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# Structure et régulation des assemblages de coraux scléractiniaires dans la région de Toliara, sud-ouest de Madagascar

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# Résumé

Les récifs coralliens sont des écosystèmes d'une complexité exceptionnelle, abritant une biodiversité élevée et fournissant des ressources essentielles à la population humaine. En raison de la pression croissante du changement climatique et des facteurs de stress locaux, ces écosystèmes font actuellement face à un déclin des coraux, ainsi qu'à une diminution de l'abondance et de la biodiversité des organismes qui y sont associés. L'augmentation de la fréquence et de l'intensité de ces facteurs de dégradation, laissant des délais de récupération de plus en plus courts, implique de mieux comprendre la résilience des récifs coralliens.

Dans cette thèse, nous avons examiné les processus clés impliqués dans la structuration, la dynamique et la résilience des communautés de coraux dans la région de Toliara, au sud-ouest de Madagascar. Plus précisément, nous avons étudié les stratégies de reproduction, les caractéristiques du recrutement et les mécanismes de régulation des assemblages coralliens. Ces informations permettront de proposer des mesures de gestion et de conservation efficaces.

Nos résultats montrent que les conditions climatiques et environnementales locales favorisent des événements de ponte synchronisée chez les *Acropora* de la région de Toliara. En revanche, ces événements de ponte n'ont pas pu être observés chez le *Galaxea fascicularis* et le *Platygyra daedalea*. Ces résultats sont cohérents avec le fort recrutement et la dominance des Acroporidae et des Pocilloporidae dans les assemblages de recrues, de juvéniles et d'adultes. Les communautés de coraux dans la région de Toliara présentent une forte variabilité entre les habitats, les stations et les années de suivi. Cette variabilité spatiale et interannuelle se manifeste dans le recouvrement benthique, la richesse spécifique, la densité des colonies (recrues, juvéniles et adultes) et la taille des colonies. Les analyses de corrélation entre les trois stades de vie indiquent une relation de type « stock-recrutement » pour les Acroporidae, tandis que les Poritidae sont plutôt régulés par une relation de type « limitation par le recrutement ». Chez les Pocilloporidae, les populations semblent régulées par les deux types de relations.

Les différences de processus de régulation entre les taxons coralliens mises en évidence dans notre étude suggèrent la mise en œuvre d'actions de conservation qui bénéficient à tous les stades de la vie. Par exemple, le maintien de la biomasse de poissons herbivores et d'invertébrés pour contrôler la biomasse d'algues peut favoriser le recrutement des coraux et diminuer la mortalité des juvéniles et des adultes. Nos résultats suggèrent également que les sites situés sur la pente externe et sur les massifs coralliens lagonaires, qui présentent des taux de recrutement élevés, et une forte richesse spécifique, abondance et couverture corallienne, constituent des sites de conservation à privilégier.

**Mots-clés :** Récifs coralliens ; Coraux scléractiniaires ; Structure des communautés ; Reproduction ; Recrutement ; Variabilité spatio-temporelle ; Régulation des populations ; Facteurs environnementaux ; Grand Récif de Toliara ; Madagascar.

# Abstract

Coral reefs are exceptionally complex ecosystems, harboring high levels of biodiversity and providing essential resources for human populations. Increasing pressures from climate change and local impacts mean that these ecosystems are currently facing a decline in not only coral populations but also the abundance and biodiversity of other reef organisms. The increasing frequency and intensity of disturbances leaves shorter recovery times and implores a better understanding of coral reef resilience.

In this thesis, we examined the key processes involved in the structure, dynamics and resilience of coral communities in the Toliara region, Southwest Madagascar. Specifically, we studied reproductive seasonality, recruitment patterns and regulation processes of coral assemblages. This information will enable us to propose effective management and conservation measures.

Our results show that local environmental conditions favor synchronized spawning events in Acropora from the Toliara region. However, spawning events could not be observed in Galaxea fascicularis and Platygyra daedalea. These results are consistent with the high recruitment and dominance of Acroporidae and Pocilloporidae in recruit, juvenile and adult assemblages. Coral communities in the Toliara region show strong variability between habitats, stations and years of monitoring. This spatial and inter-annual variability is reflected in benthic cover, species richness, colony density (recruits, juveniles, and adults) and colony size. Correlation analyses between the three life stages indicate a "stock-recruitment" relationship for Acroporidae, while Poritidae are regulated by a "recruitment-limitation" relationship. In Pocilloporidae, populations appear to be regulated by both types of relationships.

The discrepancies in regulation processes between coral taxa highlighted in our study support the implementation of conservation actions that benefit all life stages. For example, maintaining herbivorous fish and invertebrate biomass to control algal biomass can promote coral recruitment and reduce juvenile and adult mortality. Our results also suggest that sites located on the outer slope and on patch reefs, with high recruitment rates and high coral species richness, abundance and cover, are favorable conservation sites.

**Keywords:** Coral reefs; Scleractinian corals; Community structure; Reproduction; Recruitment; Spatio-temporal variability; Population regulation; Environmental factors; Great of Toliara; Madagascar.

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# Chapitre 1 :
# Introduction générale

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## 1.1. Contexte général

Les récifs coralliens sont des écosystèmes marins complexes et dynamiques majoritairement bioconstruits par les coraux scléractiniaires et abritant également d'autres organismes tels que des algues, des éponges, des mollusques et des poissons. Leur structure physique complexe offre un lieu d'interaction écologique idéal pour les organismes qui y sont associés. Ces groupes d'animaux et de végétaux contribuent ensemble à la santé des écosystèmes récifaux et jouent un rôle dans le maintien de la résilience, de la stabilité et de la récupération des récifs coralliens suite à des perturbations naturelles et anthropiques (Maragos et al. 1996). Lough et al. (2018) estimaient que les récifs tropicaux abritent près de 25% des espèces marines. Ces récifs sont souvent liés aux écosystèmes adjacents, tels que les herbiers de phanérogames et les forêts de mangroves. L'interconnexion entre ces écosystèmes est souvent matérialisée par les animaux comme les tortues, les poissons et les requins qui y passent au moins une partie de leur cycle de vie pour se reproduire, se réfugier, grandir ou se nourrir.

Les récifs coralliens se répartissent dans plus de 100 pays situés dans les zones tropicales. Leur concentration est plus importante dans certaines parties du globe, à l'intérieur des latitudes de 30° Nord et 30° Sud, entre le tropique du Cancer et le tropique du Capricorne (Souter & Linden 2000, Budd et al. 2010). On peut regrouper les récifs coralliens dans deux grandes zones : i) la zone tropicale de l'Atlantique Ouest, regroupant les eaux tropicales et subtropicales situées entre les Bermudes et le Brésil, comprenant la mer des Caraïbes et le golfe du Mexique ; ii) la zone Indo-Pacifique, couvrant toutes les zones de l'Afrique de l'Est, de la mer Rouge, de l'Asie orientale à l'Océanie (Burke et al. 2011). Plus de la moitié des récifs de la planète se trouvent dans six pays : l'Australie, l'Indonésie, les Philippines, la Papouasie-Nouvelle-Guinée, les Fidji et les Maldives. Dans l'ensemble de ces étendues géographiques, on peut trouver six grands types géomorphologiques de récifs : les récifs barrières, les atolls, les bancs récifaux, les récifs frangeants, les massifs coralliens lagonaires et les complexes massifs d'îles. Ces récifs coralliens ne couvrent qu'une petite portion de la surface du globe (soit 284 300 km$^2$) mais ont des effets significatifs sur les aspects physiques et les cycles biogéochimiques de la Terre, et sont les hôtes de près de 30 embranchements d'animaux (Paulay 1997). En raison de leur position et de leur structure, les récifs coralliens associés aux mangroves offrent une protection efficace contre les vagues, les houles, l'érosion et les cyclones le long des côtes (Pascal et al. 2016, Beck et al. 2018, Hoegh-Guldberg et al. 2019, Bravo et al. 2021). À une profondeur et une rugosité appropriée, les récifs coralliens peuvent servir de briselames naturels. Avec une crête basse et submergée, ils offrent des avantages en termes de réduction des inondations en dissipant l'énergie des vagues (Beck et al. 2018).

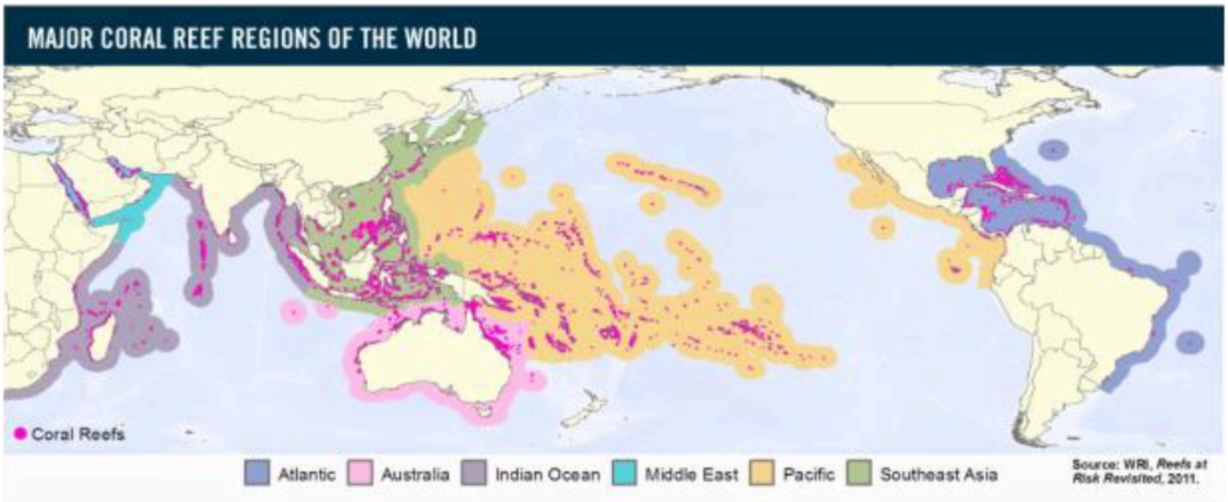


**Figure 1.1.** Aire de distribution des principaux récifs coralliens mondiaux. Source : WRI - Reefs at Risk Revisited (2011).

Au niveau mondial, la valeur de la protection côtière fournie par les récifs coralliens est estimée à plus de 4 milliards de dollars en termes de dommages évités lors des tempêtes courantes (Beck et al. 2018, Rivera et al. 2020). Cette protection côtière bénéficie à 197 millions de personnes vivant à moins de 10 m d'altitude et à moins de 50 km des récifs (Ferrario et al. 2014, Woodhead et al. 2019). La dégradation des habitats récifaux entraîne une diminution de leur structure tridimensionnelle, ce qui limite leur capacité à absorber l'énergie des vagues et augmente la force de celles-ci sur les plages, les forêts, les villes et autres structures côtières. Pour faire face à ce problème d'érosion, de nombreux pays optent pour l'installation de récifs artificiels en mer. La protection du littoral est donc essentielle pour préserver la vie humaine ainsi que les activités économiques liées aux plages (Pascal et al. 2016). Les récifs coralliens et la santé humaine sont également étroitement liés, notamment grâce à la recherche de molécules actives en biomédecine (Higa et al. 2001, Bruckner 2002, Su et al. 2012, Yu et al. 2013, Cooper et al. 2014). Plusieurs organismes présents sur les récifs possèdent des biomolécules potentiellement actives pour la guérison des maladies cardiovasculaires (Zhao et al. 2015), le cancer (Fenical 1996, Adey 2000, Venugopal 2008, Zhao et al. 2015), les ulcères (Venugopal 2008), l'Alzheimer (Kabir et al. 2021, Hafez Ghoran & Kijjoa 2021) ou encore la malaria (Zhao et al. 2015, Nii-Trebi 2017). À travers la pêche, les récifs coralliens constituent également l'un des principaux leviers économiques des pays riverains (Gough et al. 2020). En effet, la pêche sur les récifs coralliens est estimée à 143 milliards de dollars au niveau mondial (The State of World Fisheries and Aquaculture 2018) et est particulièrement importante pour les populations insulaires qui dépendent essentiellement de la pêche côtière pour leurs sources de revenus et de nourriture (Eddy et al. 2021). Ainsi, les activités liées aux récifs coralliens contribuent non seulement à l'économie, mais également à la sécurité alimentaire et à la nutrition de plusieurs millions de personnes dans le monde (Bravo et al. 2021).

La beauté des coraux et les paysages de plage constituent également des lieux attrayants pour l'industrie du tourisme. Au niveau mondial, les activités touristiques liées aux récifs coralliens génèrent 35,8 milliards de dollars par an (Spalding et al. 2017, Woodhead et al. 2019). Rien que pour l'Australie, la Grande Barrière de Corail a accueilli plus de 22 millions de visiteurs en 2016, et le tourisme dans la région du Queensland génère à lui seul 6,4 milliards de dollars australiens par an (Authority 2019, Rivera et al. 2020).

Dans certaines cultures, comme celle des Vezo dans le sud-ouest de Madagascar par exemple, les récifs coralliens servent également de base pour des événements culturels, des fêtes ou des rituels (Cinner et al. 2013). Pour la population de cette région de Madagascar, plusieurs cérémonies culturelles, notamment les mariages, les inaugurations de maisons et les cérémonies d'incantation appelées localement "tromba", nécessitent le prélèvement de blocs de coraux et de coquillages utilisés comme décorations. Les espèces récifales, comme les tritons (nom d'espèce) ou les oreilles d'éléphant (nom d'espèce), sont quant à elles utilisées comme instruments pour appeler la population à rejoindre une réunion villageoise ou pour alerter d'éventuelles menaces (par exemple, en cas de vol de zébus). Des chercheurs ont également rapporté l'efficacité des « tabous » dans plusieurs pays insulaires comme en Polynésie française (Cinner 2005, Artaud 2014), ou à Madagascar (Cinner 2005, Rakotoson & Tanner 2006, Artaud 2014). Ces formes de protection de la nature se manifestent par l'interdiction de consommer certaines espèces d'animaux ou par l'interdiction d'accès à des zones spécifiques (une île qui sert de cimetière par exemple). Malgré les biens et services qu'ils fournissent, les récifs coralliens mondiaux sont soumis à des pressions constantes d'origine naturelle et anthropique.

### 1.2. Un écosystème menacé

Le changement climatique, l'acidification des océans et d'autres pressions locales telles que la surpêche, la déforestation, l'extraction minière ou la pollution (engrais, eaux usées, métaux lourds), la maladie et l'explosion des prédateurs ont déjà causé la perte d'espèces clés et la réduction de la biodiversité marine à l'échelle mondiale (Hoegh-Guldberg et al. 2007, Boschetti 2016). Depuis les années 80, l'observation du déclin des récifs tropicaux montre une réduction moyenne de 30 à 50 % des récifs coralliens mondiaux. Selon Burke et al. (2011), la proportion des récifs qui pourraient subir les effets des pressions locales et des changements climatiques devrait augmenter à 90 % d'ici 2030. Ces facteurs de stress modifient l'écologie et la géomorphologie des récifs coralliens qui ne ressemblent plus à leur état naturel d'origine (Jackson & Sala 2001, Halpern et al. 2008). La combinaison de ces facteurs de stress entraine ainsi des changements durables dans la composition et la structure des communautés (Nyström et al. 2008), la réduction de la complexité topographiques (Alvarez-Filip et al. 2009, Bellwood et al. 2019, Tuttle et al. 2020, Good & Bahr 2021, Tuttle & Donahue 2022) et la diminution de l'abondance des espèces clés associées aux récifs coralliens (Done 1992, Aronson & Precht 2000, Hughes et al. 2003).

L'accroissement démographique sur les littoraux, la proximité des marchés et l'augmentation de l'effort de pêche sont fortement liés à la dégradation de l'habitat récifal (Newton et al. 2007, Mora 2008, Cinner et al. 2013, Brewer et al. 2013). De plus, les pratiques des méthodes de pêche destructrices, telles que la pêche à l'explosif, la senne de plage et le retournement des coraux, contribuent aux dommages physiques subis par les coraux.

Outre, les besoins en infrastructures, la déforestation, l'agriculture ainsi que l'extraction de minerais et de pierres précieuses ont conduit à l'artificialisation des sols, contribuant indirectement à la dégradation des récifs coralliens, notamment par les apports terrigènes causant une hyper-sédimentation en milieu marin (Saffache 2006, Maina et al. 2012, 2013, Carlson et al. 2019) et le rejet des eaux usées des villes, des engrais chimiques et de tous les autres déchets chimiques responsables de l'enrichissement du milieu marin et de la prolifération des maladies chez les coraux (Fabricius 2005, Mann 2011).

Sur le plan climatique, l'augmentation de la température de surface de l'eau provoque un stress physiologique qui est à l'origine de l'expulsion des zooxanthelles (Glynn 1991, Baird et al. 2009a, Obura et al. 2018). L'événement de blanchissement de 1998 suivi d'une mortalité massive de coraux, a détruit environ 16% des récifs coralliens mondiaux (Reaser et al. 2000, Wilkinson 2000, McClanahan et al. 2009). Le blanchissement de 2015-2016 a été d'une intensité supérieure à celui de 1998-1999, en termes de température maximale, de surface affectée, de nombre de pays et de taux de mortalité (Claar et al. 2018). Une analyse globale de l'impact du phénomène de 2015-2016 a montré que 75% des écosystèmes récifaux appartenant à plus de 100 pays ont subi un blanchissement modéré à sévère (Hughes et al. 2018a, 2019). Plusieurs études prévoient l'augmentation de la fréquence et de l'intensité des événements massifs de blanchissement au cours des prochaines décennies (Hoegh-Guldberg 2014, Claar et al. 2018, Hughes et al. 2019).

Suite à l'élévation de la température associé au réchauffement climatique, le volume des océans monte et les glaciers fondent, provoquant ainsi une augmentation du niveau de la mer (Nicholls & Cazenave 2010). Van de Wal et al. (2022) estime que pour un réchauffement global de 2°C, une montée des eaux de 0,9 m ou plus sera observée d'ici 2100 et jusqu'à 2,5 m en 2300. Une augmentation de la profondeur des océans peut ainsi modifier l'hydrodynamisme, générer des vagues plus grosses, et augmenter l'érosion côtière, ce qui peut avoir des répercussions sur la turbidité de l'eau, et de nombreux processus biologiques comme le recrutement, l'alimentation, ou la croissance (Brierley & Kingsford 2009, McLean & Kench 2015).

Plus de 30% du $CO_2$ émis dans l'atmosphère par les activités humaines sont dissous dans les océans. La dissociation du $CO_2$ libère des ions hydrogène et réduit le pH de l'eau de mer, et conduit à l'augmentation de son acidité (Hoegh-Guldberg 2011). Cette acidification de l'eau interfère ou empêche la formation des carbonates de calcium par les organismes marins présentant des structures calcaires (comme les coraux, les algues calcaires, les mollusques, les crustacées et les échinodermes ; Ferrari et al. 2012, Anthony 2016). Chez ces organismes, l'acidification des eaux réduit la croissance et la calcification (Havenhand et al. 2008), limite la motricité des spermatozoïdes et donc la fécondation (Havenhand et al. 2008, McDonald et al. 2009, Morita et al. 2010), diminue la survie des jeunes stades (Kurihara 2008, Albright et al. 2008, 2010, McDonald et al. 2009, De Putron et al. 2011), ainsi que la capacité de récupération des coraux, ce qui diminue la résilience des récifs coralliens. Les effets de l'acidification sur les coraux durs peuvent également être indirects via des effets délétères sur des organismes favorisant les processus du recrutement corallien, comme certaines algues calcaires encroûtantes (Albright & Langdon 2011, Fabricius et al. 2017).

Les maladies des coraux persistent naturellement à faible prévalence dans les communautés coralliennes, mais peuvent se transformer en épidémies destructrices dans des conditions favorables (Greene et al. 2020). Elles peuvent provoquer des pertes importantes des tissus coralliens et la mort de colonies. Les agents pathogènes peuvent être des bactéries, des virus ou des champignons (Morais et al. 2022). Leur apparition est liée à l'augmentation des stress environnementaux, notamment l'élévation de la température, la variation de la salinité, le changement de la qualité des eaux et l'augmentation de la pollution, la sédimentation et la turbidité (Dalton & Smith 2006, Aeby et al. 2011, Vega Thurber et al. 2020). La susceptibilité à une maladie varie entre les espèces de coraux, ce qui peut causer des changements importants dans la structure et la composition des communautés coralliennes (Hobbs et al. 2015). Les études récentes effectuées dans la péninsule arabique (Aeby et al. 2019, 2020, 2021) et dans sud-ouest de l'Océan Indien (Séré et al. 2015) ont démontré une forte prévalence de maladies chez les coraux *Acropora*, *Platygyra*, *Pavona*, *Echinopora* et *Porites* (Séré et al. 2015, Aeby et al. 2019, 2020, 2021).

La majorité des corallivores (poissons, annélides, crustacées, échinodermes et gastéropodes) ne génèrent pas de dommages importants sur les communautés coralliennes, seules quelques espèces peuvent provoquer des dégradations sévères (Glynn & Krupp 1986, Hayes 1990, Baums et al. 2003, Rotjan & Lewis 2008, Souza et al. 2011, Kayal et al. 2012). Rice et al. (2019) rapportait par exemple que certaines espèces de Scaridés broutent les tissus vivants à la surface des colonies et dégradent en même temps une partie du squelette calcaire. Parmi les espèces corallivores dites spécialisées, *Acanthaster* spp. sont des étoiles de mer qui se nourrissent de polypes coralliens. Elles se trouvent sur les récifs tropicaux à travers le monde, à l'exception de l'océan Atlantique (Mohsen et al. 2012). Dans un récif corallien « sain », ce complexe d'espèces est présent mais peu abondant, et a par conséquent peu d'impact sur les assemblages coralliens (Glynn 1973, Zann et al. 1990, Pratchett 2005). Mais lors de périodes de pullulation, les fortes densités d'*Acanthaster* spp. provoquent de fortes mortalités au sein des assemblages de coraux (Pratchett 2005). Ces pullulations d'*Acanthaster* ont été rapportées dans de nombreux récifs de l'Indo-Pacifique, notamment dans le Pacifique occidental, l'Océan Indien, et la Mer Rouge, avec des mortalités coralliennes jusqu'à 90% (Birkland & Lucas 1990, Schleyer 1998, Pratchett et al. 2017, Ramah et al. 2021). Ces pullulations peuvent non seulement causer une réduction de la diversité, du recouvrement et de l'abondance des coraux, mais sont généralement suivies d'une augmentation du recouvrement en macroalgues et en gazons à microalgues (Birkland & Lucas 1990, Kayal et al. 2012). Ces prédateurs peuvent également inhiber la croissance et la reproduction sexuée des coraux, en enlevant des tissus vivants et du squelette calcaire (De'ath et al. 2012).

Les impacts des autres évènements extrêmes comme les cyclones sont tout aussi ravageurs que les pressions citées précédemment. Ces aléas tendent également à augmenter en fréquence et en intensité du fait des changements climatiques. Knutson et al (2020) prédisent qu'au niveau mondial, le nombre de jours d'occurrence des cyclones tropicaux de catégories 4 et 5 augmentera de 35 % vers la fin du 21éme siècle, tandis que le nombre de cyclones de cette même catégorie augmentera de 21% (Knutson et al. 2015, 2021). Knutson et al. (2020, 2021) prédisent qu'une augmentation globale de +2°C de la température entrainera une intensification de +5% de la vitesse maximum du vent, ce qui accentuera le potentiel de destruction des coraux. La force des vagues et des courants générés par les cyclones est en premier lieu responsable de dégradation physique du milieu récifal. Les cyclones sont également souvent accompagnés par des fortes pluies, augmentant le débit des rivières ce qui accroît la turbidité et réduit la salinité du milieu récifal.

## 1.3. Les coraux scléractiniaires

### 1.3.1. Caractères généraux

Les coraux constructeurs de récifs appartiennent à l'embranchement des Cnidaires, à la classe des Anthozoaires, à l'ordre des Scléractiniaires et se distinguent des coraux non constructeurs par une symbiose intracellulaire mutualiste et obligatoire avec des algues dinoflagellés unicellulaires, appelées zooxanthelles (Bythell et al. 2018). Les coraux sont des organismes diploblastiques présentant une symétrie radiale. Ils sont constitués d'une cavité gastro-vasculaire centrale couronnée de tentacules dotés de cnidoblastes. Ces derniers permettent aux cnidaires de capturer leur nourriture en injectant un filament urticant, qui libère des venins au contact des proies. Ils se nourrissent de zooplancton et de bactérioplancton. Les coraux n'ont pas de système respiratoire dédié, la respiration est de type cutané, les échanges gazeux s'opérant au niveau de chaque cellule. Bien qu'ils ne possèdent pas de système circulatoire ni d'organes excréteurs, ils disposent d'un système nerveux et d'un système digestif rudimentaires.

Les coraux scléractiniaires communément appelés coraux hermatypiques sont des organismes fixés, solitaires ou coloniaux. Cet ordre est représenté par environ 1605 espèces dont près de 50% sont zooxanthelées et constructeur de récifs (Hermatypiques) (Hoeksema et al. 2019). Les espèces appartenant à ce groupe sont formées de deux entités qui vivent en symbiose : les polypes et les zooxanthelles, responsables de l'apport d'énergie à travers la photosynthèse (Maragos et al. 1996). La seconde entité est la partie non vivante du corail, qui constitue son squelette calcaire. Les polypes des coraux scléractiniaires assurent la sécrétion de leur squelette calcaire en association avec les zooxanthelles dès la fixation des larves planulas (Maragos et al. 1996). Pour prospérer, les coraux présentent des exigences physiologiques et environnementales spécifiques. Ils ne se développent que dans des eaux peu profondes et claires, dont la température est comprise entre 18 et 32 °C (Souter & Linden 2000). La lumière constitue également un paramètre important pour la survie des coraux, qui ne se trouvent généralement donc qu'à moins de 100 mètres de profondeur (Hoegh-Guldberg et al. 2019). Une fluctuation importante de la salinité de l'eau peut également influencer leur distribution, les coraux préférant des eaux dont la salinité se situe entre 35 et 40 (Souter & Linden 2000). Enfin, les récifs coralliens se développent difficilement dans des zones excessivement approvisionnées en sédiments, en eaux douces venant des rivières et lors de cyclones (Maragos et al. 1996). L'action individuelle ou simultanée de ces pressions (naturelles ou anthropiques) sur le récif corallien est à l'origine de dommages physiques sur la structure et la qualité des habitats coralliens. Les mécanismes de récupération et de maintien des populations de coraux sont fortement liés à la reproduction sexuée, à travers de l'apport local en larves, à la composition taxonomique des parents à l'échelle locale ou régionale, au mode de dispersion des larves, et au recrutement et à la survie jusqu'aux stades juvénile et adulte.

### 1.3.2. Reproduction sexuée

Le cycle de vie des coraux scléractiniaires se compose de deux phases distinctes : une phase larvaire planctonique, qui dure de quelques jours à quelques semaines après la reproduction sexuée (la ponte), et une phase benthique, qui se déroule de la fixation des larves sur le substrat jusqu'au stade adulte (Harrison 2011, Adjeroud et al. 2017).

La reproduction sexuée des coraux scléractiniaires se caractérise par deux modes différents : les coraux à fécondation externe ou "broadcast spawners" et les coraux à fécondation interne ou "brooders" (Fadlallah 1983, Richmond & Hunter 1990, Kruger & Schleyer 1998, Petersen et al. 2007, Gilmour et al. 2016). Pendant la ponte, les coraux à fécondation externe libèrent les gamètes mâles ou femelles dans la colonne d'eau où la fécondation s'effectue (Richmond & Hunter 1990, Shlesinger et al. 1998a, Levitan 2005, Harrison 2011). Ce mode de reproduction est utilisé par plus de 80 % des espèces de coraux (Baird et al. 2009c, Foster & Gilmour 2018, Hughes et al. 2019, Lin et al. 2021). La gamétogenèse ne se produit généralement qu'une fois par an et dure plusieurs mois avant la ponte, qui est souvent massive et synchronisée (Guest et al. 2008, Foster & Gilmour 2018, Ibrahim et al. 2021). Par exemple, la ponte des coraux broadcast spawners a été documentée pour la première fois sur la Grande Barrière de Corail en Australie en 1984, impliquant 130 espèces qui se sont reproduites une semaine après la pleine lune (Harrison et al. 1984). Depuis lors, les stratégies de reproduction des communautés de coraux ont été étudiées dans d'autres régions du monde, telles que les Caraïbes (Hudson et al. 2020), la Mer Rouge (Bauman et al. 2011, Bouwmeester et al. 2015, 2016, 2021), la Polynésie française (Carroll et al. 2006) et l'Océan Indien (Kruger & Schleyer 1998, Mangubhai & Harrison 2008b a, 2009, Massé et al. 2013, 2019, Sola et al. 2016). La durée de vie des larves détermine ensuite le schéma de recrutement des coraux. Par exemple, les larves issues de fécondation externe ont une durée de vie planctonique de quelques jours à quelques semaines, ce qui leur permet de se disperser et de coloniser des récifs distants (Connolly & Baird 2010, Gilmour et al. 2016). En libérant les gamètes de manière synchronisée, les broadcast spawners maximisent la rencontre entre les gamètes mâles et femelles (Harrison & Wallace 1990, Harrison 2011, Levitan et al. 2011, Sakai et al. 2020). Pour les brooders, la fécondation se produit à l'intérieur des polypes (Harrison 2011, Gilmour et al. 2016). Le développement des gamètes pour ces espèces est souvent très court, moins d'un mois, mais elles peuvent présenter plusieurs cycles de gamétogenèse pendant l'année (Foster & Gilmour 2018). La phase planctonique des larves dure quelques minutes à quelques heures avant la fixation (Harrison & Wallace 1990, Thomas et al. 2020). La majorité des espèces de ce groupe privilégient l'auto-recrutement en se fixant directement près de leurs parents (Harrison & Wallace 1990, Figueiredo et al. 2013, Hughes et al. 2019, Thomas et al. 2020). Il convient de noter que les stratégies reproductives d'une espèce peuvent varier non seulement entre espèces, mais également entre populations d'une même espèce, comme documenté chez *Pocillopora damicornis, P. verrucosa*, et *P. meandrina* (Ward 1992, Schmidt-Roach et al. 2012).

Les coraux scléractiniaires peuvent être divisés en deux catégories selon leur sexualité : les hermaphrodites et les gonochoriques (Fadlallah 1983, Szmant 1986, Baird et al. 2009c, Harrison 2011). Une espèce est considérée comme hermaphrodite lorsqu'elle produit à la fois des gamètes mâles et femelles dans le même polype ou la même colonie, on parle dans ce cas d'hermaphrodisme simultanée. L'hermaphrodite séquentiel concerne les espèces qui changent de sexe à différent moment de leur cycle de vie (Fadlallah 1983), comme c'est le cas de certains Fungiidae (Loya & Sakai 2008, Eyal-Shaham et al. 2020). Une espèce est, en revanche, considérée comme gonochorique si les gamètes mâles et femelles sont produits par des colonies différentes (Harrison 2011). Chaque mode de développement, fécondation externe ou fécondation interne, peut présenter les deux types de sexualité. Par exemple, les espèces hermaphrodites à fécondation externe représentent plus de 80 % des espèces de coraux mentionnées précédemment (Baird et al. 2009c).

Les facteurs environnementaux jouent un rôle clé dans la régulation du cycle de reproduction des coraux, et ils affectent notamment le moment de la ponte et la synchronisation des événements de reproduction entre les différentes colonies (Keith et al. 2016, Sakai et al.

2020, Lin et al. 2021). La ponte des coraux est par exemple régulée par une combinaison de facteurs environnementaux qui influencent la période des événements de ponte, la nuit et l'heure de la ponte (Richmond & Hunter 1990, Shlesinger & Loya 2019, Sakai et al. 2020, Lin et al. 2021, Lin & Nozawa 2023). Les principaux facteurs sont la température (Nozawa 2012, Keith et al. 2016, Paxton et al. 2016, Sakai et al. 2020, Bouwmeester et al. 2023, Lin & Nozawa 2023), la marée (Keith et al. 2016), la pluviométrie (Mendes & Woodley 2002), le vent (Keith et al. 2016, Sakai et al. 2020), et la phase lunaire (Guest et al. 2002, Kaniewska et al. 2015, Lin et al. 2021). La synchronisation de la ponte peut varier considérablement entre les espèces de coraux d’un même récif, et entre différentes régions, le long du gradient latitudinal notamment (Richmond & Hunter 1990, Bouwmeester et al. 2021) La synchronisation des pontes chez les coraux semble être une adaptation pour maximiser le succès de la fécondation des gamètes, notamment lors de conditions météorologiques favorables, comme pour les pontes massives pendant les mortes-eaux où la vitesse du vent et la force des vagues sont réduites (Jones & Hoegh-Guldberg 2001, Jamodiong et al. 2018a, Gan et al. 2021).

