neutral or positive (Kinne 1980). Many examples, however, highlight that the boundaries between those statuses are not rigid and that the symbiotic interactions are much more correctly illustrated by a symbiotic continuum (Parmentier and Michel 2013). In this continuum, the sum of the interactions between a symbiont and its host defines the status of the symbiosis, which is variable depending on the life cycle of both host and symbiont or the environmental conditions. Cryptochirid crabs may have a negative impact on their coral hosts by (i) reducing their growth by feeding on coral tissues (Simon-Blecher et al. 1999) or due to abnormal growth of the skeleton (Simon-Blecher and Achituv 1997); (ii) leading to the death of polyps due to the crab settlement and (iii) favouring algal and fungal growth in and around the pit which leads to an energy loss for the coral (Simon-Blecher et al. 1999). On the other hand, cryptochirid crabs may have a positive impact on their coral hosts by bringing nutrients and organic matter to coral polyps in being active filter feeders. If these crabs are considered parasites because they bore into the skeletons of their hosts, Mokady et al. 1998 relativized this phenomenon among boring bivalves suggesting that the benefit provided through nutrient enrichment may significantly outweight the cost of localized structural damage. At the level of *Seriatopora* populations, the impact of *H. marsupialis* is negligible: corals in low infested or highly infested sites do not show any sign of disease. At the level of colonies, the main negative impact of *H. marsupialis* is the abnormal skeletal development forcing corals to spend energy to create the galls. However, at the level of individuals, histological analyses show that polyps into the galls are normal and sexually functional. Feeding habits of *H. marsupialis* do not match with a parasitic association as they feed on organic particles brought by the water flow. While they can gather mucus from the host surface to eat trapped particles, it may not represent a metabolic drain (Carricart-Ganivet et al. 2004; Badaro et al. 2012). The two last observations would indicate that the symbiosis is at least neutral for the hosts. In conclusion, this marine association perfectly illustrates that the placement of the coral gall crab in a symbiosis category is not applicable and that, instead, the use of the symbiotic continuum is the best way to characterise it.

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Annexe 6: Summary of the costs of the value chain for coral aquaculture

Analysis of costs		Naming	Price (MGA)	Unit	Quantity	Unit cost per nubbin	Initial investment	Amortization (year)	Annual cost	Annual amortization
Supplies	NVC	Coral tables	25,000	1	48	177.30	1,200,000	5		240,000
		Cutting pliers	4,000	1	8	7.88	32,000	3		10,667
	VC	Plastic cup	5,000	50	2.13	212.77			612,766	
		Cement	23,000	50 kg	0.1	46.00			132,480	
		Sand	20,000	100 L	0.2	40.00			115,200	
		Elastic	7,000	50	2	280.00			806,400	
	Total				**MGA**	**763.95**	**1,232,000**		1,666,846	250,667
					EUR	**0.22**	**352**		476	72
Production	NVC	Materials and office supplies	3,500,000	1	1	23,333.33	*3,500,000*	*5*		*700,000*
	NVC (annual	Technician	1,200,000	annual	1	1,181.10			*1,200,000*	
		Secretary	7,200,000	annual	1	7,086.61			*7,200,000*	
		Communication cost	2,645,965	annual	1	2,604.30			*2,645,965*	
		Villagers (farmers)	600,000	annual	8	4,705.88			4,800,000	
	Total				**MGA**	**38,911.23**	**3,500,000**		15,845,965	700,000
					EUR	**11.12**	**1,000**		4,527	200
Packing	NVC	Plastic wash tub	15,000	1	3	8.86	45,000	5		9,000
		Water pump	85,000	1	3	83.66	255,000	3		85,000
		Scales	30,000	1	1	5.91	30,000	5		6,000
		Oxygen pump	300,000	1	1	98.43	300,000	3		100,000
		Water filter	1,560,000	1	1	307.09	1,560,000	5		312,000
	VC	Roll	9,000	10 m	0.4 m	360.00			365,760	
		Styrofoam box	16,000	1	3.00	564.71			573,741	
		Elastic	7,000	50	1	140.00			142,240	
	Total				**MGA**	**1,568.64**	**2,190,000**		1,081,741	512,000
					EUR	**0.45**	**626**		309	146
	NVC (annual	Village-Toliara airport (return)	315	1 km	40 km	296.47			302,400	
		Transit (cost)	60,000	1 sending	1	705.88			720,000	
		Transit company (service fees)	300,000	1 sending	1	3,529.41			3,600,000	