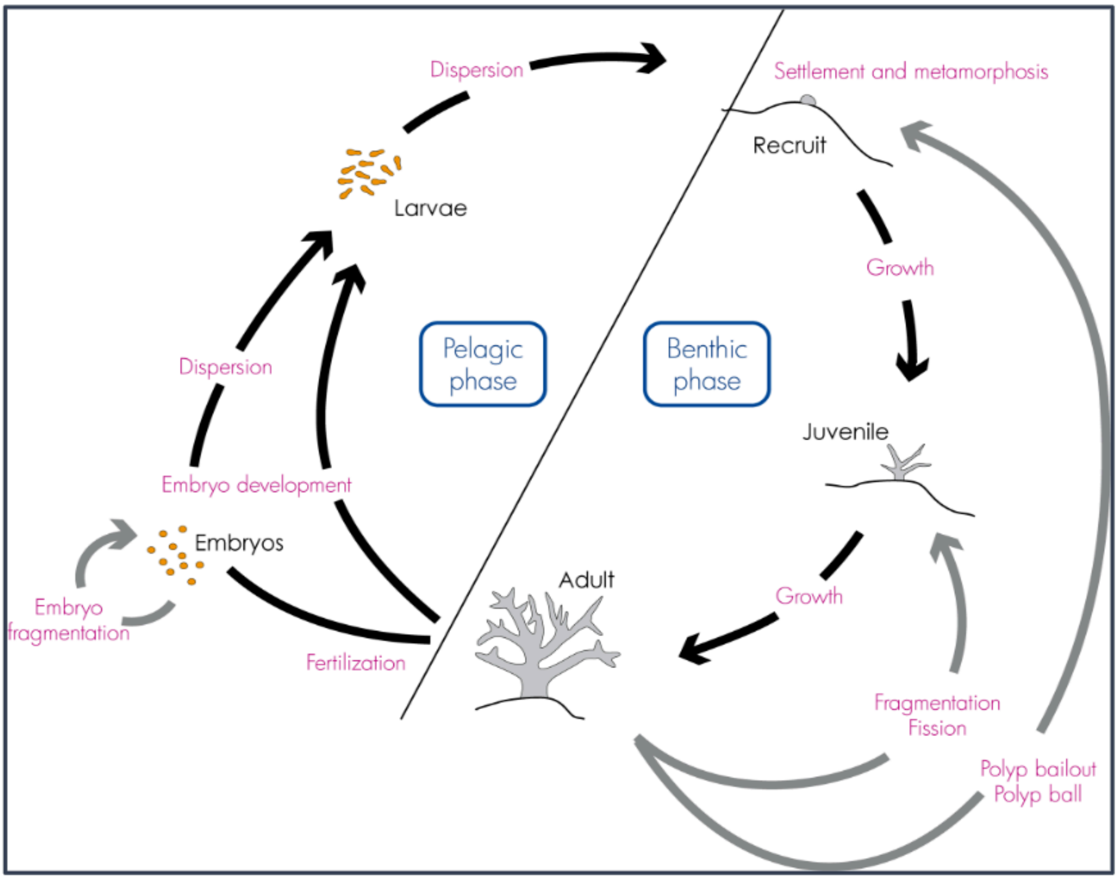


**Figure 1.2.** Cycle de vies des coraux scléractiniaires. Sauf rares exceptions, les adultes sont fixés au substrat. La reproduction sexuée conduit à l’émission de larves ou de gamètes. Les larves planulas connaissent alors une phase pélagique, puis se fixent au substrat et se métamorphosent, démarrant ainsi leur phase benthique. Après la fixation et la métamorphose, on parle de recrues. Au bout d’un an environ,

les colonies atteignent une taille centimétrique et sont appelées juvéniles. Après trois à quatre ans, les colonies sont généralement capables de reproduction sexuée et considérées comme adultes. Les coraux se reproduisent également par voie asexuée (Adjeroud et al. 2017).

### 1.3.3. Processus du recrutement

Durant leur phase pélagique et au fil de leur développement, les larves planulas perdent peu à peu leur flottabilité positive et développent une capacité de nage grâce aux cellules ciliées épidermiques (Babcock & Heyward 1986, Harrison & Wallace 1990, Richmond 1997). Ces cellules leur permettent de réguler leur position verticale dans la colonne d'eau (Szmant-Froelich et al. 1980, Chia et al. 1984, Harrison & Wallace 1990). Les larves de coraux utilisent ces cellules sensorielles pour détecter les variations de température de l'eau, la pression barométrique, la distribution de la lumière et la chimie de l'eau (Stake & Sammarco 2003, Gleason & Hofmann 2011, Pysanczyn et al. 2023). Elles utilisent ces signaux pour se diriger vers le fond à la recherche de substrats appropriés pour leur installation (Babcock & Mundy 1996). Une fois qu'elles ont trouvé un substrat adéquat, elles commencent à se fixer et à sécréter leur squelette calcaire. Si les conditions sont favorables, elles se métamorphosent et survivent dans leur nouvel environnement jusqu'à atteindre l'âge adulte et la maturité sexuelle (Richmond & Hunter 1990). Le recrutement correspond aux processus par lesquelles les individus nouvellement formés intègrent les populations adultes (Sale 1990). Le recrutement est une phase cruciale pour le maintien et le repeuplement des récifs. Le recrutement des coraux est caractérisé par une grande variabilité spatiale, à toutes les échelles étudiées : entre les bassins océaniques, entre différentes régions, entre différents récifs de la même région, et à l'échelle locale entre les sites, les plaques de recrutement (plaques de substrat artificiel d'environ 10 × 10 cm utilisées pour étudier le recrutement corallien) et même entre les surfaces des plaques (dessus, dessous et bord ; Fisk & Harriott 1990, Hughes et al. 2002, Adjeroud et al. 2007, 2017, 2022, Jouval et al. 2019. La fixation est largement influencée par l'hydrodynamique, l'énergie des vagues, ainsi que la profondeur (Ritson-Williams et al. 2009, Edmunds et al. 2010, Adjeroud et al. 2017). Des facteurs biologiques favorisent la fixation des larves, tels que certaines espèces d'algues calcaires encroûtantes (Lei et al. 2021), alors que des facteurs inhibiteurs, tels que la sédimentation (Babcock & Davies 1991, Babcock & Mundy 1996, Babcock & Smith 2002, Birrell et al. 2005, DeMartini et al. 2013, Wakwella et al. 2020), l'intensité lumineuse (Babcock & Mundy 1996), ou la prédation réduisent les taux de fixation (Ritson-Williams et al. 2009). La compétition avec les macroalgues affecte également la distribution spatiale des recrues et des adultes (Kuffner et al. 2006, Dixon et al. 2022). Une fois établies, les recrues et les juvéniles de coraux font face à une forte mortalité causée par la compétition avec d'autres organismes benthiques, la prédation ainsi que la sédimentation (Tuttle et al. 2020, Wakwella et al. 2020, Tuttle & Donahue 2022).

Le recrutement corallien se caractérise également par une variabilité saisonnière et inter annuelle (Fisk & Harriott 1990, Dunstan & Johnson 1998, Soong et al. 2003, Adjeroud et al. 2007, 2022, Green & Edmunds 2011, Jouval et al. 2019, Edmunds 2021b). Cette variation temporelle du recrutement est fortement liée aux caractéristiques de la reproduction des coraux (Adjeroud et al. 2017). Le changement des conditions climatiques et océanographiques, notamment la température de l'eau, affecte la fécondité des coraux, et par conséquent, les processus de recrutement (Harrison & Wallace 1990, Hughes & Tanner 2000, Adjeroud et al. 2007, 2017). Ces variations de fécondité peuvent être causées par des perturbations à grande échelle telles que les épisodes de blanchissement, ainsi que des facteurs de stress chroniques tels que la pollution de l'eau (Adjeroud et al. 2007, 2017). La mortalité des adultes et des larves causés par ces perturbations réduit la disponibilité des larves pour le recrutement (Edmunds 2021b). Dans ce contexte d'hétérogénéité spatiale et temporelle des assemblages coralliens, la régulation des populations et le maintien de la biodiversité des coraux constructeurs de récifs dépendent très fortement des patrons de recrutement et les événements post-fixation (Connell et al. 1997, Hughes & Tanner 2000, Adjeroud et al. 2007, 2022).

### 1.3.4. Modèles de régulation des populations de coraux

Sous la pression constante des perturbations environnementales que subissent les récifs coralliens, le succès de la reproduction et du recrutement des coraux sont les principaux facteurs qui assurent la résilience des populations et des communautés coralliennes (Bouwmeester et al. 2021). L'approvisionnement en larves de corail et les caractéristiques du recrutement sont également fondamentaux pour la répartition et l'abondance des coraux adultes (Connell et al. 1997, Edmunds 2000, Hughes et al. 2000, Penin et al. 2007, Jones et al. 2009, Adjeroud et al. 2017).

Les mécanismes de régulation des populations de coraux peuvent être séparés en trois modèles, qui se distinguent par le type et l'intensité des liens entre les jeunes stades vie, recrues et juvéniles, et les adultes (Caley et al. 1996, Chesson 1998, Edmunds et al. 2010, Penin & Adjeroud 2013, Adjeroud et al. 2017, 2019). D'une part, le modèle de « limitation par le recrutement » *(recruitment limitation* ou *recruitment regulation*) stipule que l'abondance des populations adultes est directement fonction de l'apport larvaire. Dans ce cas, la mortalité intervenant aux stades recrues et juvéniles ne serait pas suffisamment importante ou variable pour masquer l'influence du recrutement dans la taille des populations adultes, et par conséquent, les variations spatiales ou temporelles de l'abondance des adultes sont positivement corrélées à celles des jeunes stade vie (recrues et juvéniles). Dans ce modèle, il est donc important de déterminer si la structure spatiale des adultes, juvéniles et recrues sont similaires et si la mortalité post-fixation est densité indépendante (Fraschetti et al. 2002).

Le modèle de stock-recrutement stipule que l'apport larvaire et, par conséquent, le recrutement sont fonction de l'abondance des populations adultes (Hughes et al. 2000, Adjeroud et al. 2017). Une diminution importante de stock reproducteur (les adultes) pourrait donc diminuer de façon drastique l'abondance des recrues. Chez les coraux, cette relation peut être démontrée par une forte corrélation entre la fécondité et l'abondance des adultes et l'abondance des recrues (Hughes et al. 2000, Dubé et al. 2017). Ce modèle est très dépendant de l'impact des perturbations et stress locaux (cyclones, blanchissement, pollution et prédation) sur l'abondance et la structure de taille des assemblages coralliens adultes, ainsi que sur la fécondité, la production et la qualité des larves (Coma & Lasker 1997, Hughes et al. 2000, Dubé et al. 2017). Ce modèle suppose généralement une forte rétention larvaire à l'échelle locale (Hughes et al. 2000, Dubé et al. 2017). Comme pour le cas du modèle de limitation par le recrutement, une forte proportion de reproduction asexuée par fragmentation et de recrutement allochtone peut masquer cette relation (Hughes et al. 2000, Thomson et al. 2021).

Enfin, le modèle de prédation/compétition se caractérise par l'absence de corrélation entre la distribution spatiale des jeunes stades (juvéniles et recrues) et les adultes (Bak & Engel 1979, Edmunds 2000, Penin et al. 2007, Adjeroud et al. 2017). Ce modèle suggère que le recrutement initial est suffisamment élevé pour saturer l'habitat, et que c'est la mortalité post-fixation précoces et la disponibilité limitée des ressources et de l'espace qui influencent la structure des populations adultes (Hereu et al. 2012, Nozawa et al. 2013).

## 1.4. État des connaissances sur les récifs coralliens de Madagascar

### 1.4.1. Récifs de Madagascar

Madagascar est un État insulaire de l'Océan Indien situé à 400 km au large du Mozambique, au sud-est du continent africain. C'est la quatrième plus grande île mondiale avec une superficie de 592 800 km$^2$, entourée de 5000 km de côte. Géographiquement, l'île se localise entre la latitude 12°S et 26°S et la longitude 43°E et 51°E. Madagascar fait partie des îles de l'Océan Indien au même titre par exemple que l'île de La Réunion, l'île Maurice, les Comores ou les Seychelles. Sa population est estimée à 27 249 564 habitants, soit une densité de 46,40 habitants/km² (INSTAT 2020). De par sa localisation, Madagascar bénéficie d'un climat tropical soumis aux régimes de vents de mousson et d'alizé (Randriamarolaza et al. 2022). Il existe deux saisons : la saison des pluies (saison chaude) de novembre à avril et la saison sèche (saison fraîche) de mai à octobre (Kameni Nematchoua et al. 2020). Les cyclones tropicaux frappent chaque année, essentiellement dans la région nord-est, généralement de novembre à avril (Mavume et al. 2009, Rakotobe et al. 2016).

Les écosystèmes marins de Madagascar sont principalement composés de mangroves, d'herbiers de phanérogames et de récifs coralliens. La superficie des récifs coralliens y est estimée à 12 600 km², dont les plus développés se trouvent : i) dans le sud-ouest, en allant depuis le sud du village d'Androka vers le nord jusqu'à Morombe ; ii) dans le nord-ouest, de Sahamalaza en passant par la baie d'Ambaro avec l'archipel de Nosy Be, Nosy Mitsio et jusqu'à Nosy Hara ; iii) les récifs de la côte nord-est depuis Vohemara, incluant la presqu'île Masoala et les récifs autour de Toamasina et de Sainte-Marie (Cooke 2012). Les récifs coralliens de Madagascar sont majoritairement de type « frangeant », suivi des récifs barrières, des bancs coralliens et des récifs immergés (Cooke 2012).

Madagascar est considéré comme un hotspot de biodiversité marine dans la région sud-ouest de l'Océan Indien, car elle abrite près de 35,8% des récifs de la région et contribue à la biodiversité élevée de la région avec ses 380 espèces de coraux, sur un total mondial de 1542 (McKenna et al. 2003, Obura et al. 2011). Cependant, ses récifs sont confrontés à de nombreuses menaces de dégradation, similaires à celles rencontrées dans le monde entier. Les principales menaces sont le réchauffement climatique, l'hyper-sédimentation et la surpêche (Bruggemann et al. 2012, Cooke 2012, Maina et al. 2012, 2013, Andréfouët et al. 2013). Les événements climatiques tels que les épisodes d'El Niño de 1998 et de 2015-2016 ont provoqué un réchauffement significatif des eaux de l'océan, avec des impacts contrastés sur les écosystèmes coralliens de Madagascar. Les épisodes de blanchissement observés après ces événements, ainsi que d'autres événements ponctuels d'élévation de température tels que ceux de 2002, 2010 et 2020, ont entraîné des mortalités massives de coraux dans certaines régions de Madagascar (Ahamada et al. 2002, Obura et al. 2017). Dans le nord-est, par exemple, le stress thermique de 1998 n'a provoqué qu'un faible blanchissement de 5% à 9,9% des colonies touchées, tandis que dans le sud-ouest, à Andavadoaka, 42% des récifs ont été affectés et 62% à Belo sur Mer (Ahamada et al. 2002). Malgré ces événements, les récifs coralliens de

Madagascar conservent une grande biodiversité et représentent une importante source de revenus pour les communautés locales (Harris 2007). La différence de réponse au stress thermique entre les régions nord et sud de Madagascar est attribuable à la présence d'upwelling d'eau froide, résultant du passage du Courant Sub-Equatorial le long de la côte nord-est et de sa bifurcation vers le nord. En outre, la forte précipitation dans le nord ainsi que l’apport importante en eau douce peuvent atténuer le stress thermique subis par les coraux. Dans la région sud-ouest de l'île, le faible niveau de précipitations par an et l'assèchement des principales rivières n'ont que très peu d'effet sur la température de l'eau. Toutefois, le rejet des nutriments et des sédiments par les rivières, accentué par la mauvaise gestion des terres agricoles et les activités minières en amont, provoque des dommages irréversibles sur les récifs situés en aval des embouchures (Webster & McMahon 2002, Nadon et al. 2008, Maina et al. 2013). Malgré cela, la pêche récifale reste la principale source de protéines pour plusieurs millions de Malgaches vivant sur les côtes (Webster & McMahon 2002). La pression anthropique sur les récifs coralliens de Madagascar est particulièrement importante et se manifeste de différentes manières. Tout d'abord, l'augmentation de la population et l'évolution des modes de vie ont conduit à une intensification de la pêche et à une surpêche des espèces clés, telles que les herbivores qui jouent un rôle crucial dans la régulation des macroalgues. Par ailleurs, la croissance économique et le développement urbain ont entraîné un accroissement des polluants déversés dans les milieux marins, ainsi qu'une dégradation des habitats côtiers, tels que les platiers friables. Enfin, les activités minières, les pratiques agricoles inadaptées et les méthodes destructrices de pêche ont également des impacts néfastes sur les récifs coralliens (Andréfouët 2008, Harris et al. 2010, Maina et al. 2012, 2013, Andréfouët et al. 2013).

Ces pressions ont eu des conséquences importantes sur la santé des récifs coralliens malgaches. Une étude publiée en 2017 a montré une diminution du recouvrement corallien de 50 à 30% entre 1998 et 2016, consécutive notamment aux événements de blanchissement (Obura et al. 2017). En outre, la surpêche des herbivores a favorisé le développement des macroalgues, au détriment des coraux, conduisant à un changement de la composition des communautés benthiques récifales. La diminution de l'abondance des poissons herbivores observée au cours des deux dernières décennies souligne l'ampleur du déclin des récifs coralliens de Madagascar.

### 1.4.2. Historique des recherches

Les récifs coralliens de Madagascar sont parmi les sites les plus étudiés de la région sud-ouest de l'Océan Indien. Les premières recherches ont été menées dès les années 1950 par l'ORSTOM (devenu depuis l'Institut de Recherche pour le Développement), sur le site de Nosy Be, qui est aujourd'hui le Centre National de Recherches Océanographiques (CNRO), et par l'Université d'Aix-Marseille et sa Station Marine d'Endoume, sur le site de Toliara, qui est aujourd'hui l'Institut Halieutique et des Sciences Marines depuis 1961 (IHSM). Ces premières études ont porté sur les inventaires floristiques et faunistiques, la géomorphologie et la sédimentologie, les facteurs environnementaux, le plancton et l'étude des peuplements des récifs coralliens et des mangroves (Angot 1950, Guilcher 1954, Pichon 1964, 1972, 1978, Thomassin 1970, 1971, Clausade et al. 1971, Battistini 1977, 1995, Vasseur et al. 1988, Vasseur 1997, Salomon 2009, Menu & Roederer 2013). Grâce à ces années de recherche, près de 6000 espèces ont été identifiées dans la région de Toliara, et près de 400 rapports et publications scientifiques ont été produits (Vasseur 1997, Harris et al. 2010).

Après l'arrêt des recherches en 1972 suite au départ des chercheurs français, aucune recherche portant sur la thématique des récifs coralliens n'a été effectuée pendant environ une décennie (Vasseur 1997). Depuis, une réorientation de la recherche vers des secteurs plus stratégiques, tels que la pêche industrielle et l'aquaculture, a été observée. Suite à la recommandation de l'UICN en 1984 et à la conférence de Madagascar sur la conservation des ressources naturelles en 1985, un premier bilan complet de l'état de santé du récif corallien de Toliara a été réalisé en 1987. L'objectif était la création de réserves marines dans la région de Toliara (Vasseur 1997). Cette étude est donc la première à détecter les signes de dégradation des écosystèmes récifaux, l'importance des impacts humains et à proposer des études à conduire pour une bonne gestion des écosystèmes côtiers et la mise en place d'aires marines protégées (Vasseur 1997). Cette étude a également suscité plusieurs travaux sur la pêche (langouste et poissons), la valorisation des nouvelles ressources (algues) et les essais d'aquaculture (concombre de mer, crevette). Vers les années 2000, plusieurs initiatives se sont succédées pour mettre à jour l'état de santé de plusieurs récifs de Madagascar, inventorier les espèces marines (invertébrés, coraux, poissons, phanérogames et palétuviers), évaluer la tendance actuelle des dégradations des habitats et l'état des stocks des espèces à forte valeur économique comme les langoustes, concombres de mer et crabes. Malheureusement, ces recherches étaient très ponctuelles, ce qui ne permet pas d'évaluer la variation temporelle de l'état de santé de ces habitats (Webster & McMahon 2002, Nadon et al. 2008, Harris et al. 2010, Brenier et al. 2011, Maharavo 2011, Obura et al. 2011, Bruggemann et al. 2012, Maina et al. 2012, Andréfouët et al. 2013, Sheridan et al. 2014).

Au niveau des récifs coralliens, des inventaires de la biodiversité marine des côtes nord-ouest et nord-est de Madagascar par l'ONG Conservation International (CI) et le Centre National de Recherche sur l'Environnement (CNRE) ont permis de déceler une forte diversité de coraux (380 espèces ; Obura et al. 2011, Maharavo 2009) associée à celle d'autres groupes récifaux comme les poissons (788 espèces) et les mollusques (525 espèces ; McKenna & Allen 2003, Maharavo 2009). Plusieurs travaux ont montré que certains récifs malgaches, notamment dans le sud-ouest de l'île, se sont considérablement dégradés durant les 60 dernières années (Nadon et al. 2008, Maharavo 2009, McClanahan et al. 2009, Harris et al. 2010, Sheridan et al. 2014). Ces dégradations sont principalement dues à la surpêche, l'hyper-sédimentation, aux effets du réchauffement climatique (Quod et al. 2000, Harris et al. 2010, Andréfouët et al. 2013, Rasoamanendrika 2014) et des cyclones tropicaux (Carter et al. 2022). Cette dégradation se manifeste également chez les communautés de poissons coralliens, pour lesquelles seules 63 % des espèces inventoriées en 1972-1979 ont pu être observées en 1987 (Vasseur 1998).

## 1.5. Objectif et structure de la thèse

L'objectif principal de cette étude est d'approfondir notre compréhension des processus clés liés à la structuration, à la dynamique et à la résilience des communautés de coraux dans la région de Toliara, située au sud-ouest de Madagascar. Plus précisément, cette étude se concentre sur plusieurs aspects essentiels : la structure spatiale, la reproduction, le recrutement et les mécanismes de régulation des assemblages coralliens. En combinant ces différentes approches, notre objectif est d'obtenir une vision plus précise de l'état de santé, des mécanismes de maintien et du potentiel de résilience des communautés de coraux de cette région. L'objectif est également de fournir des informations rigoureuses pour orienter les efforts de conservation et de gestion de ces écosystèmes vulnérables et menacés.

Le présent manuscrit est organisé en sept chapitres. Le chapitre d'introduction expose le contexte général de l'étude, tandis que le deuxième chapitre détaille les matériels et méthodes utilisés dans notre travail. Les chapitres suivants (3, 4, 5, 6) explorent respectivement la structure spatiale, la reproduction, le recrutement, et la régulation des assemblages de coraux. Ces chapitres sont rédigés sous forme d'articles scientifiques, publiés, en révision, ou récemment soumis dans des journaux scientifiques internationaux. Enfin, le septième chapitre constitue une synthèse générale des conclusions obtenues dans l'ensemble des chapitres, et propose quelques perspectives à ce travail, notamment en termes de gestion et de conservation des récif coralliens.

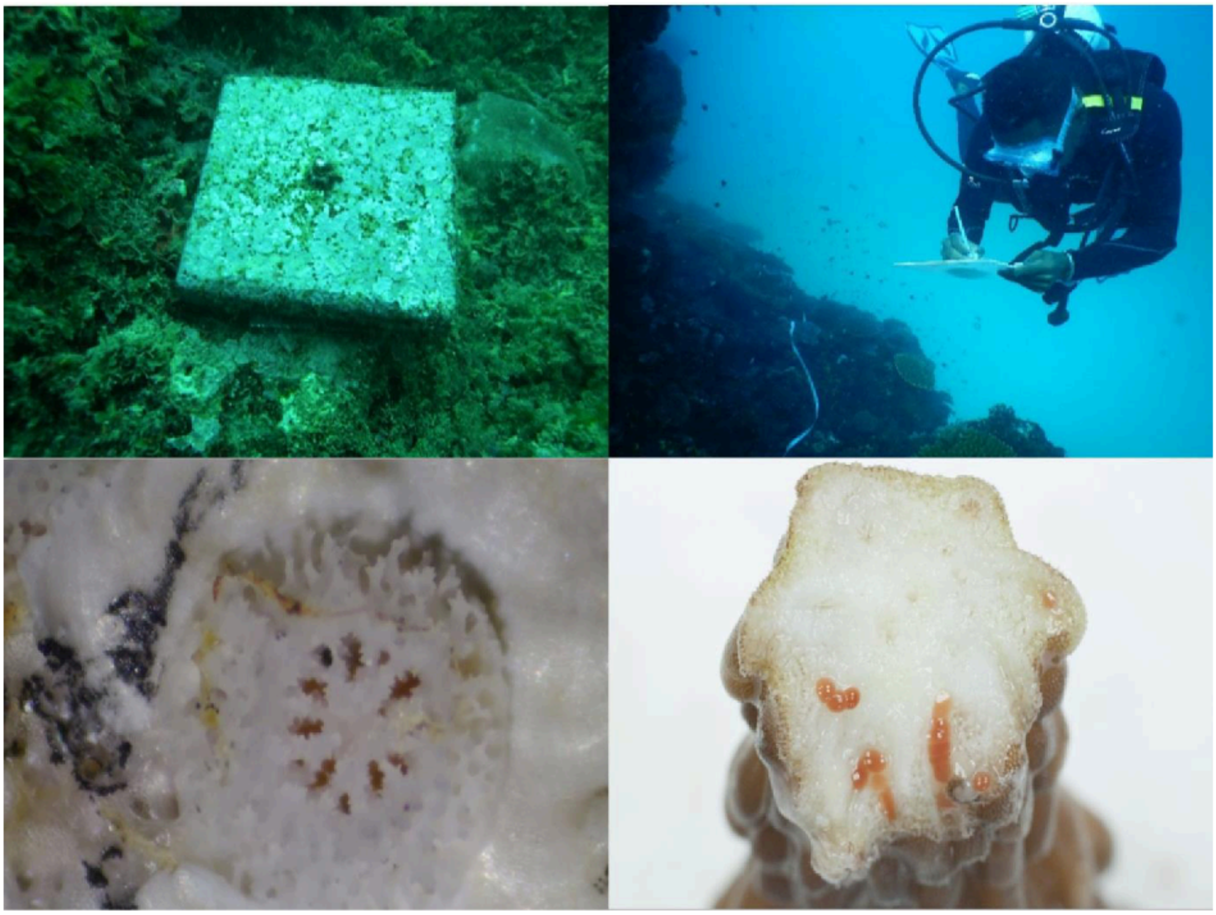
Dans le chapitre 3, intitulé « **Structure spatiale des communautés coralliennes dans la région de Toliara, sud-ouest de Madagascar, et implications pour la conservation et la gestion** », nous examinons la variation spatiale des communautés coralliennes au sein et entre les principaux habitats récifaux (massifs coralliens lagonaires, pente interne, et pente externe). Ce chapitre examine notamment l'hétérogénéité spatiale du recouvrement des principaux groupes benthiques (coraux vivants, macroalgues, gazons algaux, algues calcaires, coraux mous, coraux morts, débris, sable, autres organismes) ainsi que les huit principaux genres de coraux, entre les 10 stations d'étude. La richesse générique, la composition taxonomique, l'abondance des colonies adultes (tous taxons confondus et pour les huit principaux genres) et la structure de tailles des coraux adultes ont également été quantifiées. L'implication de nos résultats en termes de conservation et de gestion des récifs de Toliara est discutée.

Dans le chapitre 4, intitulé « **Reproduction sexuée de quelques espèces de coraux du Grand Récif de Toliara, sud-ouest de Madagascar** », nous déterminons les périodes et le degré de synchronisation des pontes de quatre espèces de coraux présentes sur le Grand Récif de Toliara, durant deux années de suivi. Le lien entre les modes de reproduction et les facteurs environnementaux (température de l'eau, vitesse du vent, et phase de la lune) est également examiné. Les résultats permettent non seulement d'apporter les premières connaissances sur la reproduction des coraux dans la région de Toliara, mais aussi de mieux comprendre les caractéristiques du recrutement.

Dans le chapitre 5, intitulé « **Recrutement des coraux dans la région de Toliara, sud-ouest de Madagascar : variabilité spatio-temporelle, influence de la composition du substrat et implication pour la conservation des récifs** », nous évaluons la variation spatiale multi-échelles (au sein et entre les trois principaux habitats récifaux, mais aussi à l'échelle des stations et des plaques de recrutement) et la variation interannuelle (sur une période de trois ans) de l'abondance et de la composition des assemblages de recrues coralliennes. L'influence de la composition du substrat sur le recrutement des coraux est également examinée.

Dans le chapitre 6, intitulé « **Mécanismes de régulation des populations de coraux scléractiniaires dans la région de Toliara, sud-ouest de Madagascar** », nous comparons la variation spatiale de l'abondance des recrues, des juvéniles, et des adultes à l'échelle des habitats et des stations sur une période de trois ans. L'objectif est d'évaluer la prépondérance des modèles de régulation (limitation par le recrutement, stock-recrutement, et prédation/compétition) pour différents taxa coralliens aux traits d'histoire de vie contrastés. Ces résultats, couplés à ceux des chapitres précédents, permettent de mieux appréhender les processus liés au maintien et à la dynamique des assemblages coralliens, et d'estimer leur capacité de résilience.

# Chapitre 2 :
# Matériels et méthodes



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## 2.1. Zone d'étude : les récifs coralliens du sud-ouest de Madagascar

Situé dans le sud-ouest de Madagascar, la région administrative Atsimo Andrefana se trouve dans l'ex-province de Toliara, dont la capitale est la ville de Toliara. Elle couvre une superficie de 66 502 km$^2$ correspondant à 11,4% de la superficie de Madagascar (CREAM 2013). La population est estimée à 1 352 456 habitants avec un taux d'accroissement de 5%. Le climat de la région est de type tropical subaride marqué par la saison fraiche et sèche (d'avril à septembre) et la saison chaude et humide d'octobre à mars (INSTAT 2020). La saison des pluies est relativement courte (de novembre à mars), avec une faible précipitation moyenne (< 600 mm ; CREAM 2013). Les environs de la région sont affectés par des cyclones provenant de l'Océan Indien ou du canal de Mozambique, mais leur fréquence est moins importante que dans la partie nord-est de Madagascar ou dans d'autres régions du sud-ouest de l'Océan Indien. Ces phénomènes météorologiques sont généralement accompagnés de fortes précipitations, entraînant ainsi d'importantes inondations (CREAM 2013). La période d'insolation est longue, en moyenne de 225 jours par an. Les marées maritimes sont du type semi-diurne avec alternance de vives et mortes eaux selon la lune (Harmelin-Vivien 1981). L'amplitude maximale de la marée est de 3 m, et dans ce cas les platiers compacts émergent à marée basse (Pichon 1978, Harmelin-Vivien 1981). Les marées basses de vives-eaux s'observent généralement au milieu de la journée et au milieu de la nuit. Le vent dominant souffle du sud-sud-ouest qui engendre une houle qui se propage en direction de nord-nord-est (Weydert 1974, 1979). L'amplitude moyenne est de1,5 à 2 m soumettant le front récifal à une agitation importante (Weydert 1974). La température de l'eau varie généralement de 22°C à 30°C tout au long de l'année avec quelques pics pouvant dépasser le 31°C (Botosoamananto et al. 2021).

Le récif corallien de la région de Toliara se situe entre la baie de Saint Augustin au sud (où débouche le fleuve Onilahy) et la baie de Ranobe au nord (Clausade et al. 1971, Vasseur 1997). Les formations récifales de la région de Toliara sont extrêmement variées. Elles se présentent sous différent types : récif barrière, récif frangeant, et banc corallien (Weydert 1974, 1979, Pichon 1978). Elles sont implantées sur le rebord et sur le plateau continental qui se prolonge vers la large plaine côtière quaternaire (Battistini 1964, Weydert 1974). Le Grand Récif de Toliara (GRT) et la barrière récifale d'Ifaty sont les récifs les plus développés du sud-ouest de Madagascar. Ils intègrent quatre types d'habitats distincts :

i) la pente externe, une formation de type éperons et sillons, constituant l'habitat où les coraux sont les diversifiés et abondants ;

ii) le platier compact, qui est peu profond et fortement dégradé, correspond à la combinaison de la levée détritique et du platier friable ;

iii) la pente interne qui est également peu profonde, à faible diversité et recouvrement corallien, fortement dégradée et qui partage les mêmes pressions que le platier compact ;

iv) les récifs du lagon, composés des massifs coralliens lagonaires et de bancs coralliens, qui sont relativement profonds et possèdent une richesse taxonomique et un recouvrement corallien élevés.

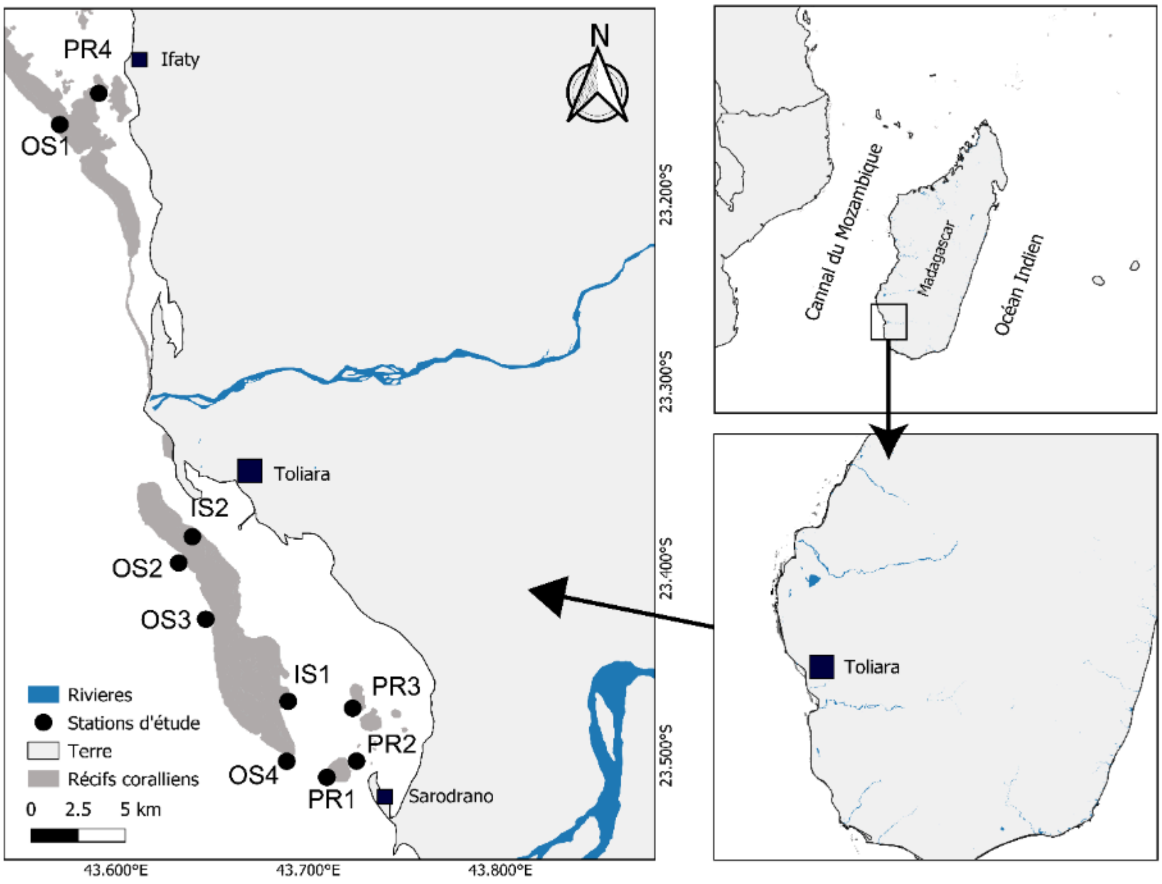


**Figure 2.1.** Localisation de la zone d'étude et des dix stations d'échantillonnage sur les récifs de la région de Toliara, sud-ouest de Madagascar. PR : massif coralliens lagonaires (*patch reefs*), IS : pente interne (*inner slope*), et OS : pente externe (*outer slope*).

La diversité corallienne dans la région de Toliara est fortement variable selon les zones géographiques et les types de récifs ; les sites présentant la plus grande diversité étant situés sur des récifs isolés et sur le récif barrière externe dans des eaux plus profondes, là où ils sont moins exposés aux pressions de pêches traditionnelle et industrielle (Nadon et al. 2008). Le premier bilan de la biodiversité de la région fait état de 6000 espèces marines (Clausade et al. 1971, Weydert 1974), mais le niveau de connaissances par taxon n'est pas homogène. Une récente évaluation de la biodiversité de la région sud-ouest a inventorié 166 espèces de coraux scléractiniaires reparties sur 55 genres et 17 familles (Harding et al. 2006), soit 53 espèces de plus que les 113 espèces observées par Pichon (1978). Cette étude fait également état de 385 espèces de poissons appartenant à 182 genres et 57 familles et 258 espèces de mollusques appartenant à 112 genres et 71 familles.

Les récifs de la région de Toliara jouent un rôle à la fois économique, social, et culturel pour la population riveraine (Harris et al. 2010, Bruggemann et al. 2012, Maina et al. 2013). Ainsi, les récifs du sud-ouest de Madagascar n'échappent au contexte national et international de dégradation. Les principales pressions sur les récifs du sud-ouest de Madagascar sont classiques des pays tropicaux en développements, à savoir : la pratique d'activités de pêche, parfois destructrices (pêche à pieds, seine, empoisonnement, collectes d'organismes clés comme les poissons et invertébrés herbivores), la pollution et l'hyper-sédimentation issus du développement urbain, de la déforestation, du développement de l'agriculture et des activités minières qui se trouvent en amont des deux principales rivières (Fiherenana et Onilahy), l'extraction des bloc de coraux pour la construction de maisons et tombeaux (Nadon et al. 2008, Harris et al. 2010, Bruggemann et al. 2012, Maina et al. 2012).

La gestion des récifs coralliens à travers la création d'Aires Marines Protégées (AMP) dans plusieurs régions côtières de Madagascar a connu des progrès significatifs. Dans la région sud-ouest, la mise en place d'AMP gérées localement a obtenu un soutien important de la part des acteurs locaux tels que les associations de pêcheurs, les opérateurs touristiques, les sociétés d'exportation de produits de la mer et les organismes gouvernementaux (Rakotoson & Tanner 2006, Ratsimbazafy et al. 2019). Grâce à des lois locales et au consentement des différentes parties prenantes, des sanctuaires de biodiversité et des réserves temporaires ont été créés dans le but d'accroître la productivité des pêches (Brenier & Vogel 2017, Ratsimbazafy et al. 2019). Malgré l'importance étendue des récifs coralliens dans notre zone d'étude (d'une longueur de 19 km), la gestion urgente face aux perturbations anthropiques et naturelles, ainsi que le manque de données sur leur état de santé, n'ont pas encore permis la mise en place de réserves marines jusqu'à présent.

## 2.2. Choix et codification des stations d'étude

Cette étude a été menée sur les communautés récifales de 10 stations réparties dans les trois habitats principaux des récifs de Toliara, à savoir les massifs coralliens lagonaires, la pente interne et la pente externe (voir Figure 2.1). Les codes des stations sont abrégés comme suit :

les deux premières lettres indiquent les habitats récifaux (PR pour les « patch reefs » ou massifs coralliens lagonaires, IS pour la « inner slope » ou pente interne, et OS pour la « outer slope » ou pente externe), suivies des numéros des stations. Ainsi, quatre stations ont été sélectionnées sur les massifs coralliens lagonaires (PR1, PR2, PR3, PR4), deux stations sur la pente interne (IS1 et IS2) et quatre autres stations sur la pente externe (OS1, OS2, OS3 et OS4). Les échantillonnages ont été réalisés entre 8 et 12 mètres de profondeur pour l'ensemble des dix stations.

**Tableau 2.1.** Principales caractéristiques des 10 stations étudiées dans la région de Toliara, au sud-ouest de Madagascar.

| Stations | Habitat | Latitude | Longitude | Profondeur (m) |
|---|---|---|---|---|
| **PR1** | Massifs coralliens lagonaires | -23.50291 | 43.725132 | 8 |
| **PR2** | Massifs coralliens lagonaires | -23.51153 | 43.709762 | 8 |
| **PR3** | Massifs coralliens lagonaires | -23.4746 | 43.723102 | 8 |
| **PR4** | Massifs coralliens lagonaires | -23.14571 | 43.591147 | 8 |
| **IS1** | Pente interne | -23.47272 | 43.68718 | 8 |
| **IS2** | Pente interne | -23.38282 | 43.6398 | 8 |
| **OS1** | Pente externe | -23.16239 | 43.570894 | 8 |
| **OS2** | Pente externe | -23.39685 | 43.63275 | 12 |
| **OS3** | Pente externe | -23.42697 | 43.6468 | 10 |
| **OS4** | Pente externe | -23.503 | 43.688823 | 10 |

## 2.3. Structure des communautés coralliennes

Le pourcentage de recouvrement des principales catégories de substrat a été évalué par la méthode des photo-quadrats (Kohler & Gill 2006). Cette technique, largement utilisée en écologie récifale, permet d’obtenir un nombre de photos élevé tout en limitant le temps de plongée. A chaque station, trois transects fixes de 10 m ont été placés parallèlement à la côte. Dans le cas des éperons-sillons sur la pente externe, ces trois transects sont placés parallèlement au prolongement des éperons. A l’aide d’un appareil photo sous-marin (Nikon Coolpix, 13,5 mégapixels) fixé un quadrat de 0.25 m$^2$, le plongeur se déplace le long du transect et prend des photos tous les mètres. Ces photos sont ensuite analysées au laboratoire à l'aide du logiciel CPCe (Coral Point Count with Excel extensions). Sur chaque photo, 100 points sont aléatoirement disposés et la catégorie de substrat sous chacun de ces points est identifiée (corail dur, corail mou, éponge, gorgone, hydraire, algues, et les catégories abiotiques coraux morts, débris, et sable). Pour les coraux durs, les colonies sont identifiées au genre. L'estimation du pourcentage de recouvrement des différentes catégories de substrat a été réalisée une fois par an, de 2017 à 2020.

## 2.4. Caractérisation de la stratégie reproductive des coraux

### 2.4.1. Suivi de la maturation des gamètes

Pour déterminer les périodes et le degré de synchronisation de la ponte des coraux scléractiniaires de la région de Toliara, nous avons choisi quatre espèces en fonction de leur abondance et de leur facilité d'identification (Tableau 2.2).

**Tableau 2.2.** Liste des espèces sélectionnées pour l'étude des stratégies reproductives.

| **Familles** | **Espèces** |
|---|---|
| ***Oculinidae*** | *Galaxea fascicularis* |
| ***Acroporidae*** | *Acropora nasuta* |
| ***Acroporidae*** | *Acropora digitifera* |
| ***Faviidae*** | *Platygyra daedala* |

Les échantillonnages consistent à prélever des fragments de colonies adultes en milieu naturel, afin de suivre la variation de la maturité des gamètes. L'observation a été faite tous les mois pendant la période froide et de manière plus intensive au fur et à mesure de l'entrée dans la saison chaude, avec des échantillonnages toutes les deux semaines, puis hebdomadaires, et enfin journaliers. Pour les espèces branchues, on coupe, à l'aide d'un sécateur, trois branches de 6 cm de longueur sur une colonie possédant un diamètre supérieur à 15 cm (Kruger & Schleyer 1998) de façon à ne pas endommager la colonie. Pour les autres formes de colonies (massives, encroûtantes), un tube métallique de 20 mm est utilisé pour prélever des carottes de squelette et tissus (Massé 2014). Au retour de chaque plongée, les échantillons sont disséqués et observés à la loupe binoculaire pour détecter la présence ou l'absence des gonades et gamètes, et leur état de maturité. La taille approximative ainsi que la couleur des gonades et des gamètes sont notées (Figure 2.2.). Plusieurs états de maturité sont distingués : « mature » si les ovocytes sont pigmentés, « immature » si les ovocytes sont pâles ou blancs et de petites tailles, et « absent » s'ils sont indétectables à l'œil nu (Olivier et al. 1988, Baird et al. 2002, Carroll et al. 2006, Mangubhai 2007, Gilmour et al. 2016). L'état de maturité permet d'estimer la période de ponte des coraux.

### 2.4.2. Suivi des pontes

L'observation de l'état de maturité des gonades et des gamètes permet d'avoir une indication sur la période probable de ponte des colonies coralliennes. En complément, des colonies identifiées ont été suivies en milieu naturel. En période de ponte probable, des sorties quotidiennes ont été réalisées. L'objectif était d'être présent le jour de la ponte, et de pouvoir ainsi documenter les modalités de la ponte pour les espèces sélectionnées : heure de ponte (certaines espèces pondent au crépuscule, d'autres en milieu ou en fin de nuit), la durée de ponte (brève, étendue sur toute ou une partie de la nuit, etc.), la synchronisation à l'échelle locale pour une même espèce (toutes les colonies d'une même espèce à une station pondent-elles au même moment ?) et pour l'ensemble des espèces d'une station. L'influence des conditions environnementales (température, vitesse du vent, phase de la lune, marée) sur la maturation et le déclanchement de la ponte a été évaluée.

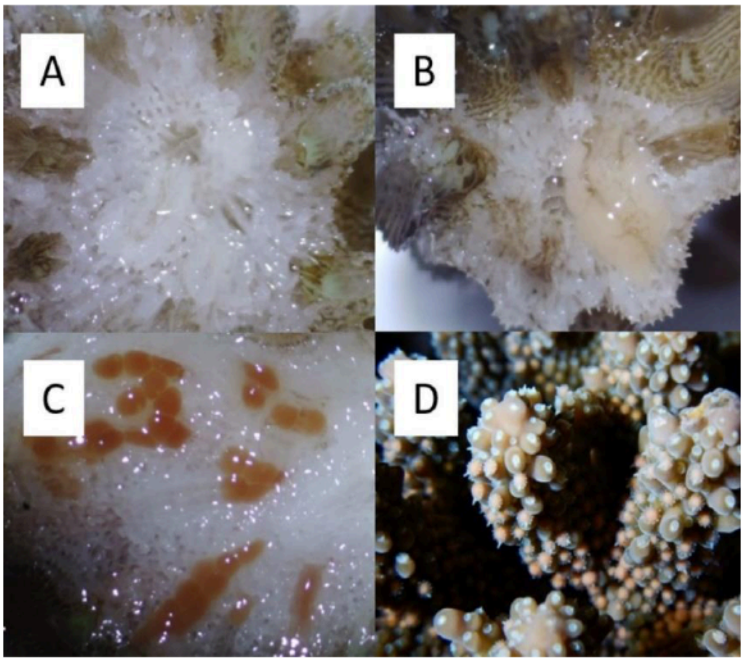


**Figure 2.2.** Section de branches de colonies d'*Acropora* montrant les différents stades de maturation des gamètes retenus dans notre travail : A) œufs absents, B) œufs pâles immatures, C) œufs pigmentés et matures ; et photos d'une colonie d'*Acropora* sur le point de pondre (D).

## 2.5. Variation spatiale et temporelle du recrutement des coraux

Dans l'étude de recrutement des coraux, nous avons choisi d'utiliser des plaques artificielles de fixation en terre cuite de dimension 11 × 11 × 1 cm. Chaque plaque est installée sur une platine en inox à l'aide d'un écrou papillon (Figure 2.3.). Les platines sont solidement fixées au substrat par deux chevilles en plastique. Cette méthode d'étude du recrutement des coraux, largement utilisée, est détaillée dans Mundy (Mundy 2000) et Adjeroud et al. (2007, 2022). A chaque station, 20 plaques ont été mises en place et retirées après quatre mois durant l'été austral (octobre à janvier).

Au laboratoire, ces plaques ont été plongées dans de l'eau de Javel pendant 24 h puis séchées au soleil, afin de les débarrasser des parties vivantes et ne laisser que les squelettes de recrues coralliennes (Adjeroud et al. 2010). Après ce traitement, les plaques sont observées à la loupe binoculaire. À ce stade de développement, les structures calcaires, sur lesquelles se basent l'identification des coraux, ne sont pas suffisamment développées pour permettre une identification à haut niveau taxonomique, et seules trois familles peuvent être identifiées (Babcock et al. 2003) : les Acroporidae, les Pocilloporidae, et les Poritidae. Une catégorie « autres » regroupe les recrues des autres familles, lesquelles ne peuvent pas être identifiées par observation à la loupe binoculaire (Figure 2.4). Une cinquième catégorie, celle des « cassées », regroupe toutes les recrues dont les structures calcaires sont trop endommagées pour être placées dans une des quatre catégories précédentes.

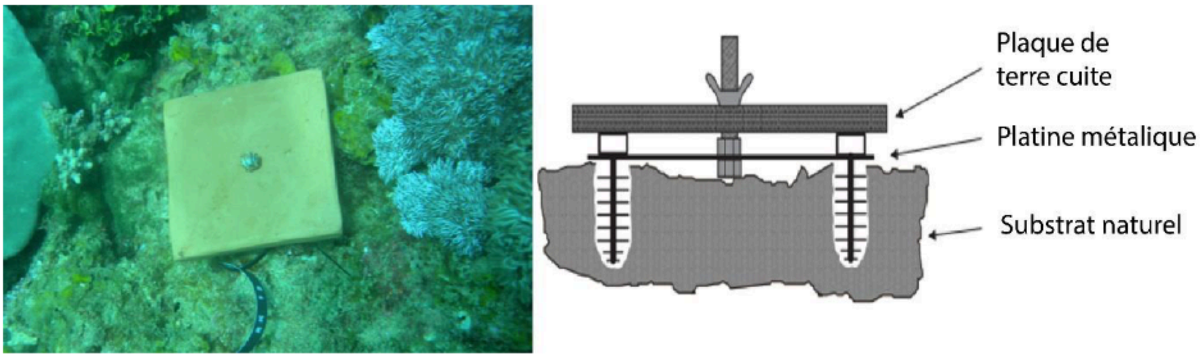


**Figure 2.3.** Méthode d'attachement direct de plaque de recrutement. A gauche : plaque en terre cuite *in situ* lors de sa pose (elle n'est pas encore colonisée) ; à droite : schéma décrivant les différents éléments du dispositif de recrutement (d'après Jouval et al. 2019).

**Figure 2.4.** Illustration des trois principales familles de recrues (Pocilloporidae, Acroporidae et Poritidae). Identification basée sur les descriptions de la morphologie du squelette (Babcock et al. 2003).

## 2.6. Mécanismes de régulation des populations de coraux

Pour les coraux scléractiniaires, les juvéniles sont définis comme des colonies immatures visibles à l'œil nu et dont le diamètre est inférieur ou égal à 5 cm, alors que les colonies dont le diamètre est supérieur à 5 cm sont considérées comme des adultes capables de se reproduire sexuellement (Penin et al. 2007, Adjeroud et al. 2017). L'estimation de l'abondance des juvéniles et des adultes a été réalisée dans 3 transect-couloirs de 10 m2 (10 × 1 m) à chaque station, qui sont les mêmes transects que ceux utilisés pour la caractérisation de la structure des communautés coralliennes (Figure 2.5 ; Penin et al. 2007, Penin & Adjeroud 2013). Chaque extrémité du transect a été matérialisée par un piquet en fer à béton, afin de faciliter le repérage lors des échantillonnages suivants. Dans ces transects-couloirs, tous les juvéniles et les adultes ont été comptabilisés et identifiés au niveau du genre, une fois par an, en 2018, 2019 et 2020.

**Figure 2.5.** A gauche : juvénile de *Stylophora* et à droite : transect de comptage et identification des juvéniles et adultes.

## 2.7. Analyse statistique des données

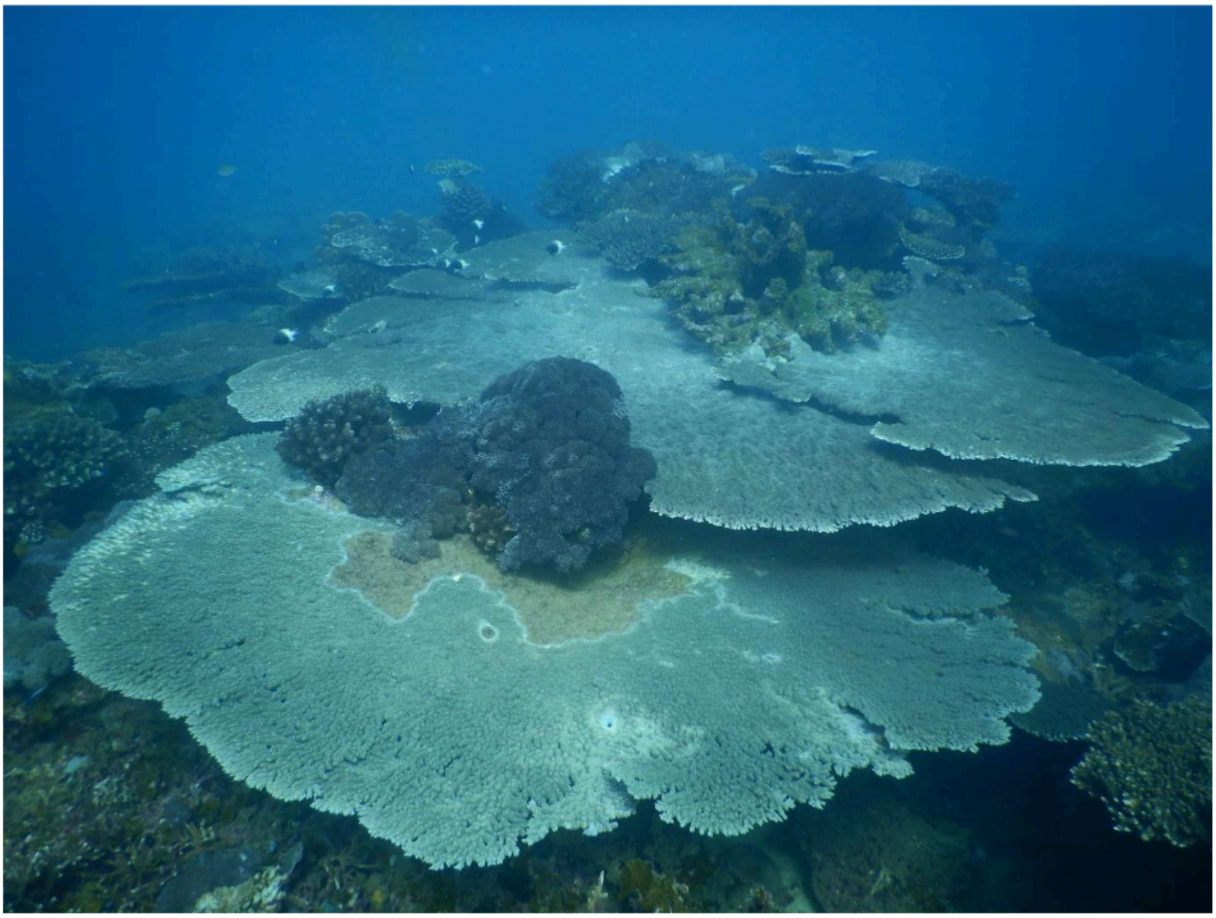
De manière générale, les collectes des données s'étalent de 2017 à 2021 (Annexe 1, 2, 3). Les échantillonnages ont été hiérarchisés à l'échelle des années de suivi, des habitats et des stations, avec comme unité d'échantillonnage le transect pour l'abondance des colonies adultes et juvéniles, le photoquadrat pour la couverture benthique, et la plaque de terre cuite pour le recrutement. Les paramètres environnementaux, comme la température ou la vitesse du vent, ont été évalués à l'échelle régionale, à partir des données satellitaires.

L'analyse statistique des données est spécifique aux différents chapitres et à la nature des données collectées. Une liste récapitulative des sources de variation, descripteurs et les types d'analyse est fournie dans le tableau 2.3.

**Tableau 2.3.** Résumé des principales analyses statistiques utilisées pour chacun des quatre chapitres d'analyse de données réalisées dans ce travail de thèse.

| Chapitre | Source de variation | Descripteurs | Analyse statistique |
|---|---|---|---|
| 3 | Habitats, Stations | Richesse générique | ANOVA |
| | | Composition taxonomique | MDS |
| | | Taux de recouvrement | ANOVA |
| | | Abondance des colonies | ANOVA |
| | | Classe de taille des colonies | ANOVA par permutation |
| 4 | Saisons, Mois | Maturation des gamètes | Descriptif (proportion) |
| 5 | Années, Habitats, Stations | Abondance des recrues | GLMM (négative binomiale) |
| | | Taux de recouvrement | |
| 6 | Années, Habitats, Stations | Abondances des recrues, juvéniles et adultes | GLMM (négative binomiale) |
| | | | Corrélation de Spearman |

# Chapitre 3 :
# Structure spatiale des communautés coralliennes dans la région de Toliara, sud-ouest de Madagascar, et implications pour la conservation et la gestion



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**Botosoamananto RL**, Todinanahary G, Razakandrainy A, Randrianarivo M, Penin L, Adjeroud M (2021) Spatial patterns of coral community structure in the Toliara region of southwest Madagascar and implications for conservation and management. *Diversity 13: 486 (https://doi.org/10.3390/d13100486)*

## Résumé

Les récifs coralliens de Madagascar présentent l'une des biodiversités les plus élevées de l'Océan Indien occidental. Le Grand Récif de Toliara (GRT), sur la côte sud-ouest, a abrité des communautés récifales florissantes dans les années 60, mais a depuis été affecté par des épisodes de blanchissement, une sédimentation élevée, une surpêche et des activités de collecte, entraînant un déclin des coraux signalé pour la dernière fois en 2008. Dans ce travail, nous avons examiné l'hétérogénéité spatiale de la structure des assemblages coralliens au sein et entre les principaux habitats récifaux de la région de Toliara. En 2017, nous avons enregistré une couverture corallienne élevée, avec des valeurs supérieures à 40% dans six des 10 stations, associée à une forte abondance des colonies coralliennes. Nous avons également constaté le retour à un assemblage corallien dominé par les coraux du genre *Acropora*. Bien que ces résultats positifs suggèrent un retour récent à des assemblages coralliens plus sains, ils doivent néanmoins être tempérés, car la diversité que nous avons enregistrée était inférieure à celle des années 60. De plus, nous avons constaté une forte couverture de macroalgues à plusieurs stations, suggérant que l'écosystème récifal est probablement proche du point de basculement vers un changement de phase. Enfin, la structure de taille des principaux taxa coralliens était positivement asymétrique, avec peu de grandes colonies pour assurer le renouvellement des populations locales. La forte variabilité spatiale décrite dans ce travail suggère que les Aires Marines Protégées doivent intégrer une superficie suffisamment grande pour capturer l'échelle de cette hétérogénéité spatiale.

**Mots-clés :** Récifs coralliens ; coraux scléractiniaires ; structure des communautés ; variabilité spatiale ; Madagascar.

## Abstract

Coral reefs of Madagascar have one of the highest biodiversity of the Western Indian Ocean. The Great Reef of Toliara (GRT), on the southwestern coast, has been documented as harbouring flourishing reef communities in the ‘60s, but has since been affected by bleaching events, high sedimentation, overfishing, and gleaning activities, causing a coral decline last reported in 2008. Here, we examined the spatial heterogeneity in community structure of coral assemblages among major reef habitats in the region of Toliara. In 2017, we recorded high coral cover, with values > 40% at six of the 10 stations, which was associated with high abundance of coral colonies. We also documented the return to an *Acropora* dominated coral assemblage. While these positive results suggest a recent return to healthier coral assemblages, they must be tempered, as the diversity that we recorded was lower than in the ‘60s. Moreover, we found a high cover of algae at several stations, suggesting that the ecosystem is likely close to the tipping point toward a phase shift. Finally, the population size-structure of major coral taxa was positively skewed, with few large colonies to ensure the replenishment of local populations. The marked spatial variation suggests that marine protected areas should integrate a sufficiently large area to capture the scale of this spatial heterogeneity.

**Keywords:** Coral reefs; scleractinian corals; community structure; spatial variability; Madagascar.

## 3.1. Introduction

Surrounded by coral reefs of ~2,400 km$^2$ along 1,400 km of coastline, Madagascar is a hotspot of biodiversity in the Western Indian Ocean (Myers et al. 2000, Ganzhorn et al. 2001, Brooks et al. 2006, Cooke 2012). With 380 coral and 788 reef associated fish species, the overall diversity of Madagascar coral reefs is comparable to that of the coral triangle (Veron & Turak 2003, McKenna et al. 2003, Obura et al. 2011, Cooke 2012). This high diversity of reef organisms is probably due to the size and diversity of reef habitats that are particularly well-developed in the northeast, northwest, and southwest coasts (Obura 2008, Ahamada et al. 2008). With ~33 km$^2$ of shallow reef area, the Great Reef of Toliara (GRT), in the southwest coast, is the largest reef complex of Madagascar and the Western Indian Ocean, and has been a refuge for diverse reef taxa, including 714 species of reef fishes (Pichon 1978, Harmelin-Vivien 1981, Rasoarimalala 2001) and 135 species of scleractinian corals (Pichon 1978, Sheppard 1998). This coral reef provides both costal protection and an artisanal fishery for the city of Toliara (Laroche & Ramananarivo 1995, Humber et al. 2017, Lemahieu et al. 2018). The GRT was intensively surveyed in the '60s-'70s, following the establishment of a marine research center in 1961 (currently Institut Halieutique et des Sciences Marines). The diversity and zonation of scleractinian coral assemblages, the primary reef-building species, was first studied by Pichon (1978).

However, like most coral reefs worldwide, those of Madagascar have been increasingly exposed to various types of large-scale natural and anthropogenic perturbations and local stressors that have worsened their socio-ecological vulnerability and resilience (Ahamada et al. 2002, Obura 2005, Harding et al. 2006, 2008, Obura et al. 2011, Cochrane et al. 2019). Overfishing, sedimentation, and thermally induced coral bleaching events have particularly affected the island's coral reefs located around populated cities (Harding et al. 2008, Obura et al. 2017, Gough et al. 2020). Some coral habitats of the GRT have been affected by high sedimentation caused by discharge of the Fiherenana river in the north (36 million tons of sediment/Ha/year) and Onilahy river in the south (84 million tons of sediment/Ha/year) (Payet et al. 2012), favoring the prevalence of coral diseases (Sheridan et al. 2014). Since the '80s, overfishing, destructive fishing, water pollution, and gleaning activities, all linked to the rapid growth of the human population (53% between 1993 and 2008), have also been a major concern for the health of the GRT (Harris et al. 2010, Bruggemann et al. 2012, Andréfouët et al. 2013). In addition, bleaching episodes associated to El Niño events have affected coral and other reef associated species, particularly in 1998 and 2015-2016 (Quod & Bigot 2000, Obura 2005, Obura et al. 2017). All these episodic disturbances and chronic stressors have caused a decline in coral cover and abundance in the last 50 years, particularly for architecturally complex coral taxa such as *Acropora* and *Pocillopora*, with coral cover decreasing from ~50% to 5% during this period at several shallow habitats (Harris et al. 2010, Andréfouët et al. 2013, Todinanahary et al. 2018). This decline has been associated with the increase of fleshy macroalgae or other non-reef building species, such as zoanthids and soft corals in habitats previously dominated by *Acropora* (Nadon et al. 2008, Ahamada et al. 2008, Harris et al. 2010), an undesirable state which provides fewer ecosystem goods and services. Coral diversity has also been affected, with a decline from 38 to 30 genera in shallow habitats, and a loss of 18 genera in seagrass beds over the past 40 years (Bruggemann et al. 2012, Todinanahary et al. 2018).

Despite these increasing threats and the general trend of coral decline, no quantitative studies have recently examined the spatial patterns and community structure of coral assemblages in various coral habitats, thus precluding a precise indication of the current status and the resilience capacities of the GRT. This type of information is however crucial to implement adequate conservation measures that are critically needed considering ongoing human development and importance of reef resources in this area (Harris et al. 2010). Though some Locally Managed Marine Areas (LMMA) have been implemented in the region of the GRT with some success, they focused on fisheries and did not address coral assemblages (Vermeij et al. 2007, Williams et al. 2013).

In this context, the major aim of the present study was to investigate spatial patterns and community structure of coral assemblages among major reef habitats in the region of Toliara, including the GRT. Composition, generic richness, cover (including other benthic taxa), and size-structure of coral assemblages have been quantified and compared among 10 stations. Implications of our results in terms of conservation and management actions are also discussed. The original data set examined here constitutes a reference baseline for evaluating future changes in coral communities, and may help identify effective conservation actions.

## 3.2. Materials and Methods

### 3.2.1. Study area

The present study was conducted in Madagascar’s southwestern region of Toliara, including the Great Reef of Toliara (GRT), located 2 km seaward of Toliara city (Figure 3.1.). Approximately 19 km long and 1-3 km wide, the GRT is a major barrier reef system of the SW

Indian Ocean. High sedimentation comes from mining activities in the highland by the region's two main rivers, Fiherenana in the north and Onilahy in the south. Madagascar is characterized by two main seasons: winter from April to September, when sea surface temperature (SST) falls down to 18°C, and summer from October to March, when rainfall and SST (up to ~30°C) are higher. Dominant winds are from the SW direction. Tropical storms and cyclones generally hit Madagascar from November to May, and are common in the northern and eastern part of the island (94 tropical cyclones recorded from 1948 to 2010) (Doropoulos et al. 2015). The southwest region is less affected as the passage or formation of cyclones in the Mozambique channel is relatively rare (Mahafina 2011, Ratsimbazafy et al. 2019). Malagasy coral reefs have suffered from bleaching events caused by abnormal increases in SST, with major events in 1998 and 2015-2016. These bleaching events have caused an important decrease in coral cover (~20 and 25%, respectively) associated to an increase in algal cover (Ahamada et al. 2002, Obura et al. 2017). In contrast to some other regions of the Western Indian Ocean (Maina et al. 2012), no evidence of significant degradations by outbreaks of the coral predator sea star *Acanthaster* spp. have been reported in Madagascar (Matyas 2015).