Transport	VC	Transit (Gasynet)	0,5%*V	V=20,000 MGA	1	100.00			101,600	
		T-A : freight cost	7,875	MGA/kg	0.82	6,457.50			6,560,820	
		T-A : freight tax	1,050	1 envoi	1	12.35			12,600	
		T-A : freight insurance	30%*V	V=20,000 MGA	1	6,000.00			6,096,000	
		T-A : freight letters	14,000	1	0.012	164.71			168,000	
		A-P: freight cost	16,625	MGA/kg	0.82	13,632.50			13,850,620	
		A-P: freight handling	175	MGA/kg	0.82	143.50			145,796	
		A-P: freight fuel	3,360	MGA/kg	0.82	2,755.20			2,799,283	
		A-P: freight tax	490	MGA/kg	0.82	401.80			408,229	
	Total				**MGA**	**34,199.32**	**0**		34,765,348	0
					EUR	**9.77**	**0**		9,933	0
Total			**NVC per unit**		**MGA**	**44,132.12**			Total charges	Total amortization
					EUR	**12.61**				
			VC per unit		**MGA**	**31,311.03**				
					EUR	**8.95**				
			Total		**MGA**	**75,443.15**	**6,922,000**	Initial investment	**53,359,900**	**2,925,751**
					EUR	**21.56**	**1,978**		**15,246**	**836**

NVC Non variable costs
VC Variable costs
T-A Toliara - Antananarivo by plane (freight)
A-T Antananarivo - Client International airport (based on Paris)
V Declared value of the article (a coral nubbin)

Annexe 7: Analysis of Variance Tables corresponding to statistical tests in Chapitre 4

4.3.1 Influences of water volumes.

4.3.1.1 Growth and survival of the nubbins

	Df	Sum Sq	Mean Sq	F value	Pr(>F)
Code (volumes)	8	0.22455	0.028068	3.2928	0.017
Residuals	18	0.15343	0.008524		

4.3.2 Influences of increased dissolved oxygen concentration

4.3.2.1 Growth and survival of the nubbins

	Df	Sum Sq	Mean Sq	F value	Pr(>F)
CodeTreatment	2	1103.6	551.78	6.7695	0.002829
Residuals	42	3423.4	81.51		

Evaluation du potentiel biologique, économique et social de la coralliculture dans le sud-ouest de Madagascar

Dans le contexte de la baisse globale de la biodiversité des récifs coralliens et compte tenu du développement du marché des coraux vivants, la coralliculture est une technique prometteuse à développer dans un futur proche. A Madagascar, les aquacultures villageoises représentent une alternative à la pêche et aux collectes des organismes sauvages. La présente étude a été menée dans le cadre du programme PIC ("Programme Interuniversitaire Ciblé") de l'ARES-CCD intitulé "Développement des polyaquacultures au niveau des villages côtières du sud-ouest et du nord de Madagascar". Les principaux objectifs de l'étude consistent (i) à identifier la biodiversité des scléractiniaires, afin d'évaluer leur potentiel de recrutement et de choisir les premières espèces, meilleures candidates pour la coralliculture (ii) à identifier la meilleure technique de transport pour l'exportation des coraux d'élevage et (iii) à évaluer le potentiel de la coralliculture dans les villages du Sud-Ouest de Madagascar.

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