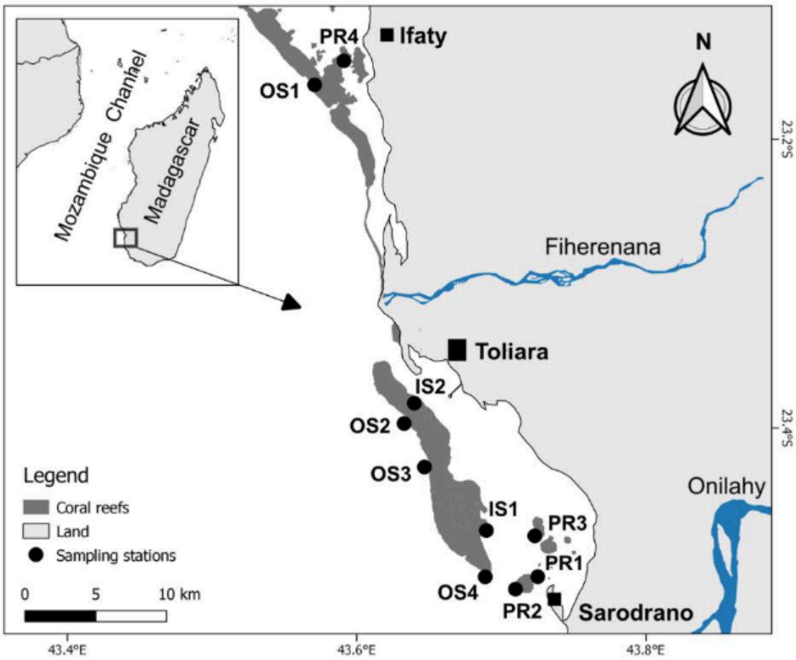

**Figure 3.1.** Map of the southwest coast of Madagascar showing the location of the 10 sampling stations in the Toliara region, including the Great Reef of Toliara (GRT). Stations were located on the three major habitat types: patch reefs (PR), inner slope (IS), and outer slope (OS).

### 3.2.2. Sampling strategy

Sampling was undertaken from February to July 2017. A total of 10 stations were located between the village of Ifaty in the north and the village of Sarodrano in the south, on the three major habitat types: four stations on patch reefs (PR1 to PR4), two stations on the inner reef slope (IS1 and IS2), and four stations on the outer slope (OS1 to OS4; Figure 3.1). These stations were located on the bioconstructed reef framework, between 6 and 12 m depth (see Supplementary Table S1). The percent cover of major living and abiotic substrate was estimated using the photoquadrat method (Kohler & Gill 2006). At each station, 30 photoquadrats of 0.25 $m^2$ (50 × 50 cm) were taken along 3 transects of 10 m length with an underwater camera (Nikon W300). Percent cover was estimated using the Coral Point Count with Excel extension (CPCE 4.1) (Kohler & Gill 2006) software. On each photo, 100 random points were used to quantify percent cover of major benthic categories: hard corals (Scleractinian corals and the calcareous hydrocoral *Millepora*), dead corals (defined as recently dead coral with skeletons covered by thin layer of turf algae), soft corals (Alcyonacea, mainly represented by *Xenia* sp. and *Sarcophyton* sp.), algae (coralline algae, macroalgae, turf), other living taxa (including sponges, hydroids, zoanthids, corallimorphs, tunicates and sea anemones), and abiotic substrates (rubble, and sand).

In addition, generic richness and abundance of adult coral colonies (> 5 cm in diameter) were estimated at each station using three randomly replicated belt-transects of 10 $m^2$ (10 × 1 m), laid parallel to depth contours and separated by ~1 m, following the method described in Adjeroud et al. (2019). The size-structure of the major coral genera was recorded using the same belt-transects. Coral colonies with > 50% of their living tissue area contained within each belt-transect were assigned to the following size classes for maximum diameter: 6-10, 11-20, 21-40, 41-80, 81-160, and 161-320 cm.

### 3.2.3. Data analysis

Spatial variations of percent cover of benthic categories, generic richness (GR), and abundance of coral colonies among habitats and stations were explored using nested ANOVA, with habitat and station as fixed factors. Data were appropriately transformed (log(x+1)) for GR and abundance, and arcsin(x) for percent cover, to meet the assumptions of normality and homogeneity of variance. ANOVA were complemented by pairwise *t*-test comparisons to determine which samples showed significant differences. The overall spatial variation in the composition and abundance of coral assemblages among the 10 stations was analyzed using nonmetric multidimensional scaling (nMDS), based on the Bray-Curtis dissimilarity index, and followed by ANOSIM to identify significant differences among habitats. ANOVA per permutation was used to compare the size frequency distribution among each habitat based on the colony abundances.

## 3.3. Results

Overall, benthic substrate was dominated by hard corals (46.8 ± 3.4%, mean ± SE), turf algae (17.3 ± 3.8%), macroalgae (12.7 ± 4.0%), and rubble (12.1 ± 4.9%). Percent cover of corals was significantly variable among habitats (ANOVA, F=3.4, p=0.036) and among stations within habitats (ANOVA, F=4.8, p=0.002; Supplementary Table S2; Figure 3.2.). Coral cover was lower at the inner slope (34.2 ± 3.5%, mean ± SE) compared to the outer slope (52.0 ± 4.6%) and patch reefs (48.0 ± 6.5%; pairwise *t*-test, all $p < 0.05$; Supplementary Fig. S3). At the station level, coral cover values were highly variable, ranging from 22.7 ± 13.2% at PR4 to 69.9 ± 3.7% at OS3 (Supplementary Table S4). High values were also recorded at PR1 (66.3 ± 3.3%) and PR2 (62.3 ± 10.7%).

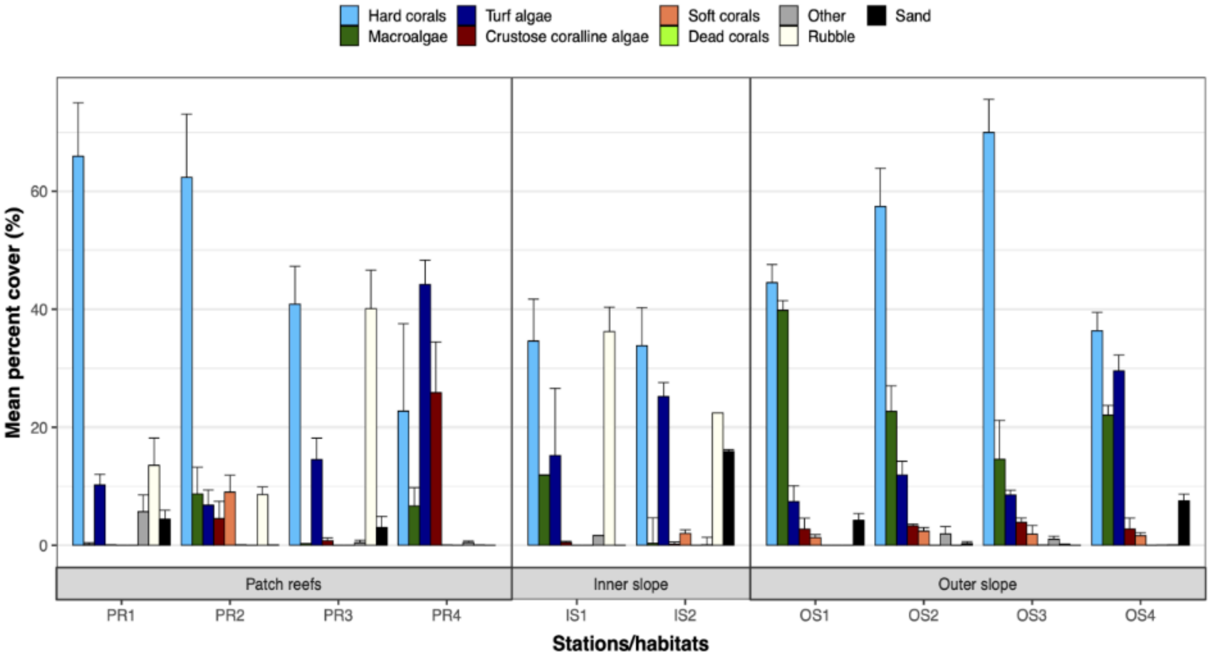

**Figure 3.2.** Mean percent cover of major substrate categories at the 10 stations located on the three major habitats (PR: patch reefs, IS: inner slope, and OS: outer slope). Error bars represent standard error.

Coral cover was dominated by *Acropora* colonies (> 50% of overall coral cover), with highest values recorded at the inner slope (37.9 ± 15.4%) and, to a lesser degree, at patch reefs

(28.8 ± 6.9%), whereas cover was lower at the outer slope (12.8 ± 2.7%; Figure 3.3.). *Pavona* cover was also high at the inner slope (27.2 ± 13.1%), whereas values were greatly reduced at patch reefs (1.5 ± 0.5%) and the outer slope (1.1 ± 0.5%). Percent cover of other coral genera was lower than *Acropora* and *Pavona* (< 7%). For *Echinopora* (4.9 ± 2.2%), *Seriatopora* (4.9 ± 1.5%), and *Porites* (3.8 ± 0.9%), highest values were recorded on the outer slope. Cover of *Seriatopora* (4.2 ± 2.0%) was also relatively important at patch reefs, together with *Galaxea* (6.4 ± 6.2%) and *Montipora* (4.0 ± 3.5%). In contrast, *Porites* (4.5 ± 2.4%) and *Pocillopora* (3.7 ± 2.0%) cover were the highest on the inner slope.

Macroalgal cover varied significantly among habitats (ANOVA, F=60.5, p=0.001) and stations (ANOVA, F=7.7, p=0.001), with values ranging from 0.1 ± 0.3% at PR1 to 39.8 ± 1.6% at OS1 (Figure 3.2.). Cover of turf algae showed a strong variation among stations (ANOVA, F=7.3, p=0.0003), with values between 6.8 ± 2.5% at PR2 to 44.1 ± 4.1% at PR4, though no difference was found among habitats (ANOVA, F=2.2, p=0.1). Similarly, cover of crustose coralline algae was variable among stations (ANOVA, F=1259.7, p=0.01), with a maximal value of 25.8 ± 8.4% recorded at PR4, but was not significantly different among habitats (ANOVA, F=53.1, p=0.5). Soft corals were not recorded at stations PR1, PR3, and IS1 and cover values were relatively low (< 2%) at most other stations, except at PR2 where cover reached 9.0 ± 2.8%. Comparisons among habitats and stations did not reveal significant differences (ANOVA, all p > 0.05). Cover of other invertebrates (sponges, zoanthids and tunicates) was also low at most stations (< 2%), with highest value recorded at PR1 (5.6 ± 2.8%), whereas no significant variation was recorded among habitats (ANOVA, F=0.3 p=0.7) and stations (ANOVA, F=2.3 p=0.06). Percent cover of rubbles was significantly different among habitats (ANOVA, F=3.7, p=0.04) and stations (ANOVA, F=2.3, p=0.001), with highest values recorded at PR3 (40.0 ± 6.5%), while almost no rubbles were recorded at outer reef stations. Sand cover was highly variable among stations (ANOVA, F=7.4, p=0.0003), with values up to 15.9 ± 0.3% at IS2, but not among habitats (ANOVA, F=2.6, p=0.09).

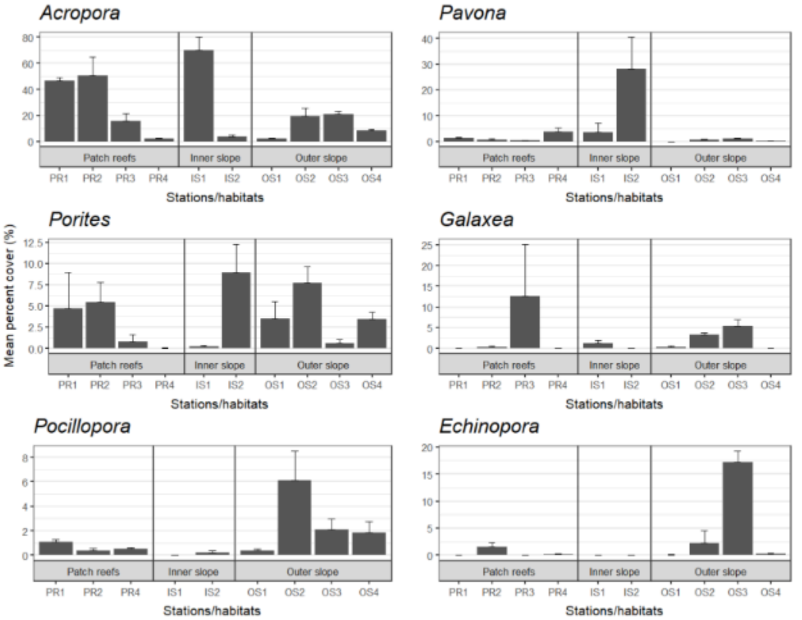

**Figure 3.3.** Mean percent cover of the eight major coral genera at the 10 stations located on the three major habitats (PR: patch reefs, IS: inner slope, and OS: outer slope). Error bars represent standard error.

A total of 43 coral genera were recorded from the 10 stations, with an overall mean of 20.1 ± 1.2 genera.10 $m^{-2}$. Generic richness (GR) was significantly variable among habitats (ANOVA, F=6.2, p=0.008) and among stations within habitats (ANOVA, F=5.2, p=0.001; Supplementary Table S5; Figure 3.4.). GR values ranged from 11.3 ± 1.2 genera.10 $m^{-2}$ at PR1 to 28.6 ± 2.0 genera.10 $m^{-2}$ at OS2, with high values (> 20 genera.10 $m^{-2}$) also recorded at PR2, PR3, and OS4 (Supplementary Tables S6 and S7). In terms of colony abundance, coral assemblages were mainly composed of eight genera (*Acropora*, *Seriatopora*, *Galaxea*, *Porites*, *Pocillopora*, *Montipora*, *Dipsastraea*, and *Favites*), while other genera such as *Blastomussa*, *Plesiastrea*, *Turbinaria*, *Astrea*, and *Diploastrea* were rarely recorded (all together < 4%) at the 10 stations (Supplementary Fig. S1). The relative contribution of these eight major genera was highly similar among the three habitats, and *Acropora* was clearly the dominant genera at all habitats and stations.

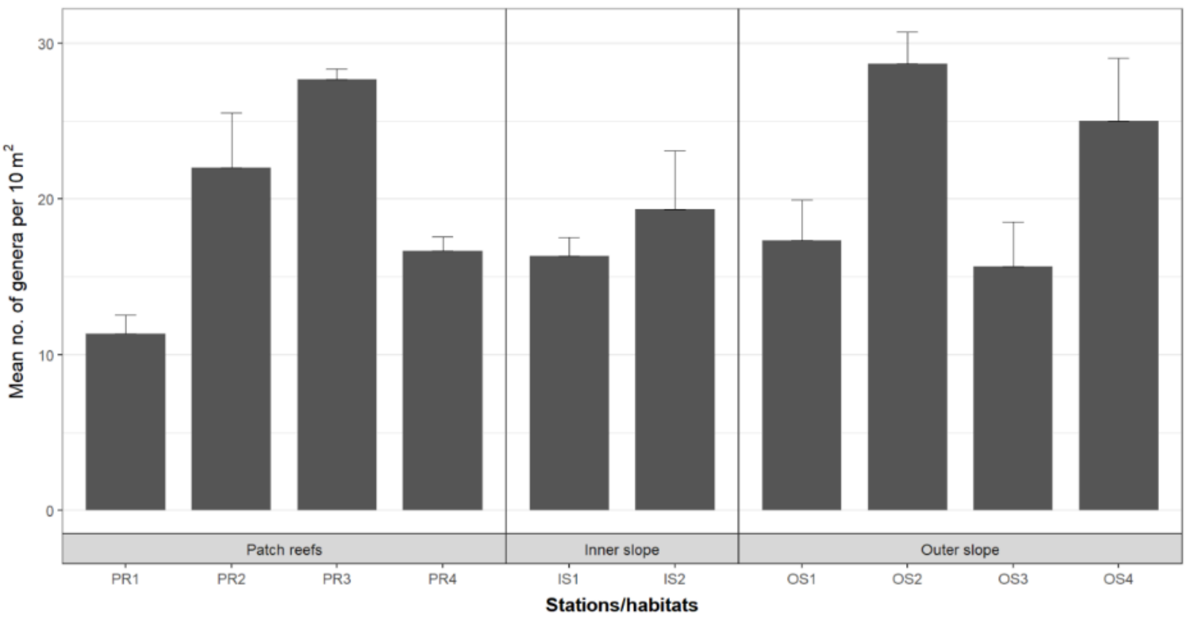

**Figure 3.4.** Mean generic richness of corals at the 10 stations located on the three major habitats (PR: patch reefs, IS: inner slope, and OS: outer slope). Error bars represent standard error.

A total of 4,644 coral colonies were recorded at the 10 stations, representing an overall mean abundance of 150.4 ± 11.1 colonies.10 m$^{-2}$. Coral colony abundance was significantly variable among habitats (ANOVA, F=4.0, p=0.03), and among stations within habitats (ANOVA, F=3.8, p=0.005; Supplementary Table S8; Figure 3.5.). Values ranged from 91.0 ± 13.0 at PR1 to 224.6 ± 18.3 colonies.10 m$^{-2}$ at OS3, with low values (< 100 colonies.10 m$^{-2}$) also recorded at IS3 and OS1 (Supplementary Tables S9 and S10). All eight major coral genera showed a significant spatial variation in abundance across habitats (ANOVA, all $p < 0.001$) and across stations within habitats (ANOVA, all $p < 0.001$; Figure 3.6.). For *Acropora*, *Seriatopora*, *Galaxea*, *Pocillopora*, *Dipsastraea, Favites*, and *Montipora,* highest values of abundance were recorded at outer slope stations, though relatively low values were also found in this habitat. Relatively high abundance of coral colonies was also recorded in other habitats, including *Pocillopora*, *Dipsastraea, Favites, Montipora,* and *Porites* in patch reefs, and *Seriatopora*, *Galaxea*, and *Porites* on the inner slope.

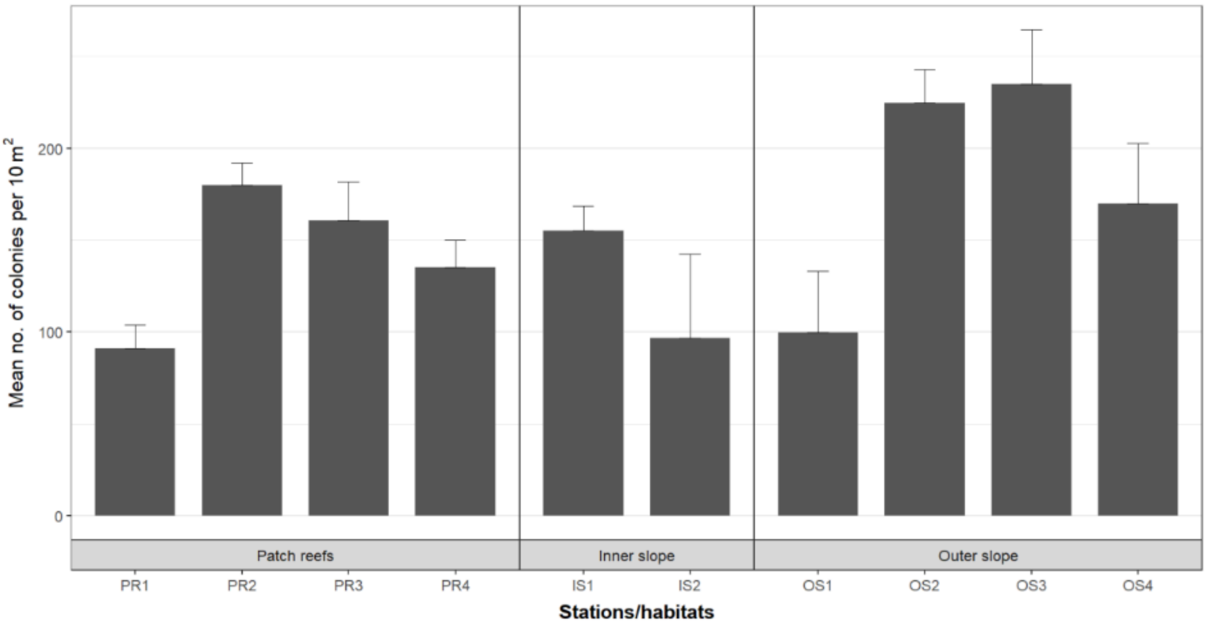

**Figure 3.5.** Mean abundance of overall coral colonies (all genera pooled) at the 10 stations located on the three major habitats (PR: patch reefs, IS: inner slope, and OS: outer slope). Error bars represent standard error.

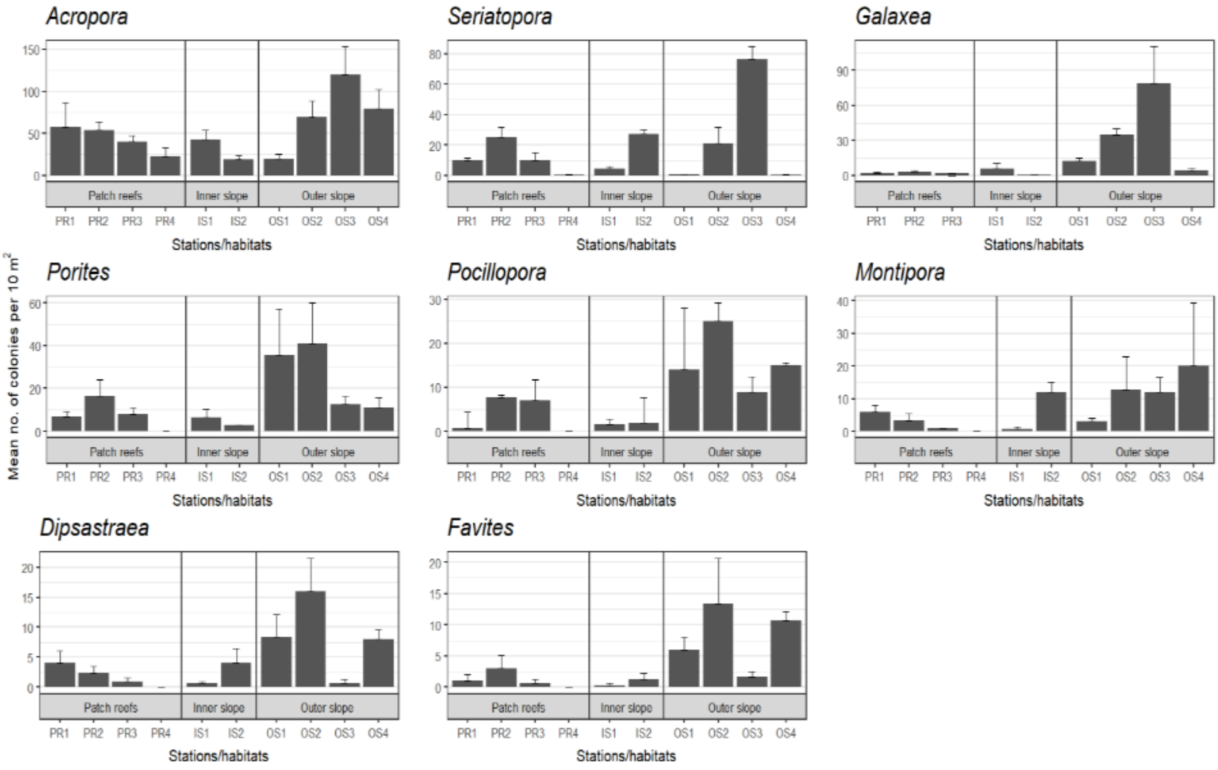

**Figure 3.6.** Mean abundance of colonies of the eight major coral genera at the 10 stations located on the three major habitats (PR: patch reefs, IS: inner slope, and OS: outer slope). Error bars represent standard error.

The composition and abundance of coral assemblages showed a significant difference among the three habitats. The nMDS, based on the Bray-Curtis dissimilarity index, first discriminated stations of the outer slope from those of the two other habitats (20% similarity; Figure 3.7.A; ANOSIM, R > 0.50, Supplementary Table S11), whereas stations of the inner slope and patch reefs were highly similar (ANOSIM, R < 0.25). Stations of the outer slope were characterized by higher abundance of *Acropora* and *Galaxea*, and a particularly high value of *Seriatopora* at OS3 (Supplementary Table S12), distinguishing this station from the three others at a higher similarity level (40%). At this similarity level, two other groups of stations were discriminated; PR1, PR2, and IS2 were characterized by a high abundance of *Fungia*, *Herpolitha*, *Stylophora*, and *Seriatopora*, whereas IS1, PR3, and PR4 were distinguished from the other patch reefs and inner slope stations by their high abundance of *Cycloseris* and *Pavona* (Figure 3.7.B).

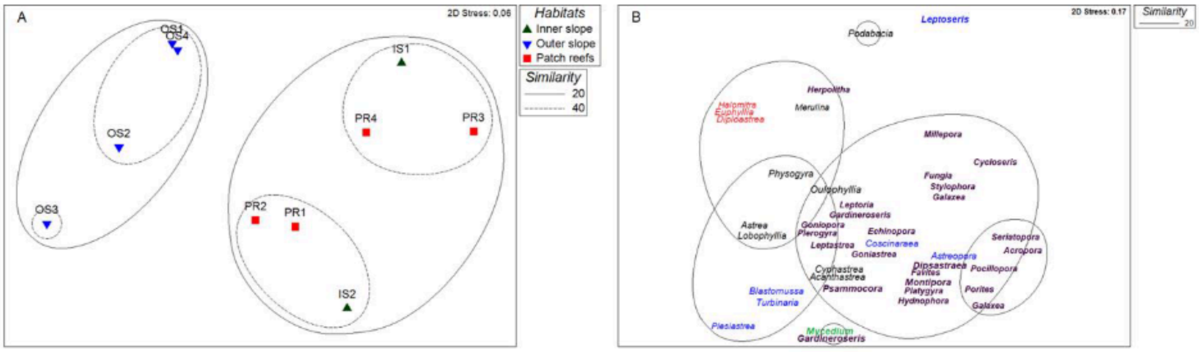

**Figure 3.7.** Non-metric multidimensional scaling (nMDS), based on the Bray-Curtis dissimilarity index, showing the spatial variation in the composition and abundance of coral assemblages among the 10 stations located on the three major habitats (PR: patch reefs, IS: inner slope, and OS: outer slope). Position of the 10 stations (A) and of the 43 genera (B) on the first two axes of the nMDS. The color code is as follows: red for patch reefs stations and coral genera exclusively recorded on this habitat, green for inner slope stations and coral genera exclusively recorded on this habitat, blue for outer slope stations and coral genera exclusively recorded on this habitat, coral genera recorded at all three habitats are indicated in purple, and coral genera recorded on more than two habitats are in black.

Coral assemblages at the 10 surveyed stations were dominated by colonies of < 20 cm in maximum diameter, representing 73% of the colonies recorded (Figure3.8.). Size frequency distribution of the eight dominant genera followed a right skewed pattern with higher abundance of small size colonies (6-10 cm and 11-20 cm in diameter) and a decrease in abundance of higher size classes (Supplementary Tables S13, S14, and S15). For most coral genera and at all three habitats, size-structure was dominated by the 11-20 cm size class, except for *Seriatopora*, *Galaxea*, and *Favites*, which had more colonies of 6-10 cm in diameter at patch reefs. The largest colonies were rare, mainly represented by branching colonies of *Acropora*, and *Seriatopora*, and massive *Galaxea*. A significant difference in the size structure was recorded among habitats (Permutational ANOVA, p < 0.001; Supplementary Table S13), except between patch reefs and inner slope (pairwise *t*-test, p > 0.05; Supplementary Table S14).

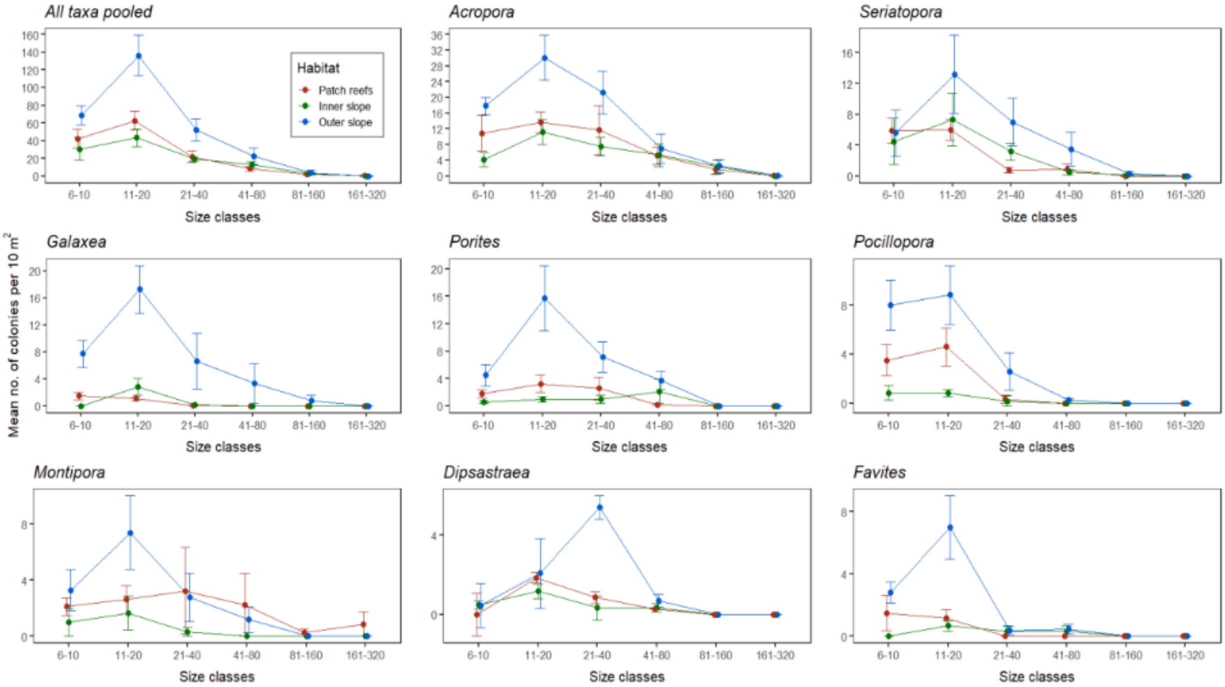

**Figure 3.8.** Size-structure of the eight major coral genera at each of the three major habitats (PR: patch reefs, IS: inner slope, and OS: outer slope) surveyed (all stations pooled). Error bars represent standard error.

## 3.4. Discussion

This study on the spatial structure of coral assemblages has allowed the assessment of the current health of coral reefs in the region of Toliara, and represents a valuable quantitative baseline for future comparisons. At most survey stations, the substrate cover is dominated by living corals (overall mean of 46.8 ± 3.4%), with values > 40% at six of the 10 stations located on patch reefs and the outer slope, and even reaching 60-70% at three stations. This high coral cover is associated with a high abundance of coral colonies (overall mean abundance of ~150 colonies.10 $m^{-2}$), notably at most outer reef and patch reef stations (up to ~220 colonies.10 $m^{-2}$). Such recent high coral cover and abundance is unexpected given the multiple large-scale disturbances and local stressors that have affected the GRT for several decades, including severe bleaching events in 1998 and 2015-2016, and important fishing and gleaning activities (Obura 2005, Obura et al. 2011, 2017, Andréfouët et al. 2013). In fact, the overall coral cover that we recorded in 2017 is much higher than values reported in 2008 (~13%) (Harris et al. 2010), but similar to the ones found in the '60s (~40%) (Pichon 1978). Similarly, the abundances of coral colonies that we recorded in 2017 were much higher than the ones reported in 2008 at various GRT stations (~50 colonies.10 $m^{-2}$) (Harris et al. 2010). Despite the different sampling techniques and strategies used by these studies that may partly explain some of the observed differences in coral cover, abundance, and diversity, our results suggest a recent trend to a return to healthier coral assemblages. Such high coral cover recorded at several sites of the GRT are in fact comparable to those in less disturbed reefs around Madagascar, such as the reef of Belo-sur-Mer (~55%) (Ahamada et al. 2002), Nosy Be (~50%) [40], northwest (~70%) (Kohler & Gill 2006), Ambodivaibe (48%) (Obura et al. 2011), or Andavadoaka (~42% on some patch reefs) (Nadon et al. 2008). The relatively good health of coral reefs in the Toliara region could be partly linked to the presence of the Southwest MAdagascar Coastal Current (SMACC), a shallow current flowing along the southwest coast toward the south, and which may facilitate larval transport from northern, less disturbed reefs and enhance the replenishment of reefs under the influence of this current (Adjeroud et al. 2019).

However, these positive and encouraging results should be taken with caution. Firstly, even if the overall diversity of corals recorded during this study (43 genera) is higher than the one reported in 2008 (30 genera) (Harris et al. 2010), it is still lower than the one found in the '60s (61 genera) (Pichon 1978). This decreasing trend in coral diversity was also documented by Bruggemann et al. (2012) with 18 of the 61 genera reported by Pichon (1978) not recorded in 2011. Some rare genera recorded in the northwest (Webster & McMahon 2002), northeast (Obura et al. 2011), and southeast Madagascar (Harding et al. 2006) were not seen (*Anomastraea, Horastrea, Craterastrea, Plesiastrea*, *Caulastrea*) or rarely recorded (*Coscinaraea, Diploastrea, Blastomussa*) at the GRT (Supplementary Table S16). In fact, as reported by Todinanahary et al. (2018), coral assemblages of the GRT have not only declined in their overall diversity, but have also changed in their composition. Secondly, turf and macroalgae are abundant at most stations, with cover higher than 20%, notably on the outer slope. This high biomass of fleshy algae is likely resulting from the decline in the abundance of herbivorous fishes recorded in the bay of Toliara and Ranobe following decades of overfishing (Harris et al. 2010, Bruggemann et al. 2012). This level of algal cover greatly reduces the availability of adequate substrate for coral settlement and growth, and induces a strong competition for space. A high cover of fleshy algae also suggests that the ecosystem is likely close to the tipping point toward a coral to macroalgal phase shift. Thirdly, the population size-structure of all major coral taxa in the Toliara region is positively skewed, with a large dominance of small colonies and relatively few large ones, as also documented in several other coral reefs (Webster & McMahon 2002, Ramanantsoa et al. 2018). Since fecundity is positively correlated to colony size (Bauman et al. 2013b, Grimsditch et al. 2017), this lack of large colonies may compromise the reproduction of local coral populations and consequently their persistence, as they will mainly rely on northern sites for their replenishment (Adjeroud et al. 2019).

As documented for several other coral reefs worldwide (Hughes & Jackson 1985, Gérard et al. 2008, Harrison 2011), GRT coral assemblages were characterized by a marked spatial variability, creating a heterogeneous mosaic of habitat patches. Generic richness, abundance, size-structure, and composition of adult coral assemblages were highly variable among the three major reef habitats (patch reefs, inner slope, and outer slope), but also among stations within habitats. The most diversified and abundant coral assemblages were located at several stations of patch reefs and outer slope habitats. Such reef scale spatial heterogeneity of coral community structure likely results from variation in physical conditions (sedimentation, hydrodynamic, light) and biotic interactions (spatial competition with fleshy algae).

In terms of colony abundance, our results highlight the marked dominance of *Acropora*. This outcome is another sign of the recent recovery to healthier coral assemblages at our study sites. In fact, *Acropora*, which was dominant in the GRT in the '60s (Pichon 1978), was greatly reduced in cover and abundance in 2008, to the benefit of more resistant taxa such as *Porites* and *Echinopora* (Harris et al. 2010). There is also an abundance of other branching taxa at our study sites such as *Seriatopora*, *Pocillopora*, and *Stylophora*, all characterized by their susceptibility to variation in environmental conditions, notably to thermally-induced bleaching events (Connell et al. 1997, Ninio & Meekan 2002, Matyas 2015). This return to a coral assemblage dominated by *Acropora*, together with these other branching taxa, is clearly a positive indication of an ongoing recovery trend to healthier coral communities.

Despite several episodes of bleaching events, and recurrent impacts linked to overfishing, sedimentation, and gleaning activities, our results suggest that coral assemblages of the GRT still have the capacities to maintain, provided that large-scale disturbances or local stressors do not increase in frequency and severity in the near future. Our survey is a snapshot in a highly dynamic system and represents a valuable baseline for long-term monitoring of the GRT. Such interannual surveys of coral assemblages of the GRT are timely for determining their status and temporal trajectories and hence, evaluating resilience capacities of this reef ecosystem. Ideally, this monitoring should not focus exclusively on corals and algae, but rather incorporate other key mechanisms of ecosystem maintenance and resilience, such as grazing pressure by herbivorous fishes and invertebrates, coral recruitment, and major impacts such as fishing, sedimentation, SST, and nutrient loading. Such monitoring should also include nearby mangroves and seagrass beds, as these adjacent habitats may have an important role in the functioning of the coral reef ecosystem. In fact, identifying major drivers of the spatio-temporal variability of reef communities, which was not within the scope of the present study, is crucial, not only to improve our knowledge on their structure and dynamics, but also to identify key biophysical processes that may be prioritized in conservation actions.

Our study also has important implications for urgently needed management and conservation of the GRT. For example, the marked spatial variation that we recorded suggests that conservation measures, such as the implementation of marine protected areas (MPAs), should integrate sufficient area to capture the scale of this spatial heterogeneity. This aspect is critical, as MPA effectiveness can be obscured by important variations at small spatial scales, despite similar adjacent habitats showing opposite trends (Cleary et al. 2016). The health of the GRT and nearby coral reefs requires a drastic reduction in the fishing pressure in this area. This may be achieved by increasing the number of community-based aquaculture projects that have shown to be a successful alternative, or even principal, source of income for some coastal populations (O'Brien et Scheibin 2018), and which may reduce the negative effects of overfishing on coral communities (Harding et al. 2006, Bruggemann et al. 2012, Gough et al. 2020). Ideally, these alternative activities must be located to minimize the impacts on nearby coral reefs and adjacent ecosystems such as mangroves and seagrass beds, and should involve end users – at least fishermen and sea farmers – in setting up the project and decision making. Furthermore, our results suggest that reef restoration activities should consider at least the genera *Acropora*, *Pocillopora*, *Seriatopora*, and *Stylophora*. These genera, which are among the most abundant in the Toliara region, have colonies with mainly branching growth forms, and are thus particularly suitable for transplantation and restoration projects (Loya et al. 2001, Guest et al. 2012). Moreover, these genera are highly sensitive to variations in abiotic conditions, and thus may act as coral sentinels to detect environmental changes (Connell et al. 1997, Ninio & Meekan 2002, Matyas 2015). Such community-based coral farming, whose technical and social feasibility has already been demonstrated, could also improve education and awareness on the importance of corals for healthy coastal ecosystems and, consequently, on their income-generating activities (O'Brien & Scheibling 2018).

The outcomes of this survey bring hope to the future of coral assemblages of the GRT by suggesting that these assemblages still have acceptable maintenance capacities, and may also be beneficial to other reef communities and the goods and services the GRT should continue to provide to local populations. But once again, this optimistic scenario can only be achieved if adequate and rigorous conservation actions are taken rapidly to limit and mitigate the local impact of disturbances that are unfortunately inevitable. In this context, the ability of local populations to become involved in community-based conservation actions is a positive aspect of their success (Williams et al. 2013, Humber et al. 2017, Todinanahary et al. 2018). The quantitative baseline examined here may support collaborative processes to evaluate future changes in coral communities and identify effective conservation actions.

# Chapitre 4 :
# Reproduction sexuée de quelques espèces de coraux du Grand Récif de Toliara, sud-ouest de Madagascar

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Ce chapitre est en préparation pour être soumis dans *Marine Biology*.
**Botosoamananto RL**, Gasimandova LM, Randrianarivo M, Penin L, Todinanahary G, Adjeroud M. Sexual reproduction of several reef corals on the Great Reef of Toliara, southwest Madagascar. *To be submitted to Marine Biology as a Short Notes*

## Résumé

La reproduction est une phase critique dans la dynamique et le renouvellement des assemblages coralliens, ainsi que dans les processus de rétablissement suite à des perturbations. Comparées à d'autres régions telles que le Pacifique occidental, les avancées sur la reproduction des coraux dans le sud-ouest de l'Océan Indien sont plus récentes et moins développées. Ici, nous avons évalué la saisonnalité et la synchronie de la reproduction des principaux coraux scléractiniaires sur le Grand Récif de Toliara (GRT), au sud-ouest de Madagascar. Pour *Acropora digitifera* et *A. nasuta*, des colonies gravides ont été enregistrées pendant la première partie des deux périodes estivales (entre septembre et décembre 2018-2019) tandis qu'aucune colonie mature n'a été observée en janvier et février 2019 et 2020. Pour *Platygyra daedalea* et *Galaxea fascicularis*, la proportion la plus élevée de colonies gravides a été enregistrée en janvier et février 2020, bien que des gamètes matures aient également été observés, mais dans une proportion plus faible, au cours de l'ensemble des période estivales. La ponte *in situ* n'a été observée que pour les espèces d'*Acropora*. En novembre 2018, *A. nasuta* et *A. digitifera* ont pondu fin novembre, une à deux nuits après la pleine lune (nAFM), tandis qu'*A. tenuis* a pondu pendant quatre nuits consécutives, trois à six nAFM. En 2019, la ponte synchronisée de 13 espèces d'*Acropora* a été observée le 19 octobre, 5 nAFM. Comme dans de nombreux autres récifs coralliens dans le monde, la maturation des gamètes et la ponte des coraux sur le GRT sont liées aux variations saisonnières des températures de surface de la mer. Nos résultats sont les premières observations détaillées de la ponte des coraux dans la région de Toliara, mais ils représentent un instantané dans le temps, et des recherches supplémentaires sont nécessaires pour déterminer si nos observations se confirment dans le temps, et pour mieux comprendre les relations avec les conditions environnementales.

**Mots-clés :** Récifs coralliens ; reproduction sexuée ; structure des communautés ; ponte multi-spécifique ; gamétogenèse ; Madagascar.

## Abstract

Reproduction is a critical phase in the dynamics and replenishment of coral assemblages and in recovery processes following disturbances. Compared to regions such as the Western Pacific, advances in documenting coral reproduction in the South Western Indian Ocean (SWIO) are more recent and less comprehensive. Here, we assessed the patterns of reproductive seasonality and synchrony of major scleractinian corals on the Great Reef of Toliara (GRT), southwest Madagascar over two summer periods, September 2018 – February 2020. For *Acropora digitifera* and *A. nasuta*, gravid colonies were recorded during the first part of the two summer periods between September to December, whereas no mature gametes were recorded in the January or February summer months. For *Platygyra daedalea*, and *Galaxea fascicularis*, the highest proportion of gravid colonies was recorded in January and February 2020, although mature gametes were also observed at a lower proportion throughout the summer periods. Spawning was recorded during field observations for *Acropora* species exclusively. In November 2018, *A. nasuta* and *A. digitifera* spawned in late November, one to two nights after the full moon (nAFM), whereas *A. tenuis* spawned for four consecutive nights three to six nAFM. In 2019, synchronized spawning of 13 *Acropora* species was observed on the 19th of October, 5 nAFM. As in many other coral reefs worldwide, gamete maturation and coral spawning on the GRT are linked to seasonal variation in sea surface temperatures. Our results are the first detailed records of spawning in the region of Toliara, but represent a snapshot in time. Further research is required to determine whether the spawning patterns recorded here are typical of spawning patterns in other years, and to investigate the relationships between the timing of spawning and potential proximate cues.

**Keywords:** Coral reefs; scleractinian corals; sexual reproduction; multispecies spawning; gametogenesis; Madagascar

## 4.1. Introduction

Scleractinian corals are the major reef-building taxa and key components of reef health and biodiversity, as they represent a habitat and a food source for numerous species (Idjadi and Edmunds 2006). However, reef corals are highly sensitive to variation in environmental conditions, such as temperature, salinity, nutrients, sedimentation, and ocean acidification. In recent decades, various large-scale natural and anthropogenic disturbances, such as mass bleaching events caused by thermal anomalies, predator outbreaks, cyclones, and overharvesting have induced mass coral mortalities in several coral reefs worldwide (Bellwood et al. 2004; Hoegh-Guldberg 2011; Hughes et al. 2017). The coral declines have caused habitat degradation and reduction of reef biodiversity (Pratchett et al. 2011; Hongo and Yamano 2013) and in some cases have led to phase shifts, with corals being replaced by macroalgae or other non-reef-building benthic organisms (McManus and Polsenberg 2004). Recovery of coral reefs following disturbances is largely dependent on the successful reproduction and recruitment of corals, which is now challenged by the increasing frequency and severity of these disturbances (Hughes et al. 2007, 2010; Graham 2015; Lam et al. 2020). Tracking coral reproduction patterns is not only fundamental to better understand the structure and dynamics of coral assemblages but also to design efficient conservation actions and restoration projects (Harrison 2011; Cameron and Harrison 2020; Cruz and Harrison 2020; Harrison et al. 2021). For example, identifying the timing and degree of synchrony of coral spawning may help identify critical periods during which environmental stressors should be minimized (Harrison 2011).

Corals, like most marine invertebrates, have a bipartite life cycle that includes a pelagic larval phase followed by a sessile benthic phase for most species, with reproduction being a crucial process in the maintenance and replenishment of local populations (Harrison and Wallace 1990; Baird et al. 2009b, 2021; Harrison 2011). Corals have complex reproductive strategies that differ among coral taxa as well as among regions and environmental conditions within the same taxa (Richmond 1990; Baird et al. 2021). The majority of corals are hermaphroditic with colonies having both male and female organs and thus producing eggs and sperm, while others are gonochoric, with colonies carrying either male or female organs during their life cycle (Richmond and Hunter 1990; Harrison 2011). Broadcast spawners, the dominant reproductive mode in corals, release gametes into the water column for external fertilization and development, occurring seasonally and generally once a year (Shlesinger et al. 1998; Baird et al. 2009b; Harrison 2011). The dispersal phase of larvae can last from days to weeks and contributes to the potential for colonization of distant reefs (Richmond 1990; Harrison and

Wallace 1990; Baird et al. 2009b). In contrast, brooders have internal fertilization and release larvae, with several spawning events per year for some species (Baird et al. 2009b; Harrison 2011). The planktonic phase is generally shorter for brooders, with larvae often settling near their parents (Ayre and Hughes 2000; Harii et al. 2002; Harrison 2011).

The timing and degree of spawning synchrony within and among coral species varies among coral reefs (Harrison and Wallace 1990; Baird et al. 2009b; Harrison 2011). Annual multispecific synchronous spawning events ('mass spawning') were first described on the Great Barrier Reef (Harrison et al. 1984), but have also been recorded in several other reefs such as Solomon Islands (Baird et al. 2009a), Singapore (Guest et al. 2002, 2005), and southern Japan (Hayashibara et al. 1993). In contrast, extended reproductive seasons have been documented at Eilat, Moorea, Hawaii, and Kenya (Richmond 1990; Shlesinger et al. 1998; Carroll et al. 2006; Baird et al. 2009b). The seasonality and synchrony of coral spawning among species and colonies are influenced by several environmental conditions, including temperature, wind speed, and lunar and tidal cycles (Babcock and Heyward 1986; Richmond 1990; Harrison and Wallace 1990; Baird et al. 2009b; Harrison 2011). Variation in sea surface temperatures (SST) and solar insolation have a major influence on the maturation of gametes, whereas moon phases, wind, and tidal fluctuation are more determinant for the spawning day/hour (Levitan et al. 2011; Kaniewska et al. 2015; Lin and Nozawa 2017; Sakai et al. 2020; Lin et al. 2021). In fact, coral spawning can be triggered by sharp increases or decreases in SST (Keith et al. 2016; Wijayanti et al. 2019). However, spawning generally occurs during the warmest period of the year in many regions (Mangubhai and Harrison 2008a; Sola et al. 2016; Jamodiong et al. 2018b; Gan et al. 2021). Biannual spawning periods have been also reported, such as in the Red Sea, with 13 species spawning between April and June, and seven species between September and November (Bouwmeester et al. 2015, 2016).

Research on coral reproduction in the South Western Indian Ocean (SWIO) has been developing more recently and remains less comprehensive than in other regions, such as the Western Pacific. Spawning of *Acropora* was recorded between September and November in Vamizi Island, Mozambique (Sola et al. 2016), and between September and October in Andavadoaka, southwest Madagascar (Gress et al. 2014), whereas in Mombasa, Kenya, it occurs from December to March (Mangubhai and Harrison 2008a). Extended gametogenesis and spawning at the end of the austral summer was documented for Pocillopora damicornis in South Africa (Masse et al. 2012). For the massive coral *Porites lutea*, broadcast spawning was observed in January at Reunion Island (Massé et al. 2019).

The present study was carried out in the context of the coral reef crisis and the critical need for information on coral reproduction to improve our understanding of the dynamics and recovery capacities of coral assemblages and efficient conservation. We aimed to assess the patterns of reproductive seasonality and synchrony of several major scleractinian corals on the Great Reef of Toliara (GRT), southwest Madagascar. Gamete maturation and timing and behaviour of gamete release were examined for four broadcast coral species during two consecutive summer seasons (September 2018 – February 2019 and September 2019 – February 2020) at 10 stations on the three major reef habitats of the GRT. The link between spawning and SST and wind speed was also examined. The GRT was harbouring flourishing reef communities in the 1960s, but various threats, such as bleaching events, high sedimentation, water pollution, and overfishing, caused coral decline and an increase of fleshy macroalgae and other non-reef building species such as zoanthids and soft corals (Pichon 1978; Bruggemann et al. 2012; Andréfouët et al. 2013). However, a recent survey has documented a recovery trend towards healthier coral assemblages with relatively high coral cover and abundance, including *Acropora*, at several habitats of the GRT (Botosoamananto et al. 2021). The present study is part of the recent initiative to better understand the structure and dynamics of coral assemblages of the GRT, and will complement surveys on coral recruitment patterns (Botosoamananto et al. in review) and regulation processes (Botosoamananto et al. submitted). The original data set compiled here will provide rigorous baseline information to monitor future changes in coral assemblages and to improve the conservation and management of the GRT.

## 4.2. Materials and methods

### 4.2.1. Study area

This study was conducted on the Great Reef of Toliara (GRT), a reef complex of 19 km long and 1-3 km wide, located 2 km seaward of Toliara, the most populated city of the southwest region of Madagascar (Fig. 1). The human population living in Toliara has increased over the last two decades, resulting in increased fishing pressure and gleaning activities (Laroche and Ramananarivo 1995; Harris 2007). The GRT is also impacted by high sedimentation resulting from poor management of mining and agricultural activities of the two main upstream rivers, Fiherenana in the north and Onilahy in the south (Maina et al. 2013; Sheridan et al. 2014). The region has two main seasons: the austral summer from October to March, a warm season with occasional rains and tropical cyclones, and the austral winter between April to September, corresponding to the cooler and dry season (Maina et al. 2012). Sea surface temperature (SST) may fall down to 18°C during the winter season and may rise to 30°C during the warm season. During our survey, SSTs were between 24-25°C in winter and 27-29°C in summer (Fig. 2). Dominant winds are from southwest direction.

The major bleaching events that have affected the GRT were reported in 1998, 1999, and 2016 (McClanahan et al. 2007; Obura et al. 2018; Gudka et al. 2020), and a minor event in March and April 2020 (Botosoamananto, personal observation). Thermal stress in 2001, 2006, 2009, and 2021 likely caused mild effects on coral assemblages of the GRT, but no mass bleaching events were reported. Cyclones are less frequent in the southwest coast of Madagascar compared to the eastern coast or to other regions in the SWIO, and no significant impacts on the GRT were reported, even for the most recent cyclone, Haruna that passed 120 km north of Toliara in February 2013 (Carter et al. 2022). Similarly, outbreaks of the coral predator *Acanthaster* spp. have not been reported in recent years on the GRT.

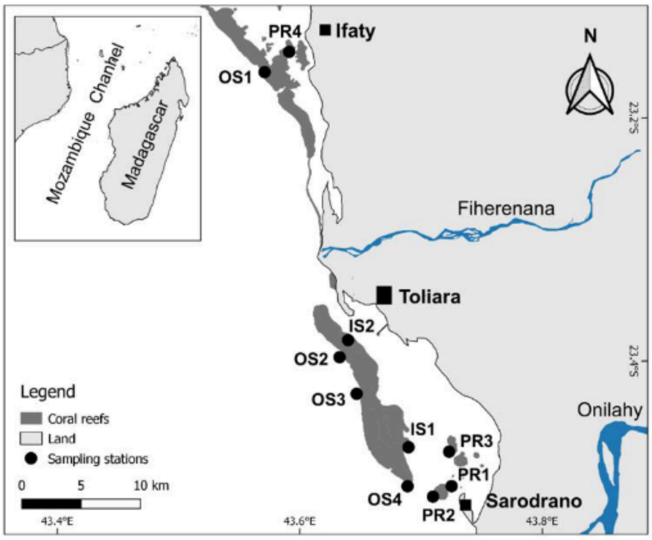


**Figure 4.1.** Map of the southwest coast of Madagascar showing the location of the 10 sampling stations in the Toliara region, including the Great Reef of Toliara (GRT). Stations were located on the three major habitat types: patch reefs (PR), inner slope (IS), and outer slope (OS).

### 4.2.2. Field surveys and coral sampling

The study was conducted at 10 stations on the three major reef habitats of the GRT: four stations on patch reefs, two on the inner slope, and four on the outer slope (Fig. 1). Station codes are abbreviated as follows: the first two letters represent the habitats (PR: patch reefs, IS: inner slope, and OS: outer slope) and the numbers specify each station. All stations were placed at 10-12 m depth. We focused on four abundant and widely distributed coral species, *Acropora* *digitifera*, *A. nasuta*, *Galaxea fascicularis*, and *Platygyra daedalea* (Botosoamananto et al. 2021). The reproductive status of coral colonies (i.e., gamete maturation) was assessed at all 10 stations, while field observations of spawning (i.e., timing and behaviour of gamete release) was conducted only at station PR2 (Fig. 1). This station was chosen for its relatively high coral diversity and abundance and because it offered the greatest security for night dives.

Gamete maturation was monitored during two consecutive summer periods (September 2018 – February 2019, September 2019 – February 2020). At each station, 2 to 3 fragments from 5 to 10 colonies per species were collected during scuba dives (Guest et al. 2002; Carroll et al. 2006; Mangubhai and Harrison 2008b). Only colonies larger than 20 cm in diameter were selected to ensure they were of sufficient size and age to be reproductively mature (Harrison et al. 1984; Chelliah et al. 2015). A distance of approximately 5 m between sampled colonies was maintained to avoid collection of genetic clones. In the field, gamete maturation was categorized based on the presence, size, and colour (pigmented or white) of gametes in the fragments (Harrison et al. 1984; Bouwmeester et al. 2016). Fragments were later transported to the laboratory for further observation and photography under a stereomicroscope (Optika Vision Lite 2.0, and Optikam Digital camera). We inferred that the large and pigmented gametes were mature and ready to be released in the days following the full moon, whereas colonies with white gametes were considered as still immature and likely to be released after two months. Colonies with no visible gametes either already spawned, or were unlikely to spawn within the next three months.

Spawning behaviour was examined through night dives conducted four days before and after the full moon from November to February for the first summer period (2018-2019) and from September to February for the second summer period (2019-2020). Night dives were conducted from 17:30 to 00:00, and spawning information on the species, the start and end time, number of days, and inter- and intraspecific synchrony were recorded.

To complement the biological data, we compiled remotely sensed data for monthly averages of SST and wind speed (from NOAA-MODIS) that were analysed using R version 4.2.1 (R Core Team 2022).

## 4.3. Results and discussion

Our field observations showed that patterns of reproductive seasonality differed among the four species, as well as between years for some taxa. For *Acropora digitifera* and *A. nasuta*, gravid colonies were recorded during the first part of the summer period, between September to December, whereas no mature gametes were recorded in January and February (Fig. 3). A high proportion (~50%) of *A. digitifera* and *A. nasuta* colonies with mature gametes was recorded September through October 2019, whereas during the first summer this proportion was lower for *A. digitifera* and extended from September to November for *A. nasuta*. For *Platygyra daedalea* and *Galaxea fascicularis*, the highest proportion of gravid colonies with mature gametes was recorded in January and February 2020. In contrast to *Acropora* species, mature gametes were observed, though at a lower proportion, during the entire summer periods, except in December 2018 for *P. daedalea*.

During our night dives conducted in both summer periods, we exclusively observed spawning of *Acropora* species, with no gamete release recorded for any other coral taxa (Fig. 4; Table 1). The timing and synchrony of *Acropora* spawning varied between the two summer periods. In 2018, spawning was synchronized among polyps as well as conspecific colonies, but not between species. Spawning was observed for *A. nasuta* and inferred (from the disappearance of mature gametes during consecutive nights) for *A. digitifera* in late November one to two nights after the full moon (nAFM), whereas *A. tenuis* spawned during four consecutive nights three to six nAFM (Table 1). Spawning started at ~18:00 (immediately following sunset) and lasted 20 minutes. In 2019, synchronized spawning of 13 *Acropora* species was observed on October 19th, 5 nAFM (Table 1). For all *Acropora* species, spawning started at ~20:00 and lasted two hours, generating larval slicks around our study site (Fig. 4). The relatively high degree of spawning synchrony in *Acropora* species recorded here reinforced previous surveys that highlighted such timing and behaviour of gamete release in this coral genera, which is hypothesized to enhance fertilisation rates by increasing gamete concentration (Hayashibara et al. 1993; Sola et al. 2016; Jamodiong et al. 2018a; Sakai et al. 2020).

As in many coral reefs worldwide, sexual reproduction of corals on the GRT is linked to variation in environmental conditions (Baird et al. 2009b; Harrison 2011). Similar to other coral reefs in the SWIO, gamete maturation and coral spawning occurred during the warm season between September to March (Massé et al. 2013; Sola et al. 2016). However, observations made in Andavadoaka (Gress et al. 2014), 170 km north of Toliara, in September 2013 showed that among eight *Acropora* species, one spawned four nights after the new moon and the seven other spawned on the fifth and sixth nights after the full moon (Gress et al. 2014). This discrepancy in the timing of spawning between Toliara and Andavadoaka may be explained by difference in seasonal variation in local SSTs, with an earlier rise in SST some years in lower latitude locations. However, these two studies over one or two spawning seasons represent a snapshot that does not integrate the potential temporal variability in reproductive processes, and should be complemented by long-term interannual monitoring to assess whether these patterns are consistent through time and the significance of latitudinal variation along the western coast of Madagascar.

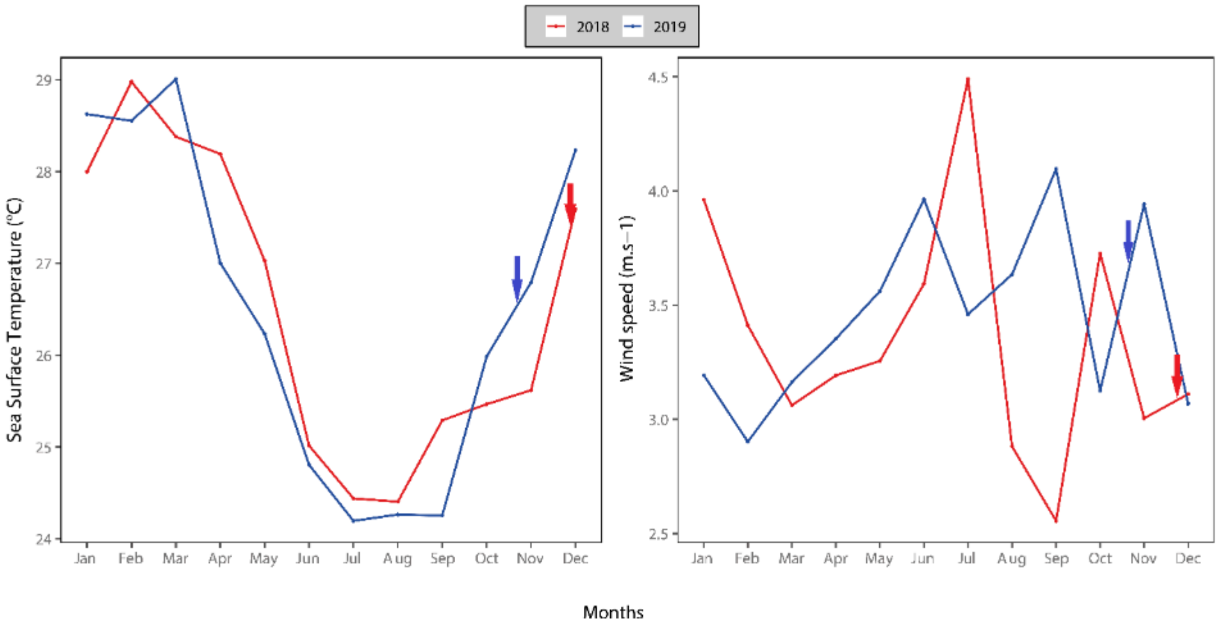


**Figure 4.2.** Monthly variation of sea surface temperature and wind speed in the region of Toliara during our survey of coral spawning and gametogenesis (2018 and 2019). Arrows indicate the beginning of the spawning observed during night dives. Data were obtained from NOAA MODIS.

At Toliara, spawning of *Acropora* corals in November 2018 occurred after a period of relatively stable SSTs (from September to early October) before an abrupt rise in late October, and during relatively low wind speeds ranging from 1.05 m.s$^{-1}$ to 3.36 m.s$^{-1}$. In 2019, the sharp rise in SSTs in October and the low wind speeds (0.62-1.17 m.s$^{-1}$) coincided with the multi-specific synchronized spawning of *Acropora*. The lunar cycle also appeared to play an important role in coral reproduction on the GRT, with spawning not occurring before but rather several days after the full moon in October or November. In contrast, the role of the tidal cycle is difficult to estimate, as spawning occurred during the spring tide in 2018 and during the neap tide in 2019.

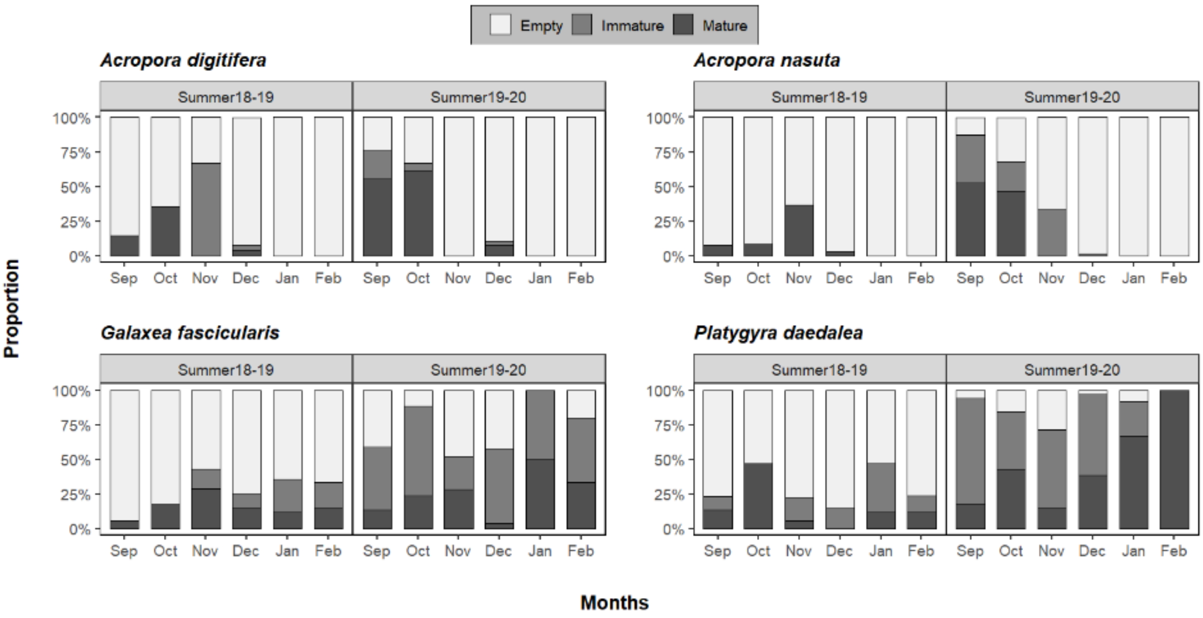


**Figure 4.3.** Proportion (%) of mature (large sized and pigmented gametes ready to spawn), immature (white gametes not ready to be released), and empty (no visible gametes) colonies of the four selected species during the two summer periods (September 2018 – February 2019, September 2019 – February 2020).

**Figure 4.4.** Colony of *Acropora* showing pink mature gametes a few minutes before spawning (left), and larval slick resulting from the synchronous multispecific spawning of *Acropora* on the Great Reef of Toliara in October 2019.

**Table 4.1.** Records of Acropora species spawning in November 2018 and October 2019 on the Great Reef of Toliara. No spawning was observed or inferred for Platygyra daedalea and Galaxea fascicularis during our survey.

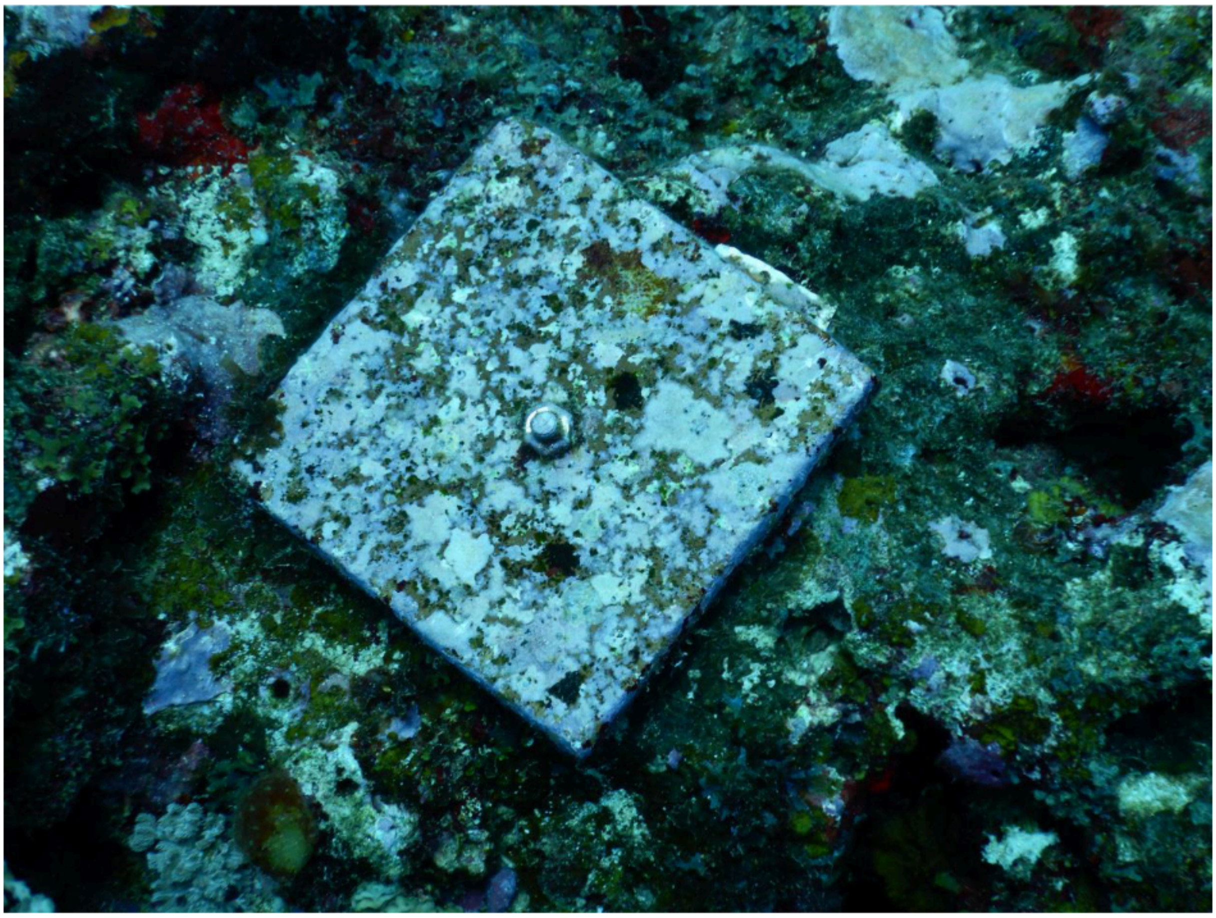
| Year | Date of spawning | Coral species | Full moon date | Nights after full moon |
|---|---|---|---|---|
| 2018 | 24-25 Nov. | *Acropora digitifera*<br>*A. nasuta* | 23 Nov. | +1/+2 |
| | 26-29 Nov. | *A. tenuis* | 23 Nov. | +3/+6 |
| 2019 | 19 Oct. | *A. abrotanoides*<br>*A. aculeus*<br>*A. appressa*<br>*A. cytherea*<br>*A. digitiferea*<br>*A. formosa*<br>*A. grandis*<br>*A. hyacinthus*<br>*A. milleporaA. nasuta*<br>*A. tenuis*<br>*A.* sp.1<br>*A.* sp.2 | 14 Oct. | +5 |

Spawning of the two non-*Acropora* species selected in our survey was not recorded during field observations. Gravid colonies with mature gametes were observed in colonies of *Galaxea fascicularis* and *Platygyra daedalea* during the entire survey periods, but no gamete release was observed or inferred. These findings are consistent with previous studies that have documented an oogenesis of seven months (from September to March) in *P. daedalea* in Kenya (Mangubhai and Harrison 2008b) and of seven to eight months (November to May/June) in the sister species *P. acuta* in Hong Kong (Chui et al. 2014).

These first detailed records of spawning in the region of Toliara will contribute to the understanding of the dynamics and maintenance of coral assemblages of the GRT, and of reproduction processes in the SWIO. However, this study represents a snapshot in time, and further research is required to determine whether the spawning patterns observed in 2018-2019 are typical, and to investigate the relationships between the timing of spawning and potential proximate cues.

# Chapitre 5 :

# Recrutement des coraux dans la région de Toliara, sud-ouest de Madagascar : variabilité spatio-temporelle, influence de la composition du substrat et implications pour la conservation des récifs



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Ce chapitre a été soumis dans *Marine Ecology*.
**Botosoamananto RL**, Todinanahary G, Gasimandova LM, Randrianarivo M, Guilhaumon F, Penin L, Adjeroud M. Coral recruitment in the Toliara region of southwest Madagascar: spatio-temporal variability, influence of substrate composition, and implications for reef conservation. *Submitted to Marine Ecology.*

## Résumé

L'étude du recrutement des coraux est essentielle pour mieux comprendre les capacités de rétablissement et de résilience des écosystèmes coralliens, ainsi que pour améliorer leur conservation. Dans cette étude, nous avons examiné variation spatio-temporelle du recrutement des coraux et l'influence de la composition du substrat dans la région de Toliara, au sud-ouest de Madagascar. Des plaques en terre cuite ont été immergées d'octobre à fin janvier sur une période de trois ans (2018-2021) à 10 stations situées dans les trois principaux habitats récifaux (massifs coralliens lagonaires, pente interne, et pente externe). Les assemblages de recrues sont dominés par les Acroporidae (45,5%) et les Pocilloporidae (45,0%), tandis que les Poritidae (1,9%) et les recrues de la catégorie "autres" (3,6%) sont rarement observés. La plupart des recrues sont observés sur les côtés des plaques (60,0%), comparativement aux faces inférieure (24,5%) et supérieure (15,5%). Les taux moyens de recrutement, allant de 219,20 recrues.m$^{-2}$ en 2018-2019 à 156,30 recrues.m$^{-2}$ en 2020-2021, sont relativement élevés par rapport à d'autres récifs du sud-ouest de l'Océan Indien. Les caractéristiques du recrutement varient au sein et entre les habitats, avec des taux plus élevés dans les stations de récifs lagonaires (187,06 recrues.m$^{-2}$) et de la pente externe (156,99 recrues.m$^{-2}$) que sur la pente interne (108,04 recrues.m-2). À l'exception des recrues de la catégorie "autres", les taux de recrutement diminuent entre 2018-2019 et 2019-2020, mais sont suivis d'une augmentation en 2020-2021, qui peut atteindre voire dépasser les valeurs initiales dans certaines stations. Les modèles linéaires généralisés à effets mixtes ont montré que l'abondance des recrues Pocilloporidae était positivement corrélée à la couverture des colonies adultes et des coraux mous, et négativement corrélée à la couverture des algues (algues calcaires encroûtantes, macroalgues, et turf). Les Acroporidae sont négativement corrélés à la couverture des algues calcaires encroûtantes, mais positivement corrélés à la couverture d'autres taxons vivants (comme les éponges). En revanche, aucune corrélation significative n'a été enregistrée pour les Poritidae et les jeunes coraux de la catégorie "autres". Cette étude a identifié des sites sur la pente externe et les massifs coralliens lagonaires qui pourraient être considérés comme des points chauds de recrutement à protéger en priorité, tandis que les sites dégradés sur la pente interne pourraient bénéficier de la transplantation de coraux. Les mesures de conservation devraient être accompagnées d'activités alternatives avec une forte implication des populations locales par le biais de zones marines gérées localement.

**Mots-clés :** Récifs coralliens; coraux scléractiniaires; recrutement; variabilité spatio-temporelle; facteurs environnementaux; Madagascar.

## Abstract

Investigating coral recruitment is critical to better understand replenishment and resilience capacities of coral reef ecosystems and to improve their conservation. Here, we examined the spatio-temporal patterns of coral recruitment and the influence of substrate composition in the region of Toliara, southwest Madagascar. Terracotta tiles were immersed from October to late January over a three-year period (2018–2021) at 10 stations located on major reef habitats. Overall recruitment rates were relatively high compared to other reefs in the South Western Indian Ocean, ranging from 219.20 recruits.m$^{-2}$ in 2018–2019 to 156.30 recruits.m$^{-2}$ in 2020–2021. Recruit assemblages were dominated by Acroporidae (45.5%) and Pocilloporidae (45.0%), whereas Poritidae (1.9%) and “other” recruits (3.6%) were rarely recorded. Recruitment patterns varied among stations and habitats, with higher rates in patch reef (187.06 recruits.m$^{-2}$) and outer slope stations (156.99 recruits.m$^{-2}$) compared to inner slope stations (108.04 recruits.m$^{-2}$). With the exception of “other” recruits, recruitment rates decreased between 2018–2019 and 2019–2020, followed by an increase in 2020–2021 that reached or even exceeded initial values at some stations. The abundance of Pocilloporidae recruits was positively correlated with the cover of confamilial adult corals and soft corals, and negatively with algae cover (crustose coralline algae [CCA], macroalgae, and turf). Acroporidae were negatively correlated with CCA cover, but positively with the cover of other living taxa (such as sponges). In contrast, no significant correlation with substrate composition was recorded for Poritidae and “other” recruits. This study identified sites on the outer slope and patch reefs to consider prioritizing for protection as recruitment hotspots, as well as degraded inner slope sites that could benefit from restoration, with the important caveat that any measures should be accompanied by alternative income-generating activities through local involvement that suits the Malagasy context, such as Locally Marine Managed Areas.

**Keywords:** Coral reefs; scleractinian corals; recruitment; spatio-temporal variability; environmental factors; Madagascar.

## 5.1. Introduction

World coral reefs have suffered in recent decades from significant impacts of various natural and anthropogenic disturbances (Bellwood et al. 2004, Hoegh-Guldberg & Bruno 2010, Hughes et al. 2017a, Obura et al. 2022). Degradation of coral reefs in the Anthropocene is mostly associated with mass bleaching events caused by thermal anomalies, exacerbated by other threats such as overharvesting, sedimentation, predator outbreaks, and cyclones (Mumby et al. 2006a, Hoegh-Guldberg et al. 2007, Hughes et al. 2018b). These threats may induce mass mortalities of scleractinian corals, the major reef-building taxa and key components of reef health and biodiversity, which in turn cause habitat degradation, and decline in reef organism diversity and abundance (Pratchett et al. 2011, Hongo & Yamano 2013). In some cases, major disturbances may cause phase shifts, which involve the replacement of corals by macroalgae or other non-reef-building benthic organisms and lead to fewer goods and services to human populations (McManus & Polsenberg 2004). One of the challenges in overcoming these coral-reef crises is for scientists and policy makers to determine the resilience of coral reefs, defined by their ability to maintain or return to their original state after being impacted by disturbances (Hughes et al. 2010, Lam et al. 2020). Two key components of resilience are resistance, the ability of an ecosystem to absorb disturbances while retaining its function and provision of services, and recovery, the capacity to return to its initial state after being transformed (Carpenter et al. 2001, McClanahan et al. 2012, Lam et al. 2020). Recovery of coral populations depends on coral recruitment, the arrival of newly settling larval recruits to adult populations (Caley et al. 1996), as well as on the growth and propagation of surviving coral colonies (Hughes & Tanner 2000, McClanahan et al. 2012, Gilmour et al. 2013, Lukoschek et al. 2013, Mumby et al. 2016, Adjeroud et al. 2018). Coral recruitment is critical to maintain and renew coral assemblages (Gilmour 1999, Doropoulos et al. 2015, 2017a, Mwachireya et al. 2015, Luter et al. 2016, Jouval et al. 2019) and is also a key indicator of resilience (McClanahan et al. 2012, Adjeroud et al. 2017, Edmunds 2018, Gouezo et al. 2019, 2020, Hughes et al. 2019, Sutthacheep et al. 2019, Guerrini et al. 2020).

Coral recruitment often shows a marked variability across spatial scales (Hughes et al. 2002, Adjeroud et al. 2007, Sola et al. 2015, Davidson et al. 2019, Jouval et al. 2019), due to the heterogeneity of environmental conditions. For example, local-scale variation in coral recruitment may be influenced by physico-chemical factors such as hydrodynamics and wave exposure, sedimentation, substrate characteristics, or water quality (Ritson-Williams et al.

2009, Edmunds et al. 2010, Edmunds 2022). Coral recruitment is also controlled by biotic factors such as predation, allelopathy, and competition with algae through space pre-emption, overgrowth, and chemical cues (Kuffner et al. 2006, Dixson et al. 2014). Recruitment patterns vary among coral taxa (Ritson-Williams et al. 2009, Kayal et al. 2015, Richmond et al. 2018, Gouezo et al. 2020, Thomson et al. 2021) in relation to contrasting life history traits such as reproductive strategies, larval preferences, and selective mortality (Mundy & Babcock 1998, Baird et al. 2003, Doropoulos et al. 2020, Shlesinger & Loya 2021). Temporal variability also characterizes coral recruitment patterns; a marked seasonal variability in recruitment rates and composition is often related to the single annual reproductive cycle for most broadcast spawning species (Harrison & Wallace 1990, Baird et al. 2009c, Richmond et al. 2018). Interannual variability in recruitment rates is documented for most coral reefs worldwide, linked to variation in climatic and oceanographic conditions and the occurrence of large-scale perturbations such as bleaching events or cyclones, all of which affect coral fecundity, dispersal, and pre- and post-settlement mortality (Mumby 1999, Mallela & Crabbe 2009, Lukoschek et al. 2013, Doropoulos et al. 2014, Hughes et al. 2019, Edmunds 2021c). Temporal pattern is thus often characterized by the succession of ‘good’ and ‘bad’ recruitment years with important implications for the structure and dynamics of adult populations (Hughes 1990, 1996, Connell et al. 1997, Hughes et al. 2000, Edmunds 2017). However, the increasing frequency and severity of large-scale disturbances and local stressors in the last five decades have resulted in a variation of coral recruitment worldwide, with a general decline in recruitment rates and a shift in recruit assemblage composition for several reefs (Hughes et al. 2019, Price et al. 2019, Edmunds & Riegl 2020, Guerrini et al. 2020), with other reefs still showing consistent, high recruitment rates (Adjeroud et al. 2022).

In Madagascar, coral reefs have confronted severe degradation since the 1980s. Major bleaching episodes associated with El Niño events in 1998 and 2015–2016 caused high mortality within coral assemblages, particularly in the northwest and southwest coasts (Obura 2005). Other threats such as overfishing, occasional use of destructive fishing methods, gleaning activities, and water pollution have also affected several coral reefs of the island. To mitigate the impacts of local stressors and large-scale disturbances on reefs and to promote their resilience, several Marine Protected Areas (MPAs) have been implemented by Malagasy authorities and NGOs, most often with the strong involvement of local populations through Locally Marine Managed Areas (LMMAs; (Ratsimbazafy et al. 2019). However, most of these

MPAs have been designed to protect fishery resources and rarely target coral assemblages (McClanahan & Jadot 2017, Ratsimbazafy et al. 2019, Randrianarivo et al. 2022).

While spatial patterns and community structure of coral assemblages around Madagascar have been documented, with recent progress on the effects of environmental factors and MPAs at local (Botosoamananto et al. 2021, Carter et al. 2022) and regional (Randrianarivo et al. 2022) scales, studies have not examined coral recruitment processes, with the exception of a preliminary study by Todinanahary et al. (2021). This lack of knowledge on coral recruitment at Madagascar contrasts with several studies conducted in the South Western Indian Ocean (SWIO) region, and investigations in Kenya (Mangubhai et al. 2007), Seychelles (Chong-Seng et al. 2014), Mozambique (Sola et al. 2015), Mascarene Islands (Jouval et al. 2019), and South Africa (Glassom et al. 2006). However, information on coral recruitment processes is crucial to implement and improve upon appropriate conservation and restoration measures for degraded reefs at Madagascar.

In this context, the present study examined the spatial and temporal patterns of coral recruitment in the region of Toliara, southwest Madagascar. Variability of recruitment rates and taxonomic composition was assessed at 10 stations located on the three major reef habitats (patch reefs, the inner slope, and the outer slope), during three consecutive years (2018 to 2021). To better understand the underlying extrinsic factors of recruitment variability, we examined the potential influence of confamilial adult corals and other benthic organisms on recruitment at the station scale. We also discuss the study's implications for reef conservation and management, such as the potential prioritization of sites with identified higher recruitment rates.

## 5.2. Materials and methods

### 5.2.1. Study area and sampling stations

This study was conducted in the region of Toliara, with a focus on the Great Reef of Toliara (GRT), one of the most developed barrier reefs of the southwest coast of Madagascar (Figure 5.1.). The human population living in Toliara City has considerably increased in recent years, with strong impacts on coral reefs through fishing and gleaning activities (Laroche & Ramananarivo 1995, Harris 2007). High sedimentation resulting from the poor management of mining and agricultural activities of the two main upstream rivers, Fiherenana in the north and Onilahy in the south, also affects coral assemblages of the GRT (Maina et al. 2013, Sheridan et al. 2014). The major large-scale natural disturbances that have impacted coral reefs of the GRT are thermally-induced coral bleachings, with major events reported in 1998, 1999 and 2016 (McClanahan et al. 2007, Obura et al. 2018, Gudka et al. 2020), and a minor event in 2020 (Botosoamananto, personal observation; Fig. S1). Thermal stress in 2001, 2006, 2009, and 2021 (Fig. S1) have likely caused mild effects on coral assemblages of the GRT, but no mass bleaching events were reported. Cyclones are less frequent in the southwest coast of Madagascar compared to the eastern coast or to other regions in the SWIO, and though Cyclone Haruna passed 120 km north of Toliara in February 2013 (Carter et al. 2022), no significant impacts on the GRT were reported. Similarly, outbreaks of the coral predator *Acanthaster* spp. have not been reported in recent years on the GRT.

A nested sampling design, with 10 stations disposed on the three major reef habitats, was selected to assess the spatial and temporal variation of coral recruitment rate and composition. Four stations were established on patch reefs (PR1, PR2, PR3, PR4), two on the inner slope (IS1, IS2), and four on the outer slope (OS1, OS2, OS3, OS4; Figure 4.1.). Station codes are abbreviated as follows: the first two letters represent the habitats (PR: patch reefs, IS: inner slope, and OS: outer slope) and the numbers specify each station. All stations were located between 7 and 12 m depth, consistent with those already established to survey the diversity, abundance, and cover of adult coral assemblages (Botosoamananto et al. 2021).

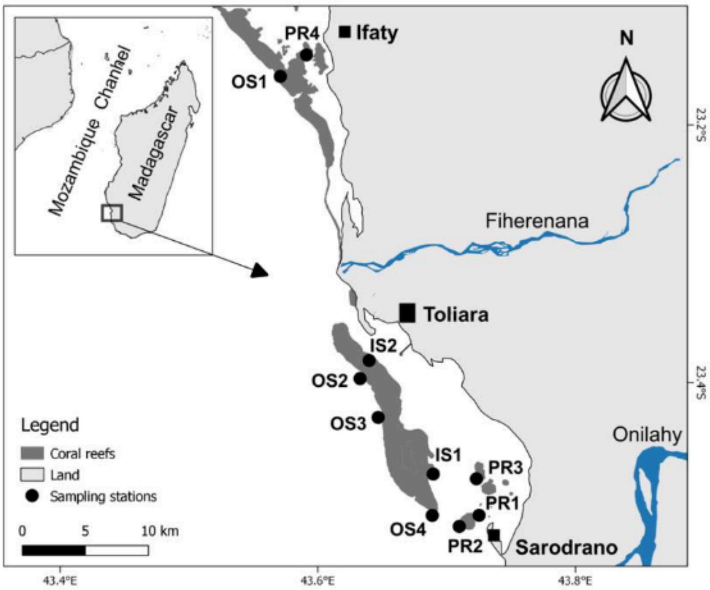

**Figure 5.1.** Map of the southwest coast of Madagascar showing the location of the 10 sampling stations in the Toliara region, including the Great Reef of Toliara (GRT). Stations were located on the three major reef habitats: patch reefs (PR), the inner slope (IS), and the outer slope (OS). See Materials and methods section for station codes.

### 5.2.2. Deployment and analysis of recruitment tiles

At each station, coral recruitment was characterized using 20 unglazed terracotta tiles (11 × 11 × 1 cm) directly attached to the substrata (Mundy 2000). Tiles were immersed for four months (October to late January) over a three-year period (October 2018–January 2019, October 2019–January 2020, October 2020–January 2021; hereafter referred to as 2018–2019, 2019–2020, and 2020–2021 recruitment events, respectively). At the end of each immersion period, tiles were retrieved and bleached to expose and identify coral recruits under stereomicroscope. For each surface of the tile (upper, lower, and sides), recruits were counted and identified. At this stage of development, three families (Acroporidae, Pocilloporidae, Poritidae) were distinguished, and all other coral families were compiled into a category named “other” recruits (Babcock et al. 2003). Broken recruits (i.e., too damaged to be identified with certainty), which represent < 4% of the overall recruits (all stations and years pooled), were not analyzed, but were considered in the overall recruitment counts (all categories pooled).

### 5.2.3. Characterization of living substrate composition

Using the station as a sampling unit, we analyzed the influence of major living substrates on the distribution and abundance of coral recruits. At each station, the percent cover of major benthic substrates was assessed in 2018, 2019, and 2020 using 30 photoquadrats of 0.25 m² (50 × 50 cm) taken along three transects of 10 m length with an underwater camera (Nikon W300; Botosoamananto et al., 2021). Percent cover was estimated using the Coral Point Count with Excel extension software (CPCE 4.1; Kohler and Gill, 2006). On each photograph, 100 random points were used to quantify the percent cover of hard corals (scleractinian corals and the calcareous hydrocoral *Millepora*), soft corals (Alcyonacea, mainly represented by *Xenia* sp. and *Sarcophyton* sp.), algae (crustose coralline algae [CCA], macroalgae, and turf), and other living taxa (including sponges, hydroids, zoanthids, corallimorphs, tunicates, and sea anemones; Botosoamananto et al., 2021).

### 5.2.4. Statistical analysis

Spatial and temporal variations of recruit abundance among the three habitat types, 10 stations, and three time periods were tested for goodness of fit of a negative binomial distribution. We used generalized linear mixed effect models (GLMM) using Lme4 (Bates et al. 2015) package in R (R Core Team 2021) with three-factor levels (years, habitats, and stations), as this approach takes into consideration unbalanced sampling and does not require the verification of parametric test assumptions (Bolker et al. 2009). Analyses were performed for the overall coral recruitment (all taxa pooled) and each of the dominant coral family categories: Acroporidae, Pocilloporidae, Poritidae, and “other” recruits. A separate GLMM was performed to compare the abundance of recruits on the three different surfaces (lower, upper, and sides) of recruitment tiles. To assess the effects of substrate composition on recruit abundance, we conducted a third negative binomial error structured GLMM with percent cover of benthic substrates as a predictor, and year as a random factor. Percent cover of corals, CCA, macroalgae, turf, soft corals, and other living taxa were selected as fixed factors. For corals, we distinguished cover of the four main coral families (Acroporidae, Pocilloporidae, Poritidae, and “other” recruits) to correlate recruit abundance with cover of confamilial adult colonies (mean of the three years). We constructed a different model for each of the four main coral families. For model selection, the Akaike information criterion corrected for small size (AICc) was used. Best models of AICc $< 4$ were selected, and model averaging was performed within them. The relative importance of each predictor in the averaged model was calculated by summing the Akaike weights for the predictor over the best models. This index ranges from 0 to 1, with a higher value for the higher relative importance. Statistical analyses were performed using R 4.1.0 (R Core Team 2021).

## 5.3. Results

### 5.3.1. Taxonomic composition

Over the three years of the study, recruit assemblages (all habitats/stations pooled) were dominated by Acroporidae (45.5%) and Pocilloporidae (45.0%), whereas “other” recruits (3.6%) and Poritidae (1.9%) were greatly less abundant. However, while the relative contribution of Acroporidae and Pocilloporidae was similar during the first two years, it changed in the last year of the study (42.6% in 2018–2019 and 41.5% in 2019–2020 for Acroporidae, and 48.2% in 2018–2019 and 47.6% in 2019–2020 for Pocilloporidae; 55.7% of Acroporidae, and 35.3% of Pocilloporidae in 2020–2021, Figure 5.2.).

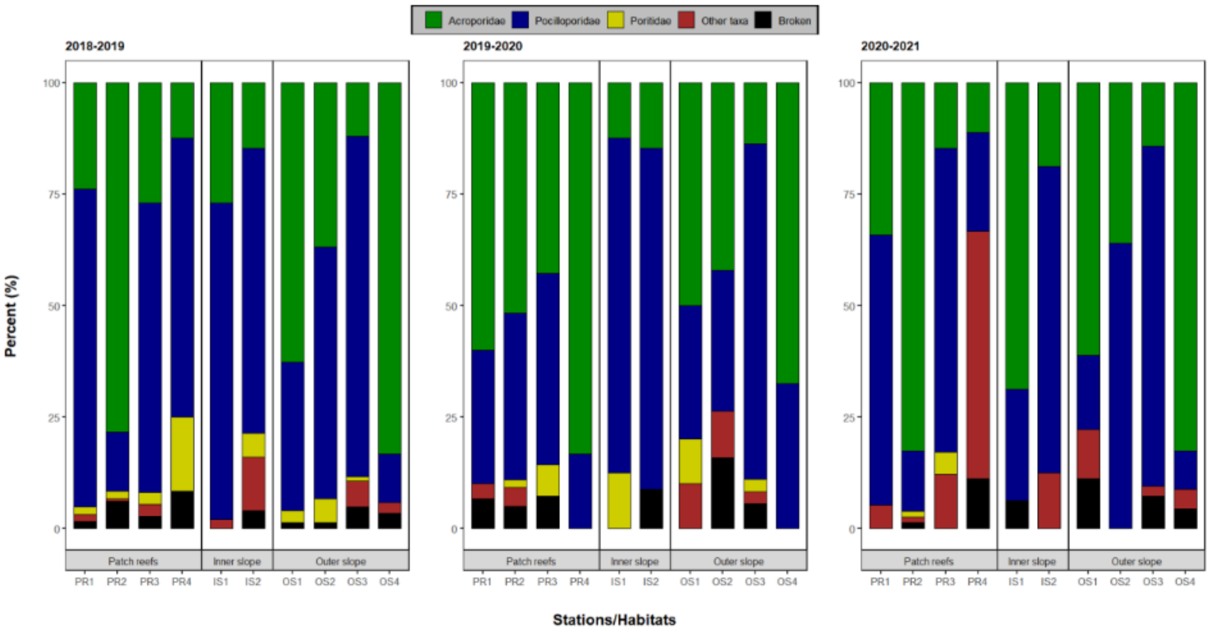

**Figure 5.2.** Variation in the relative taxonomic composition of recruit assemblages at the 10 stations established on the three major habitats during the three years of this study (2018–2019, 2019–2020, 2020–2021).

For Acroporidae, they dominated the recruit assemblage on patch reefs (representing 55.5% of the total recruits), had slightly lower relative abundance on the outer slope (41.8 %), and further reduction on the inner slope (22.4%), except at station IS1 in the final year (2020–2021). Pocilloporidae dominated the recruit assemblage on the inner slope (65.7%) as well as the outer slope (49.3%) but on patch reefs was 35.4%, with a reduced contribution at station PR2 and PR4, depending on the year. The relative abundance of Poritidae and “other” recruits was low at all three habitats (2.3% and 3.2% on patch reefs, 2.5% and 6.0% on the inner slope, and 1.6% and 3.4% on the outer slope, respectively), although station PR4 was characterized by a high contribution of “other” recruits in the last year of the study (2020–2021).

### Spatio-temporal variation of recruitment rates

The overall recruitment rate (all taxa and habitats/stations pooled) was variable among the three years (Tables S1 and S2), with a higher value in 2018–2019 (6.27 ± 0.59 recruits.tile$^{-1}$, mean ± SE, representing 219.20 recruits.m$^{-2}$), compared to both 2019–2020 (2.71 ± 0.33 recruits.tile$^{-1}$, representing 94.75 recruits.m$^{-2}$) and 2020–2021 (4.47 ± 0.77 recruits.tile$^{-1}$, representing 156.30 recruits.m$^{-2}$). Slightly higher recruitment rates (all taxa and years pooled) were recorded at patch reefs (5.35 ± 0.70 recruits.tile$^{-1}$, representing 187.06 recruits.m$^{-2}$), compared to the outer slope (4.49 ± 0.42 recruits.tile$^{-1}$, representing 156.99 recruits.m$^{-2}$) and the inner slope (3.09 ± 0.39 recruits.tile$^{-1}$, representing 108.04 recruits.m$^{-2}$; Tables S1 and S2). During the study period, a decreasing trend was observed on the inner slope (4.23 ± 0.68 in 2018–2019 to 1.77 ± 2.01

recruits.tile$^{-1}$ in 2020–2021; Figure 5.3.). At both patch reefs and the outer slope, recruitment rates decreased from 2018–2019 to 2019–2020, and, in 2020-2021 continued to decrease on the outer slope (7.25 ± 0.89 in 2018–2019 compared to 3.44 ± 0.35 recruits. tile$^{-1}$ in 2020–2021; Figure 5.3., Tables S1 and S2). However, at patch reefs, values in 2020–2021 increased and exceeded initial values (7.71 ± 1.97 in 2020–2021 compared to 6.20 ± 1.14 recruits.tile$^{-1}$ in 2018–2019).

At the station scale, stations on patch reefs showed a decrease in recruitment rates between 2018–2019 and 2019–2020, but a return to initial values in 2020–2021 at stations PR1 and PR3, and even a higher value at station PR2 (Figure 5.4.). Station PR4 was characterized by lower recruitment rates compared to other patch reef stations, with no significant temporal trend (Tables S1 and S2). The outer slope stations and one of the inner slope stations (IS1) also showed a decrease in recruitment rates between 2018–2019 and 2019–2020, followed by a slight increase in 2020–2021, except at OS3, which never exceeded initial values of 2018–2019 (Figure 5.4., Tables S1 and S2).

A marked spatial and temporal heterogeneity of recruit abundance was observed for each of the four coral categories (Figure 5.5., Tables S1 and S2). For Acroporidae, overall recruit abundance (all years pooled) was higher on patch reefs (2.97 ± 0.55 recruits.tile$^{-1}$) than on the outer slope (1.87 ± 0.23 recruits.tile$^{-1}$) and inner slope (0.69 ± 0.04 recruits.tile$^{-1}$; Figure 5.3., Tables S1 and S2). This pattern was mainly driven by the high abundance recorded at station PR2 (Figure 5.5.). At all three habitats and at most stations, abundance of Acroporidae recruits decreased from 2018–2019 to 2019–2020, but was followed by an increase in 2020–2021 that exceeded initial values at stations PR1 and PR2 on patch reefs (Figure 5.5., Tables S1 and S2).

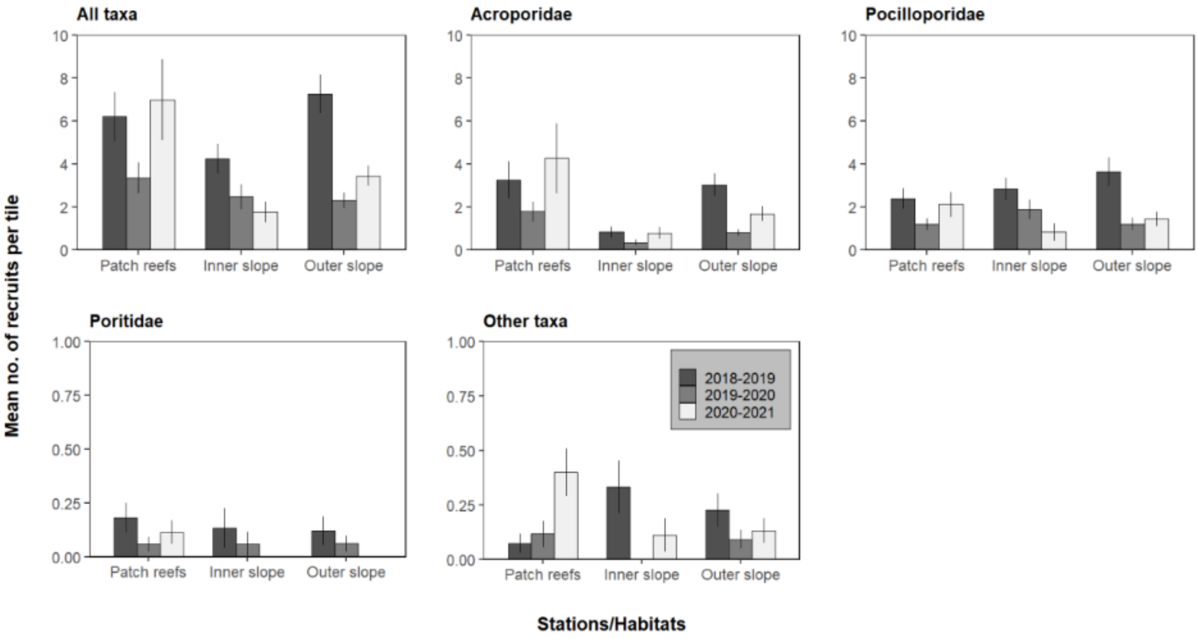

**Figure 5.3.** Spatio-temporal variation in recruitment rates of the five major categories (all taxa, Acroporidae, Pocilloporidae, Poritidae, and “other” recruits) among the three major habitats during the three years of this study (2018–2019, 2019–2020, 2020–2021).

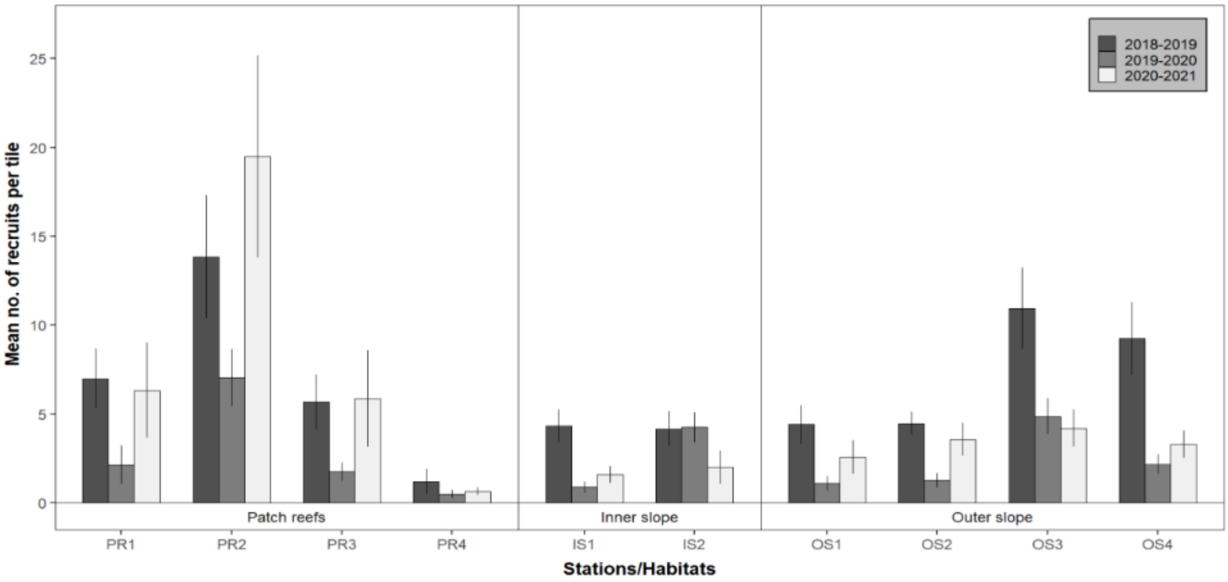

**Figure 5.4.** Spatio-temporal variation in overall recruitment rates (all taxa pooled) among the 10 stations established on the three major habitats during the three years of this study (2018–2019, 2019–2020, 2020–2021). Bars represent standard errors.

For Pocilloporidae among the habitats, overall recruit abundance (all years pooled) was slightly higher on the outer slope (2.21 ± 0.30 recruits.tile$^{-1}$) than the inner slope (2.03 ± 0.30 recruits.tile$^{-1}$) and patch reefs (1.39 ± 0.07 recruits.tile$^{-1}$; Figure 3.3., Tables S1 and S2). This pattern was mainly driven by the higher abundance recorded at station OS3 during the three years (Figure 5.5.). A decrease in the abundance of Pocilloporidae recruits between 2018–2019 and

2019–2020 was observed across all stations except PR2 and IS2; in 2020-2021 this was followed by an increase to, or approaching, initial values of patch reefs and OS2 (Figure 5.5., Tables S1 and S2).

For Poritidae, overall recruit abundance was low but slightly higher at patch reefs (0.12 ± 0.03 recruits.tile$^{-1}$) compared to the inner slope (0.07 ± 0.02 recruits.tile$^{-1}$) and the outer slope (0.07 ± 0.04 recruits.tile$^{-1}$; Figure 5.3., Tables S1 and S2). Abundance of Poritidae recruits decreased from 2018–2019 to 2019–2020 at several stations of all three habitats, and further decreased in 2020-2021 with no recruits recorded at any sites other than PR2 and PR3, which returned to values similar to the first year (Figure5.5., Tables S1 and S2).

For "other" recruits, overall abundance (all years pooled) was low and similar between the habitats (0.17 ± 0.04 recruits.tile$^{-1}$ on patch reefs, 0.18 ± 0.06 recruits.tile$^{-1}$ on the inner slope, and 0.15 ± 0.03 recruits.tile$^{-1}$on the outer slope; Figure 3.3., Tables S1 and S2). At all patch reef stations, abundance of "other" recruits increased over the three years, notably at stations PR3 and PR4, while a decreasing trend was observed on the inner and outer slopes, except OS1 (Figure 5.5., Tables S1 and S2).

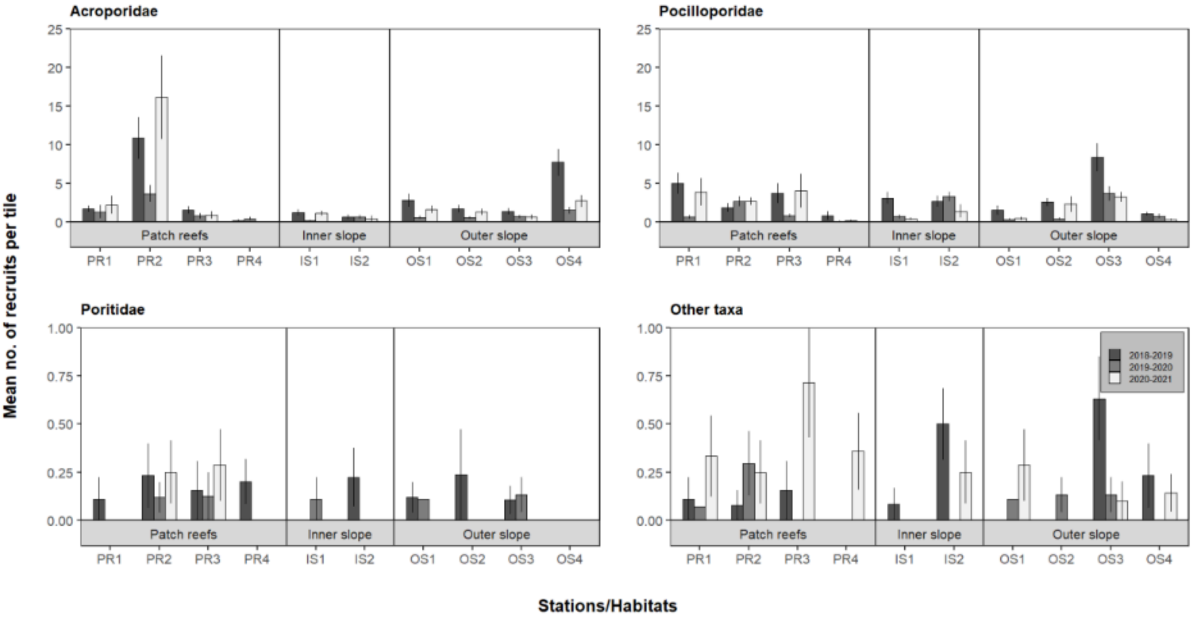

**Figure 5.5.** Spatio-temporal variation in recruitment rates of the four dominant coral categories (Acroporidae, Pocilloporidae, Poritidae, and "other" recruits) among the 10 stations established on the three major habitats during the three years of this study (2018–2019, 2019–2020, 2020–2021). Bars represent standard errors.

### 5.3.2. Variation of recruit orientation on tiles

The proportion of recruits recorded on the different surfaces of the tiles varied among years, habitats, and stations (Tables S3 and S4). In general (all taxa and all years and habitats/stations pooled), recruits were more abundant on the sides (60.0 %), compared to the lower (24.5 %) and upper (15.5 %) surfaces. This pattern was consistent for each of the four main recruit categories (Acroporidae, Pocilloporidae Poritidae and "other" recruits). In 2018–2019, the vast majority of recruits (> 80%) were recorded on the sides and the lower surface at most stations, except OS1 on the outer slope where 30% of recruits were found on the upper surface (Figure 5.6., Tables S3 and S4). In 2019–2020, an increase in the proportion of recruits on the upper surface was recorded at stations PR1 and PR2, whereas this proportion decreased at stations PR4, OS2, and OS4. In 2020–2021, the proportion of recruits on the upper surface was higher at most stations compared to previous years, particularly at one patch reef (PR2) and one outer slope (OS1) station, where ~50% of the recruits were recorded on this surface (Figure 5.6., Tables S3 and S4).

### 5.3.3. Substrate composition

Our results from the GLMM highlighted that the relationships between benthic substrates (hard corals, soft corals, algae [CCA, macroalgae, turf], and other living taxa) and recruit abundance varied among categories of recruits (Figure 5.7., Tables S5, S6, S7, S8, and S9). Significant ($p < 0.05$) correlations were recorded for all taxa combined, Acroporidae, and Pocilloporidae, whereas abundance of Poritidae and "other" recruits did not link to the selected benthic substrates. When we examined the abundance of recruits with the cover of confamilial adult colonies, we only found a significant positive correlation for Pocilloporidae. For algae cover, CCA was negatively correlated with recruit abundance of Acroporidae, Pocilloporidae, and all taxa, while turf and macroalgae cover showed a significant negative correlation with Pocilloporidae recruits. Soft coral cover (Alcyonacea, mainly represented by *Xenia* sp. and *Sarcophyton* sp.) showed a negative correlation with the abundance of recruits from all taxa, whereas a positive correlation was recorded with Pocilloporidae recruits. Cover of other living taxa (sponges, hydroids, zoanthids, corallimorphs, tunicates, and sea anemones) was positively correlated with abundance of Acroporidae recruits (Figure5.7., Tables S5, S6, S7, S8, and S9).

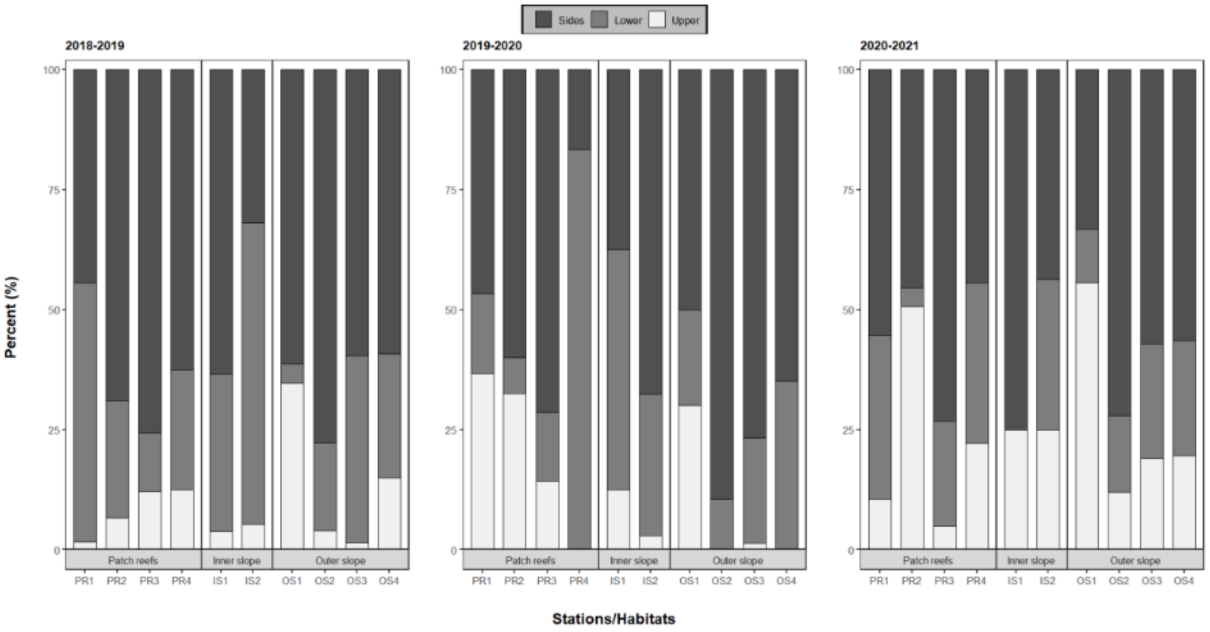

**Figure 5.6.** Relative proportion (%) of coral recruits (all taxa pooled) recorded on the different surfaces of the recruitment tiles (sides, upper, and lower) at the 10 stations established on the three major habitats during the three years of this study (2018–2019).

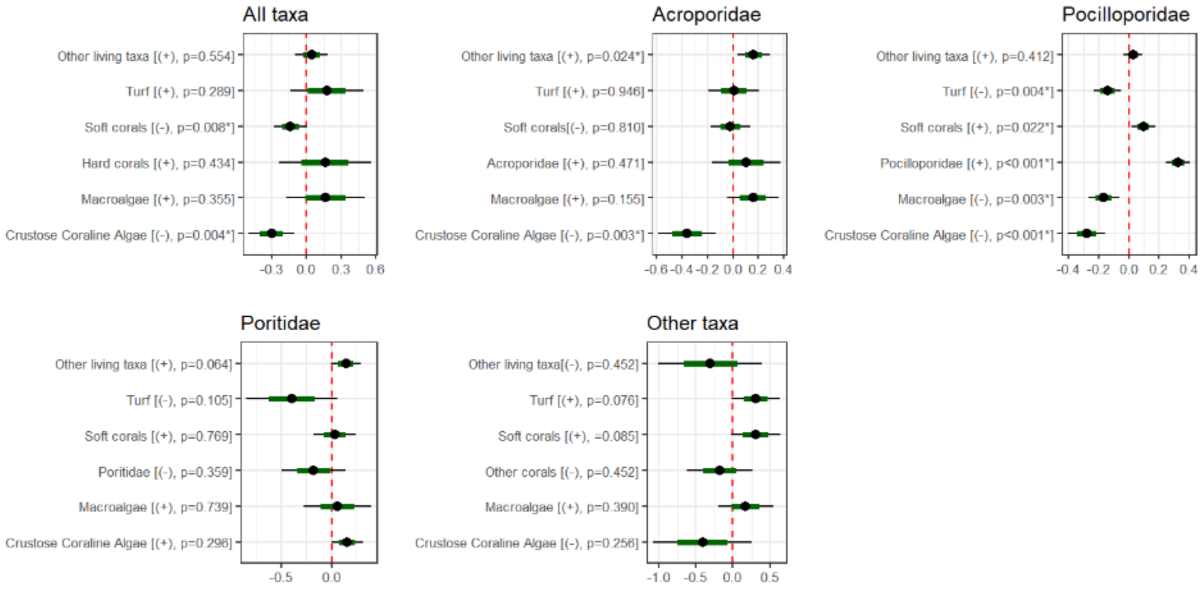

**Figure 5.7.** Mean effects of benthic substrates on the abundance of coral recruits for the five major categories (all taxa, Acroporidae, Pocilloporidae, Poritidae, and "other" recruits). Values were standardized as effect sizes, circles represent mean parameter estimates, and lines represent 95% confidence intervals. *: significant ($p < 0.05$) correlations.

## 5.4. Discussion

### 5.4.1. Spatio-temporal patterns

Our results clearly demonstrate the high degree of spatial and temporal heterogeneity in coral recruitment in the Toliara region. This is consistent with patterns recorded at several reefs worldwide, from the east African coast (Sola et al. 2015), Mascarene islands (Nzali et al. 1998, Jouval et al. 2019) and the Seychelles (Chong-Seng et al. 2014) in the SWIO, to the Great Barrier Reef (Dunstan & Johnson 1998, Doropoulos et al. 2015, Davidson et al. 2019), New Caledonia (Adjeroud et al. 2022), and French Polynesia (Adjeroud et al. 2007, Edmunds et al. 2010, Penin & Adjeroud 2013) in the Pacific, as well as the Red Sea (Glassom et al. 2004, Abelson et al. 2005, Guerrini et al. 2020) and the Caribbean (Moulding 2005, Green & Edmunds 2011, Edmunds 2021a). Overall (all taxa pooled) recruitment rates documented in the present study ranged from 17.48 ± 8.04 to 681.81 ± 198.60 recruits.m$^{-2}$ across stations and years, with highest values (> 200 recruits.tile$^{-1}$) recorded at patch reefs and outer slope stations, notably during the first (2018–2019) and last (2020–2021) year of this study. Although comparisons among surveys with different methodologies should be taken with caution, the highest values recorded at Toliara are high compared to those from other SWIO reefs, such as Kenya (Mangubhai et al. 2007), Mozambique (Sola et al. 2015), South Africa (Glassom et al. 2006), Seychelles (Chong-Seng et al. 2014), and Reunion and Rodrigues islands (Jouval et al. 2019), and reefs in the Central Pacific such as French Polynesia (Adjeroud et al. 2007), where recruitment rates are generally less than 150 recruits.m$^{-2}$. However, highest recruitment rates at Toliara remain greatly lower than those recently recorded in the southwestern lagoon of New Caledonia, with up to 13,572 recruits.m$^{-2}$ during particularly 'good' recruitment years (Adjeroud et al. 2022).

Recruit assemblages at Toliara were characterized by the similarly high (~45%) contribution of both Acroporidae and Pocilloporidae recruits, though with slight variations in contribution across sites and years, and the constantly low abundance of Poritidae and "other" recruit families. This characteristic contrasts with other SWIO reefs, where recruit assemblages are generally dominated by either Acroporidae, such as in Mozambique (Sola et al. 2015), or Pocilloporidae, such as in Reunion Island (Jouval et al. 2019), with even Poritidae dominate reefs recorded at Rodrigues (Jouval et al. 2019). The high contribution of Acroporidae in the present study may be attributable to the relatively high abundance and cover in adult assemblages (Botosoamananto et al. 2021) and to the synchronized spawning of *Acropora* corals in the region (Gress et al. 2014) potentially inducing a high concentration of larvae over a short period of time that settle on recruitment tiles. Similarly, the high contribution of Pocilloporidae recruits could be related to the high abundance of *Pocillopora* and *Stylophora* adult colonies at our study sites (Botosoamananto et al. 2021). In contrast, this suggested relationship between abundance of adults and recruits is not valid for Poritidae, since low contribution of recruits was recorded despite abundant adult colonies of *Porites* in the region of Toliara (Botosoamananto et al. 2021). The extended period of reproduction and spawning of *Porites* recorded at some reefs in the region (Mangubhai et al. 2007, Gress et al. 2014), which dilutes the larval pool over long periods of the year, may explain the low abundance of Poritidae recruits on our recruitment tiles that are immersed for four months each year.

As documented for several coral reefs worldwide (Babcock and Davies, 1991; Bauman et al., 2013; Fisk and Harriott, 1990; Ho and Dai, 2014; Maida et al., 1995, among others), we recorded a higher proportion of recruits on the lower surface and sides of recruitment tiles. The lower abundance on the upper surface likely results from either post-settlement mortality induced by high grazing levels by herbivorous organisms or by colonization of fleshy algae that compete for space with recruits and trap sediments that smother young colonies (Fisk & Harriott 1990, Babcock & Davies 1991, Maida et al. 1995, Bauman et al. 2013a, Ho & Dai 2014).

A marked spatial variability was also found among habitats and stations, with highest recruitment rates consistently recorded at patch reefs and outer slope stations, though several stations in these habitats also showed low values. In contrast, recruitment rates were consistently lower at inner slope stations during the three years of the study. This pattern may be linked to the degraded environmental conditions generally found on the inner slope, with higher sedimentation and fishing pressure and lower abundance of several adult coral taxa, notably *Acropora* and *Pocillopora*, compared to patch reefs and the outer slope (Botosoamananto et al. 2021). However, additional studies are necessary to examine more precisely the environmental characteristics of these habitats.

We recorded a significant interannual variability of recruitment rates for all coral taxa and for each of the four recruit categories, consistent with studies in many other coral reefs Adjeroud et al. 2007, 2022, Dunstan et Johnson 1998; among others). A large part of this temporal variability results from variation in the fecundity of coral populations (Hughes et al. 2000), which is driven by changes in climatic and oceanographic conditions. Sea surface temperature (SST) is a major determinant of variation in coral fecundity and thermally induced bleaching events are expected to reduce coral fecundity and recruitment in the upcoming years (Hughes et al. 2000, 2019, Ward et al. 2002). However, our results do not strictly follow this hypothesis. In fact, a minor bleaching event was observed from February 2020, resulting from elevated SST (~31°C) in January and February, but did not cause a major reduction in recruitment the following year. Instead, we recorded an increase at several sites in October 2020–January 2021, sometimes reaching or even exceeding 2018–2019 values. Moreover, the decrease in recruitment rates that we recorded in October 2019–January 2020 was not related to an increase in SST the previous years. Thus, other environmental factors such as sedimentation loads and wave energy exposure (Edmunds et al. 2010), for which we do not yet have rigorous data, are probably more related to the interannual changes in recruitment rates recorded at Toliara.

The marked variability among the three years of this study emphasizes the need for long-term interannual monitoring of coral recruitment to identify trends and potential sporadic peaks in recruitment such as reported in New Caledonia (Adjeroud et al. 2022) and to determine the drivers of variability.

### 5.4.2. Influence of substrate composition

Several studies have highlighted the importance of substrate composition on coral recruitment patterns (Dunstan & Johnson 1998, Harrington et al. 2004, Kuffner et al. 2006, Jorissen et al. 2020). Some benthic components, such as macroalgae, are generally a major inhibitor of coral recruitment whereas other taxa, such as certain CCA, may promote their recruitment (Birrell et al. 2005, Arnold et al. 2010). Our results agree with this generalization, as we recorded correlations, both negative and positive, between benthic substrates and recruitment rates. Even a single benthic category may be positively linked to the abundance of certain recruits but negatively to overall recruit abundance, such as with soft coral cover for Pocilloporidae recruits. Our results underscore that the relationships between benthic substrates and recruit abundance vary among recruit categories, from significant correlations for overall recruits (all taxa pooled), Acroporidae, and Pocilloporidae, to a lack of correlation for Poritidae and "other" recruits. This variability in the influence of benthic substrates is additional to the variable influence of spatial heterogeneity on recruitment rates among major coral families, and underlines the strong variation in recruitment patterns among taxa, in relation to contrasting life history traits.

CCA cover was negatively correlated to the abundance of Acroporidae, Pocilloporidae, and overall recruits. While several studies have demonstrated that CCA provide chemical or microbial positive cues for the settlement and metamorphosis of coral larvae and other reef invertebrates, others have failed to support this relationship (Harrington et al. 2004, Price 2010, Jorissen et al. 2020). In fact, the relationship between the coral and the CCA is very dependent on the two protagonist species (Harrington et al. 2004, Whalan et al. 2015, Jorissen et al. 2020). The negative effect of CCA may come from the chemical compounds secreted as a defence mechanism, impacting coral larvae during their settlement choice (Harrington et al. 2004, Price 2010). CCA can also inhibit coral recruitment by overgrowing and sloughing to remove the upper epithelial layers, thus eliminating small organisms including corals (Babcock & Mundy 1996, Dunstan & Johnson 1998, Harrington et al. 2004).

As in many previous studies (Vermeij 2005, Kuffner et al. 2006, Vermeij et al. 2009), our results underline the negative relationship between turf and macroalgae cover and abundance of coral recruits, in our case for the Pocilloporidae family. In fact, *competition for space with fleshy and filamentous algae may prevent coral recruitment* (Birrell et al. 2005, Arnold et al. 2010, Doropoulos et al. 2017b). Without space to settle, coral larvae spend more time in the water column searching for suitable substrate, leaving them more exposed to predation, starvation, and environmental stressors (Webster et al. 2015, Doropoulos et al. 2017b). Moreover, development of macroalgae has direct negative physical effects on coral recruits such as abrasion, shading, and smothering (McCook et al. 2001).

The negative effect of soft coral cover on the abundance of overall recruits (all taxa pooled) may be explained by several soft corals being identified as inhibitors of coral recruitment (Atrigenio & Aliño 1996, Maida et al. 2001). Soft corals such as *Sinularia flexibilis* and one of the dominant soft corals in our study sites, *Sarcophyton glaucum*, secrete toxic metabolites that cause high mortality of coral recruits (Maida et al. 1995). The soft coral *Dendronephthya* sp. releases antifouling compounds and epibiotic bacteria that inhibit larval settlement (Dobretsov & Qian 2004).

The positive link between soft coral cover and Pocilloporidae recruits, as well as the positive link between the cover of other living taxa (sponges, hydroids, zoanthids, corallimorphs, tunicates, and sea anemones) with the Acroporidae recruits, were both unexpected and are difficult to explain. Apart from the fact that it may be a significant correlation without a causal relationship, which sometimes happens with multiple correlation analyses, we hypothesize that some soft corals and other living taxa present in our study sites may have not had a sufficient inhibitory effect to significantly reduce recruitment rates of coral taxa. In this case, these positive correlations simply reflect a common higher abundance at sites where environmental conditions are favorable for some coral recruits, soft corals, and other living taxa. In any case, a complementary survey should examine in detail the species-specific interactions among corals of other benthic invertebrates of this region, which was not within the scope of the present study.

Our results highlight that the spatial variation in the abundance of Pocilloporidae recruits was positively correlated to cover of confamilial adult colonies. Such correlation may indicate the likelihood of a stock-recruitment model for population regulation (where adults drive the number of recruits), or a recruitment-limitation model (where recruits drive the number of adults; Caley et al. 1996, Baird et al. 2003, Penin et al. 2007, Adjeroud et al. 2017). This relationship may also be the result of an aggregate settlement of recruits near the established adult colonies (Edmunds 2000, Adjeroud et al. 2017, Sims et al. 2021).

The present study only examined the potential link between a small number of substrate categories and coral recruitment, but a more precise survey on other biological and physico-chemical factors influencing such variability is necessary to better understand coral recruitment processes and to improve conservation measures.

### 5.4.3. Implications for conservation

The relatively high recruitment rates recorded in the Toliara region compared to other sites in the SWIO, together with the high contribution of keystone taxa such as Acroporidae and Pocilloporidae, are encouraging results for coral conservation. These positive outcomes for recruitment processes demand implementation of management and conservation measures focused on recruitment to supports the capacity of coral assemblages to maintain a healthy state (Botosoamananto et al. 2021).

In the context of resilience-based management, actions should be taken to reduce the negative effects of nutrients and sediment loads from the Fiherenana and Onilahy rivers that have increased due to unmanaged mining, and agricultural and deforestation activities (Bruggemann et al. 2012, Sheridan et al. 2014). These actions are critical as coral recruits are particularly sensitive to increasing levels of sedimentation (Wakwella et al. 2020, Brunner et al. 2021) and nutrients (D'Angelo & Wiedenmann 2014, Evensen et al. 2021). Moreover, privileging better land and watershed management actions will also improve water quality and coral reef health, to the benefit of other reef communities.

Management of fishing activities should also be reinforced, with specific actions to protect the biomass and diversity of herbivorous fishes and invertebrates that control algal biomass to support coral recruitment processes and coral assemblage resilience. Destructive fishing methods are also part of the main cause of habitat degradation in the region of Toliara

(Harris et al. 2010, Bruggemann et al. 2012, Sheridan et al. 2014). This threat is particularly important to address as we showed that coral recruitment of Pocilloporidae, one of the dominant taxa, is highly dependent on the cover of adult colonies.

The marked spatial variability of recruitment rates and composition that we recorded also has implications in terms of area-based management actions. We identified sites on the outer slope (station OS3) and on patch reefs (station PR2) that consistently showed higher recruitment rates throughout the three years of this survey, as well as high abundance and cover of adult colonies (Botosoamananto et al. 2021). These recruitment hotspots for these habitats, and additional ones to be identified through a complementary, larger scale study, should be protected in priority and with drastic measures, such as no-take zones. These sites could act as a reservoir of coral colonies that could sustain a larval pool to replenish nearby reefs. Our results also identified sites, mainly on the inner slope, where recruitment rates are lower, and with less diverse and abundant adult assemblages (Botosoamananto et al. 2021). These sites, where the habitats are particularly degraded and unsuitable for corals, must be the subject of measures to restore the quality of environmental conditions and make them conducive to coral settlement and growth. These sites could also be candidates for restoration measures such as coral transplantation. However, as local populations are highly dependent on reef resources, it is imperative that these conservation measures be accompanied by alternative income-generating activities, such as aquaculture, with the strong involvement of local populations through Locally Marine Managed Areas (LMMAs; (Ratsimbazafy et al. 2019), which seem well suited to the Malagasy context (Todinanahary et al. 2016).

# Chapitre 6 :
# Mécanismes de régulation des populations de coraux scléractiniaires dans la région de Toliara, sud-ouest de Madagascar

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Ce chapitre est en préparation pour être soumis dans *Marine Ecology Progress Series*. **Botosoamananto RL**, Todinanahary G, Gasimandova LM, Randrianarivo M, Penin L, Adjeroud M. Regulation of coral assemblages in the Toliara region, southwest Madagascar: the link between recruits, juveniles, and adults. *To be submitted to Marine Ecology Progress Series*

**Résumé**

Comprendre les processus qui maintiennent les assemblages coralliens revêt une importance cruciale compte tenu de l'augmentation des taux de mortalité des coraux sur les récifs à l'échelle mondiale. Dans cette étude, nous avons comparé la variation spatiale de l'abondance des recrues, des juvéniles, et des adultes afin de déterminer la contribution des jeunes stades de vie dans structuration des assemblages adultes dans la région de Toliara, au sud-ouest de Madagascar. Les résultats ont mis en évidence une forte variabilité spatio-temporelle de l'abondance de tous les stades de vie au sein des principaux habitats récifaux (massifs coralliens lagonaires, pente interne, et pente externe). Nos résultats suggèrent des relations de type « stock-recrutement » pour les Acroporidae, tandis que les Poritidae et leur genre dominant *Porites* semblent plutôt régulés par des relations de type « limitation par le recrutement », avec des corrélations significatives entre l'abondance des stades juvéniles et celles des adultes des années suivantes. Nous avons trouvé des liens plus forts entre les trois stades de vie pour les Pocilloporidae, ce qui indique à la fois des relations limitation par le recrutement et stock-recrutement, principalement induites par le genre *Seriatopora* pour les corrélations juvénile-adulte. En revanche, aucune corrélation significative n'a été enregistrée pour la catégorie des "autres" familles, ce qui est probablement dû au mélange de différents taxa présentant des traits d'histoire de vie distincts. En complément, des corrélations positives entre les juvéniles et les adultes ont été observées pour les genres *Galaxea*, *Cycloseris* et *Pavona*, qui font partie de la catégorie « autres ». Les différences de processus de régulation entre les taxons de coraux mises en évidence dans ce travail suggèrent la mise en œuvre d'actions de conservation qui puissent bénéficier à tous les stades de vie. Par exemple, maintenir la biomasse des poissons herbivores et des invertébrés pour contrôler la biomasse algale peut favoriser le recrutement des coraux et réduire la mortalité des adultes. Nos résultats suggèrent également que les sites situés sur la pente externe et les massifs coralliens lagonaires, qui présentent des taux de recrutement plus élevés ainsi qu'une plus grande abondance et couverture de colonies adultes, pourraient être considérés comme des points chauds de recrutement, à conserver en priorité.

**Mots-clés :** Récifs coralliens ; coraux scléractiniaires ; variabilité spatio-temporelle ; processus de recrutement ; régulation des populations ; Madagascar.

## Abstract

Understanding the processes that maintain coral assemblages is of crucial importance given increasing rates of coral mortality on reefs globally. Here, we compared relationships among distribution patterns of recruit, juvenile, and adult corals with distinct life history traits to determine the contribution of young life stages to the structure of adult assemblages in the region of Toliara, in southwest Madagascar. Results highlighted a marked spatio-temporal variability in the abundance of all life stages within and between major reef habitats (patch reefs, inner slope, and outer slope). Indications of stock-recruitment relationships were found for Acroporidae, whereas Poritidae and its dominant genus *Porites* were likely regulated by recruitment-limitation mechanisms, with significant correlations between the abundance of juvenile stages and those of adults of the subsequent years. We found stronger links between all three life stages for Pocilloporidae, indicative of both recruitment-limitation and stock-recruitment relationships, mainly driven by *Seriatopora* for juvenile-adult correlations. In contrast, no significant correlations were recorded for the category of 'other' families, which is likely the result of mixing various taxa with different life history traits. In fact, positive correlations between juveniles and adults were found for *Galaxea*, *Cycloseris*, and *Pavona* genera, which made up the 'other' category. The discrepancies of regulation processes among coral taxa highlighted here suggest implementing conservation actions that benefit all life stages. For example, maintaining the biomass of herbivorous fishes and invertebrates to control algal biomass can benefit coral recruitment and decrease mortality of both young and adult stages. Our results also suggest that sites on the outer slope and on patch reefs, which show higher recruitment rates and abundance and cover of adult colonies, could be considered as recruitment hotspots.

**Keywords:** Coral reefs; scleractinian corals; spatio-temporal variability; recruitment process; population regulation; Madagascar.

## 6.1. Introduction

Coral reefs are crucial ecosystems in terms of biodiversity and productivity. They protect coastlands and provide goods and services that contribute to the well-being of ~850 million people from more than 100 countries (Kittinger et al. 2012, Woodhead et al. 2019). However, coral reefs are threatened by large-scale disturbances and local stressors, such as thermally induced bleaching events, cyclones, extracting activities, coastal development, algal blooms, and predators and disease outbreaks, that have increased in frequency and severity in the last five decades (Bellwood et al. 2004, Veron et al. 2009, Hoegh-Guldberg & Bruno 2010, Hughes et al. 2017a, Sully et al. 2019, Obura et al. 2022). Scleractinian corals, the primary framework builders of the reef ecosystem and key components of coral reef health and diversity, have been particularly affected with, for example, severe decline of coral cover and abundance, and reduced coral growth, fecundity and recruitment (Hughes et al. 1999, 2019, Harrison & Booth 2007, Lough et al. 2018, Price et al. 2019). This degradation of coral communities and reef habitats has also caused phase shifts in community structure, with the replacement of corals by algae or other non-reef-building benthic organisms, challenging the ecological function and the goods and services of reef ecosystems (McManus & Polsenberg 2004, Obura et al. 2022). As recovery of coral assemblages following disturbances is mainly driven by the settlement of new larval recruits, the widespread mortalities of corals are also challenging the maintenance and resilience of several coral reefs worldwide (Hughes et al. 2007b, 2010, Graham 2015, Lam et al. 2020).

Corals, like many other marine invertebrates, have a complex bipartite life cycle, which includes a pelagic larval phase followed by a sessile benthic phase for most species. Most corals require several years of benthic life to become sexually mature adults (Penin & Adjeroud 2013, Doropoulos et al. 2017a, Koester et al. 2021). Consequently, the recruitment phase includes the recruit (corals a few weeks/months old, less than 1 cm in diameter, invisible to the naked eye) and the juvenile (corals typically aged at least 1 year, 1< ∅ <5 cm) stages (Penin et al. 2010, Adjeroud et al. 2017). Recruits largely reflect the variability in larval supply, whereas juveniles are composed of successive cohorts and reflect the short-term history of settlement combined with early post-settlement mortality (Roth & Knowlton 2009, Penin & Adjeroud 2013, Koester et al. 2021). Recruitment is a critical process in the spatial patterns and dynamics of local coral assemblages, and in the recovery following disturbances (Caley et al. 1996, Adjeroud et al. 2017, Hughes et al. 2019, Guerrini et al. 2020). Several extrinsic physico-chemical factors such as hydrodynamics, light intensity, sedimentation, substrate characteristics, and water quality may affect coral recruitment patterns (Ritson-Williams et al. 2009, Edmunds et al. 2010, Gouezo et al. 2020, Edmunds 2022). In addition, biotic interactions such as predation, allelopathy, and competition with algae also influence the growth and survivorship of small corals (Kuffner et al. 2006, Wakwella et al. 2020). Chemical cues from organisms such as crustose coralline algae may enhance settlement of some coral larvae (Richmond 1997, Birrell et al. 2005, 2008, Arnold et al. 2010). For most coral species, the post settlement mortality is generally high until colonies reach an adequate size to withstand competition with other benthic organisms and predation by corallivores (Vermeij et al. 2010, Penin & Adjeroud 2013, Sarribouette et al. 2022).

The contribution of early recruits and post-settlement events on the structure and dynamics of adult populations generally varies among coral taxa with contrasting life history strategies, though spatial variation arises at multiple scales in relation to site-specific environmental conditions, notably the intensity of spatial competition and predation (Hughes et al. 2000, Penin et al. 2010, Nozawa et al. 2013, Sarribouette et al. 2022). A positive correlation between spatial distribution of recruits/juveniles and adults is considered an indication of either recruitment-limitation relationships, where young stages drive the abundance of adults, or stock-recruitment relationships, where the adults drive the abundance of recruits (Hughes 1990, Chesson 1998, Hughes et al. 2000). In contrast, dissimilarities between recruits and adults likely suggest that patterns established at settlement may be modified by variable post-settlement mortality through competition and predation, or can reflect the contrasting effects of environmental stressors on these distinct life stages (Hughes et al. 1999, Edmunds 2000, Miller et al. 2000). Supporting data for stock-recruitment or recruitment-limitation relationships, or alternative models with a predominance of predation-competition have been proposed for various coral reefs (Bak & Engel 1979, Caley et al. 1996, Chiappone & Sullivan 1996, Meesters et al. 2001, Penin & Adjeroud 2013, Doropoulos et al. 2015, 2022, Bramanti & Edmunds 2016, Pisapia et al. 2019, Jouval et al. 2020, Carter et al. 2022). However, most of these studies have either compared recruits and adults, or juveniles and adults; few have analyzed all three stages (but see Penin & Adjeroud 2013, Nozawa et al. 2013), thus limiting our understanding of mechanisms of population regulation for organisms such as corals with long and complex life cycles (Kayal et al. 2018, Sarribouette et al. 2022).

With ~2400 km$^2$ of coral reefs along 1400 km of coastline, Madagascar is a hotspot of biodiversity in the South Western Indian Ocean (SWIO). These reefs, and particularly those on the southwest coast, provide an important source of food and income for human populations.

Coral reefs surrounding the island have been confronted by several large-scale disturbances, most notably the bleaching events of 1998 and 2015-2016, along with local stressors such as sedimentation, overfishing and gleaning activities (Ahamada et al. 2002, Obura et al. 2017). Though recent advances have been made on the spatial distribution of coral assemblages at local and regional scales (Harris et al. 2010, Obura 2011, Botosoamananto et al. 2021, Randrianarivo et al. 2022), including information on juveniles (Webster & McMahon 2002, Harding et al. 2008, Nadon et al. 2008, Todinanahary et al. 2021, Carter et al. 2022) and recruits (Todinanahary et al. 2021, Botosoamananto et al. unpubl. data), the regulation of local coral populations through the combined analysis of the three main life stages (recruits, juveniles, and adults) remains unexplored. This type of information is not only crucial to better understand population maintenance and dynamics (Hughes et al. 2007b, Graham 2015, Edmunds & Riegl 2020, Gouezo et al. 2021), but also to determine appropriate conservation measures urgently needed for these reefs.

To examine regulation processes in the region of Toliara, we collected a comprehensive and original data set comparing coral abundance of the three life stages among and within major reef habitats over three consecutive years. Here, we analyze the spatio-temporal variation of recruit, juvenile, and adult corals with contrasting life history strategies. Implications of our results for conservation and management of these reefs are also discussed.

## 6.2. Materials and methods

### 6.2.1. Study area

This study was conducted in the Toliara region, southwest Madagascar, including the Great Reef of Toliara (GRT), one of the largest reef complexes of the region (Figure 6.1.). The region has two main seasons: the austral summer from October to March is a warm season with occasional rains and tropical cyclones, and the austral winter between April to September corresponds to the cooler and dry season (Maina et al. 2012). Sea surface temperature falls to 18°C during the winter season and rises to 30°C during the warm season. Coral bleaching associated with El Niño events occurred in 1998-1999 and 2015-2016, causing substantial damage to several reefs of the region. Cyclones are less frequent in the southwest coast compared to the eastern coast of Madagascar or to other regions in the SWIO, and the last major cyclone, Haruna, passed 120 km north of Toliara in February 2013 (Carter et al. 2022) with no reported significant impacts on the GRT. Outbreaks of the coral predator *Acanthaster* spp. have not been reported in recent years on the GRT. Dominant winds are from southwest direction. The total annual rainfall is ~400 mm. Two main rivers, Fiherenana in the north and Onilahy in the south, contribute the high sedimentation discharge in the region (Maina et al. 2012).

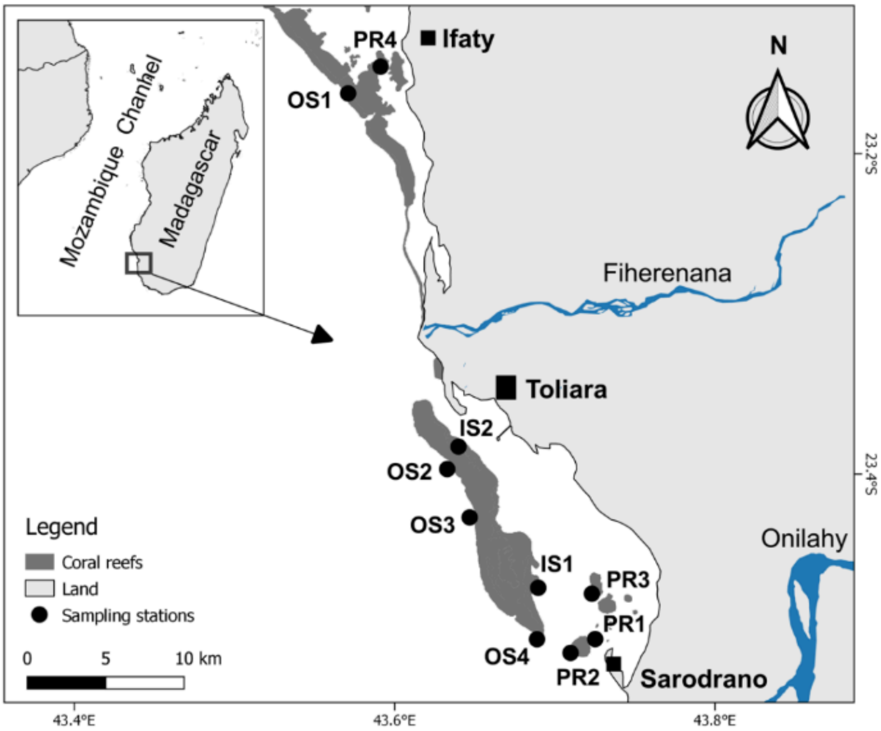

**Figure 6.1.** Location of the 10 sampling stations in the Toliara region, southwest coast of Madagascar. Stations were located on the three major habitat types: patch reefs (PR), the inner slope (IS), and the outer slope (OS). See Section 2.2 for station codes.

### 6.2.2. Sampling strategy

Ten study stations were located between the village of Ifaty in the north and the village of Sarodrano in the south, on the three major reef habitats (Figure 6.1.): four stations on patch reefs (PR1 to PR4), two stations on the inner slope (IS1 and IS2), and four stations on the outer slope (OS1 to OS4). Station codes are abbreviated as follows: the first two letters represent the habitats (PR: patch reefs, IS: inner slope, and OS: outer slope) and the number specifies each station. Stations were located between 7 and 12 m in depth to match those that were established to survey the diversity, abundance, and cover of adult coral assemblages (Botosoamananto et al. 2021).

Recruits were sampled using 11 × 11 × 1 cm unglazed terracotta tiles attached horizontally to the substratum with a stainless-steel mounting plate (Mundy 2000, Adjeroud et al. 2007). At each station, 20 tiles were deployed for a period of four months (October to January) for three consecutive years (2018-2019, 2019-2020, and 2020-2021). At retrieval, tiles were plunged into a bleach solution and rinsed in freshwater to remove all living tissues and sand. In the laboratory, recruits were counted and identified at the family level. At this stage of development, only three families (Acroporidae, Pocilloporidae, Poritidae) could be distinguished, and all other recruits were compiled into a category named ‘other’ recruits (Babcock et al. 2003). Recruits that were too damaged to be identified with certainty were not categorized as they represented < 4% of the recruits, but were however added in the overall recruitment counts (all categories pooled). See Botosoamananto et al. (in review) for further details on sampling of coral recruits.

Abundance of juvenile (∅ < 5 cm) and adult (∅ ≥ 5 cm) coral at the genera level was estimated at each station between July and August each year from 2018 through 2020. At each station, three randomly replicated belt-transects of 10 $m^2$ (10 × 1 m), laid parallel to depth contours and separated by 1 m (Penin & Adjeroud 2013) were used to sample coral colonies. See Botosoamananto et al. (2021) for further details on sampling of adult corals.

### 6.2.3. Data analysis

Spatial and temporal variation in the abundance of recruit, juvenile, and adult colonies were explored using a negative binomial error structured Generalized Linear Mixed Model (GLMM), with nested fixed factors such as years, habitats within years, and stations within habitats. We used the lme4 package (Bates et al. 2015) in R (R Core Team 2021) for our analyses. We conducted separate analyses for recruits, juveniles, and adults of the five categories (all taxa, Acroporidae, Pocilloporidae, Poritidae, and ‘other’ taxa). Our final model with stations nested within habitats as random factors was selected based on Akaike Information Criterion (AIC).

Since the data did not meet the assumption for parametric tests, Spearman rank correlations were used to analyze the relationships between recruit, juvenile, and adult abundances. Separate analyses were conducted for all taxa, Acroporidae, Pocilloporidae, Poritidae, and ‘other’ taxa. We calculated correlations between abundance of recruits and of the following year’s abundance of juveniles (e.g., recruits 2018–2019 with juveniles 2019) and of adults of year + 2 (e.g., recruits 2018–2019 and adults 2020) to examine potential recruitment-limitation relationships. We also calculated correlations between abundance of adults and abundance of recruits of the following reproductive season (e.g., adults 2019 with recruits 2019–2020) and abundance of juveniles of years + 1 and + 2 (e.g., adults 2018 with juveniles 2019 and juveniles 2020) for potential stock-recruitment relationships. To examine such relationships at a finer taxonomic scale than families, we also calculated the Spearman rank correlations between abundance of juveniles and adults of the eight dominant genera. All analyses were performed in R 4.1.0 (R Core Team 2021).

## 6.3. Results

### 6.3.1. Variation in the abundance of coral colonies

Recruit assemblages (all stations/years pooled) were dominated by Acroporidae (45.5%) and Pocilloporidae (45.0%), whereas the relative abundance was much lower for Poritidae (1.9%) and 'other' recruits (3.6%). A total of 1715 recruits were recorded during the three years of the study, and abundance of recruits was higher in 2018–2019 (6.27 ± 0.59 recruits.tile$^{-1}$, mean ± SE, representing 219.20 recruits.m$^{-2}$), compared to 2019–2020 (2.71 ± 0.33 recruits.tile$^{-1}$, representing 94.75 recruits.m$^{-2}$), and 2020–2021 (4.47 ± 0.77 recruits.tile$^{-1}$, representing 156.30 recruits.m$^{-2}$; Table S1). Recruitment rates were variable among habitats and stations, with slightly higher recruit abundance on patch reefs (5.35± 0.70 recruits.tile$^{-1}$), compared to the outer slope (4.49 ± 0.42 recruits. tile$^{-1}$) and the inner slope (3.09 ± 0.39 recruits.tile$^{-1}$; Figure 6.2.). A higher value of recruit abundance was recorded at station PR2 in 2020–2021, whereas station PR4 was characterized by lower recruitment rates compared to other patch reef stations, with no significant temporal trend. At stations PR1 and PR3, the decrease in recruitment rates between 2018–2019 and 2019–2020 was followed by a return to initial values in 2020–2021. Except station IS2, inner and outer slope stations also showed a decrease in recruitment rates between 2018–2019 and 2019–2020, followed by a slight increase in 2020–2021, except at OS3.

A total of 38 and 45 genera were recorded for juvenile and adult corals, respectively, and a significant variation of generic richness was found among habitats and stations, while no significant temporal variation was recorded (Fig. S1, Table S2). Juvenile and adult assemblages were dominated by eight genera that contributed to 63.2% of the total colonies recorded: *Acropora* (16.3%), *Seriatopora* (9.7%), *Porites* (8.4%), *Pocillopora* (6.7%), *Galaxea* (6.3%), *Cycloseris* (5.8%), *Pavona* (5.3%), and *Montipora* (4.7%). During the three years, a total of 5522 juvenile (representing 62.04 ± 5.03 colonies.10 m$^{-2}$) and 27711 adult (311.35 ± 35.63 colonies.10 m$^{-2}$) colonies were recorded.

Mean colony abundance of both juvenile and adult assemblages was highly variable among habitats and stations, for all categories of corals (all taxa pooled, Acroporidae, Pocilloporidae, Poritidae, and 'other' taxa; Figure 6.2., Tables S2, S3, S4). The highest mean juvenile and adult abundances were recorded at the outer slope (84.45 ± 9.61 colonies.10 $m^{-2}$ and 159.37 ± 16.72 colonies.10 $m^{-2}$, respectively), notably at stations OS3 for juveniles and OS2 and OS3 for adults, while the lowest values were found at the inner slope (45.27 ± 11.10 colonies.10 $m^{-2}$ and 150.44 ± 19.20 colonies.10 $m^{-2}$ for juveniles and adults, respectively), notably at station PR4. For juvenile corals, an increase in abundance was recorded the third year (2020) at the outer slope, whereas for adults, abundance values were highest in 2019 at all stations except PR4.

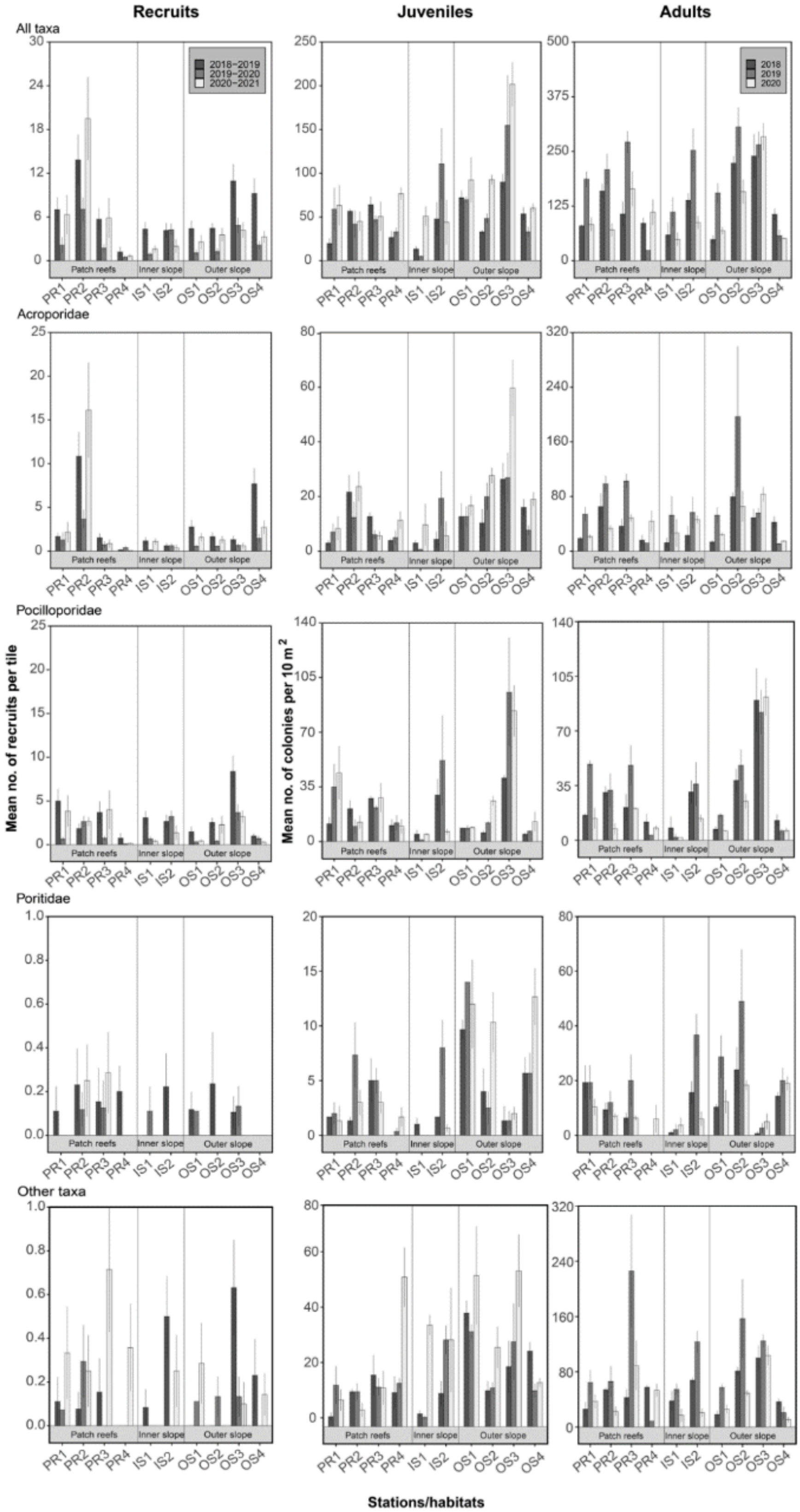

**Figure 6.2.** Spatial and temporal variation of the mean abundance of recruit, juvenile and adult corals, at the 10 stations located on the three major habitats, for the five categories (all taxa pooled, Acroporidae, Pocilloporidae, Poritidae, and 'other' taxa). Error bars represent standard error.

### 6.3.2. Relationships between recruit, juvenile, and adult corals

The relative abundance of the three life stages varied among families (Figure 6.3.), with the highest proportion of recruits bring for Pocilloporidae (10.1% of Pocilloporidae across life stages) and Acroporidae (9.6%), compared to Poritidae (1.2%) and 'other' taxa (0.8%) for which recruits represent a very low proportion of total colonies. The proportion of juveniles also differed among coral families, with a higher contribution for Pocilloporidae (25.6%), but with less variability between Acroporidae (15.4%), Poritidae (11.5%), and 'other' taxa (12.2%). The proportion of adults in the local assemblages was slightly higher for Poritidae (87.3%) and 'other' taxa (87.0%), compared to Acroporidae (75.0%) and Pocilloporidae (64.3%).

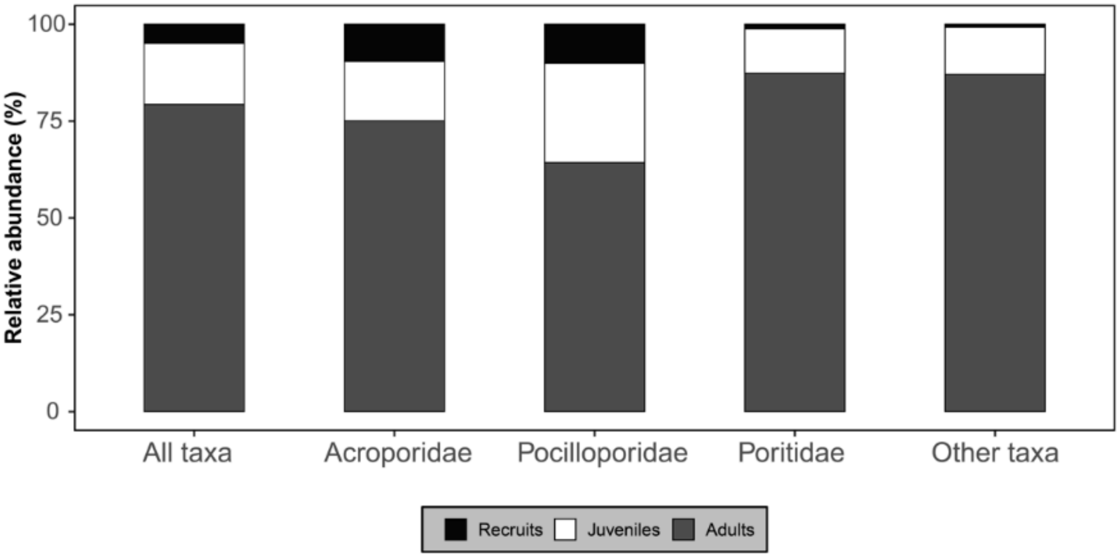

**Figure 6.3.** Relative abundance (%) of recruit, juvenile and adult colonies for each of the five categories (all taxa pooled, Acroporidae, Pocilloporidae, Poritidae, and 'other' taxa). Mean of the three years and the 10 stations.

When looking at relationships between the three life stages for specific years (Table 1), no significant correlations were recorded between abundance of recruits and juveniles for all taxa pooled, Acroporidae, Poritidae, and 'other' taxa, or between recruits and adults for Poritidae and 'other' taxa, or between juveniles and adults for 'other' taxa. For all taxa pooled, a significant correlation was recorded between abundance of adults in 2018 and recruits in 2018–2019, indicative of a potential stock-recruitment relationship. Such relationships were also signaled for Acroporidae, with positive and significant correlations between adults in 2018 and recruits in 2018–2019 and between adults in 2018 and juveniles in 2020, and for Pocilloporidae, with correlations between adults in 2018 and recruits in 2018–2019, adults in

2020 and recruits in 2020–2021, and adults in 2018 and juveniles in 2019. Recruitment-limitation relationships were suggested by positive and significant correlations between recruits in 2018–2019 and adults in 2020 for Pocilloporidae, and between juveniles in 2018 and adults in 2019 and 2020 for Pocilloporidae and Poritidae (Table 1).

Relationships between juvenile and adult abundances of the eight dominant coral genera confirm the weak relationships among juveniles and adults for Acroporidae, with only one significant correlation between adults in 2019 and juveniles in 2020 for *Montipora* (Table 2). For Pocilloporidae, we recorded significant correlations between all combination of juveniles and adults for *Seriatopora*, with no such correlation recorded for *Pocillopora*. For Poritidae, the significant correlation between juveniles in 2018 and adults in 2019 and 2020 is largely driven by *Porites*, the only dominant genera of this family. For ‘other’ taxa, we recorded positive correlations between all combinations of years for juveniles and adults *Galaxea*, and for some years for *Cycloseris* and *Pavona*, although no correlations were recorded when pooling these three genera and the other 30 that composed the category ‘other’ taxa (Table 1).

**Tableau 6.1.** Correlations between abundance of recruit, juvenile, and adult colonies for the five categories of corals (all taxa, Acroporidae, Pocilloporidae, Poritidae, and 'other' taxa). Only meaningful correlations that may represent potential stock-recruitment, recruitment-limitation, and predation-competition relationships are presented (e.g., there is no ecological sense to calculate a correlation between recruits recorded in October 2018 – January 2019 and adults recorded in July-August 2019). Spearman rank correlation coefficients (ρ) and the associated *p*-values (ns: $p > 0.05$; *: $p < 0.05$; **: $p < 0.01$; ***: $p < 0.001$) are given.

| | Recruits | | | | | | Juveniles | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | 2018-19 | | 2019-20 | | 2020-21 | | 2018 | | 2019 | | 2020 | |
| | ρ | p | ρ | p | ρ | p | ρ | p | ρ | p | ρ | p |
| **All taxa** | | | | | | | | | | | | |
| Juveniles 2019 | 0.34 | ns | | | | | | | | | | |
| Juveniles 2020 | 0.15 | ns | -0.11 | ns | | | | | | | | |
| Adults 2018 | **0.82** | ** | | | | | | | 0.35 | ns | 0.16 | ns |
| Adults 2019 | | | 0.52 | ns | | | 0.50 | ns | | | -0.16 | ns |
| Adults 2020 | 0.18 | ns | | | 0.06 | ns | 0.44 | ns | 0.36 | ns | | |
| **Acroporidae** | | | | | | | | | | | | |
| Juveniles 2019 | 0.35 | ns | | | | | | | | | | |
| Juveniles 2020 | 0.62 | ns | 0.48 | ns | | | | | | | | |
| Adults 2018 | **0.69** | * | | | | | | | 0.58 | ns | **0.63** | * |
| Adults 2019 | | | 0.21 | ns | | | 0.42 | ns | | | 0.28 | ns |
| Adults 2020 | 0.12 | ns | | | -0.40 | ns | 0.50 | ns | 0.41 | ns | | |
| **Pocilloporidae** | | | | | | | | | | | | |
| Juveniles 2019 | **0.69** | * | | | | | | | | | | |
| Juveniles 2020 | 0.40 | ns | 0.31 | ns | | | | | | | | |
| Adults 2018 | **0.63** | * | | | | | | | **0.78** | ** | 0.47 | ns |
| Adults 2019 | | | 0.60 | ns | | | **0.91** | *** | | | 0.48 | ns |
| Adults 2020 | **0.69** | * | | | **0.85** | *** | **0.62** | * | **0.68** | * | | |
| **Poritidae** | | | | | | | | | | | | |
| Juveniles 2019 | 0.13 | ns | | | | | | | | | | |
| Juveniles 2020 | 0.01 | ns | 0.07 | ns | | | | | | | | |
| Adults 2018 | -0.05 | ns | | | | | | | 0.46 | ns | 0.47 | ns |
| Adults 2019 | | | -0.17 | ns | | | **0.79** | ** | | | 0.39 | ns |
| Adults 2020 | -0.09 | ns | | | 0.00 | ns | **0.64** | * | 0.39 | ns | | |
| **Other taxa** | | | | | | | | | | | | |
| Juveniles 2019 | 0.16 | ns | | | | | | | | | | |
| Juveniles 2020 | -0.01 | ns | -0.05 | ns | | | | | | | | |
| Adults 2018 | 0.25 | ns | | | | | | | 0.15 | ns | 0.33 | ns |
| Adults 2019 | | | 0.20 | ns | | | 0.22 | ns | | | 0.06 | ns |
| Adults 2020 | -0.10 | ns | | | 0.09 | ns | 0.23 | ns | 0.38 | ns | | |

**Tableau 6.2.** Correlation between abundance of juvenile and adult corals of the overall assemblage (all genera pooled) and for the eight dominant genera (*Acropora*, *Montipora*, *Pocillopora*, *Seriatopora*, *Galaxea*, *Porites*, *Cycloseris*, and *Pavona*). Only meaningful correlations that may represent potential stock-recruitment, recruitment-limitation, and predation-competition relationships are presented. Spearman rank correlation coefficients (ρ) and the associated *p*-values (ns: p > 0.05; *: p < 0.05; **: p < 0.01; ***: p < 0.001) are given.

| | | Juveniles | | | | | |
|---|---|---|---|---|---|---|---|
| | | 2018 | | 2019 | | 2020 | |
| | | ρ | p | ρ | p | ρ | p |
| **All genera** | | | | | | | |
| | Adults 2018 | | | 0.35 | ns | 0.16 | ns |
| | Adults 2019 | 0.50 | ns | | | -0.16 | ns |
| | Adults 2020 | 0.40 | ns | 0.36 | ns | | |
| ***Acropora*** | | | | | | | |
| | Adults 2018 | | | 0.55 | ns | 0.48 | ns |
| | Adults 2019 | 0.07 | ns | | | -0.26 | ns |
| | Adults 2020 | 0.24 | ns | 0.30 | ns | | |
| ***Montipora*** | | | | | | | |
| | Adults 2018 | | | -0.16 | ns | 0.26 | ns |
| | Adults 2019 | 0.00 | ns | | | **0.67** | * |
| | Adults 2020 | 0.60 | ns | 0.21 | ns | | |
| ***Pocillopora*** | | | | | | | |
| | Adults 2018 | | | 0.14 | ns | 0.33 | ns |
| | Adults 2019 | 0.42 | ns | | | 0.39 | ns |
| | Adults 2020 | 0.54 | ns | 0.05 | ns | | |
| ***Seriatopora*** | | | | | | | |
| | Adults 2018 | | | **0.87** | *** | **0.72** | * |
| | Adults 2019 | **0.97** | *** | | | **0.76** | * |
| | Adults 2020 | **0.88** | *** | **0.95** | *** | | |
| ***Porites*** | | | | | | | |
| | Adults 2018 | | | 0.53 | ns | 0.10 | ns |
| | Adults 2019 | **0.75** | * | | | 0.31 | ns |
| | Adults 2020 | **0.74** | * | 0.54 | ns | | |
| ***Galaxea*** | | | | | | | |
| | Adults 2018 | | | **0.80** | ** | **0.82** | ** |
| | Adults 2019 | **0.82** | ** | | | **0.84** | ** |
| | Adults 2020 | **0.89** | *** | **0.76** | ** | | |
| ***Cycloseris*** | | | | | | | |
| | Adults 2018 | | | **0.70** | * | **0.84** | ** |
| | Adults 2019 | 0.57 | ns | | | 0.61 | ns |
| | Adults 2020 | **0.77** | ** | **0.66** | * | | |
| ***Pavona*** | | | | | | | |
| | Adults 2018 | | | 0.37 | ns | **0.47** | * |
| | Adults 2019 | 0.08 | ns | | | 0.29 | ns |
| | Adults 2020 | 0.06 | ns | 0.47 | ns | | |

## 6.4. Discussion

### 6.4.1. Spatio-temporal patterns of coral assemblages

Our results underline the marked spatial variability in the abundance of the three benthic life stages of coral assemblages within and between major reef habitats of the Great Reef of Toliara (GRT) region. Abundances of recruits, juveniles, and adults were higher at several stations of patch reefs, whereas lower values were generally recorded along the inner slope. This strong spatial heterogeneity of corals is consistent with patterns recorded at reefs elsewhere in the world, where marked variation of abundance, together with other coral descriptors such as cover, diversity, and size-structure are documented within and between reef habitats (Trapon et al. 2013, Penin & Adjeroud 2013, Yucharoen et al. 2015, Pratchett et al. 2017, Adjeroud et al. 2019, Botosoamananto et al. 2021, Koester et al. 2021). Although outside the scope of our survey, this heterogeneity is likely resulting from the marked variability of the environmental conditions and anthropogenic stressors in the GRT (Botosoamananto et al. 2021). Previous studies have highlighted higher fishing efforts, notably using destructive practices such as mosquito net trawl, beach seine, coral-turning fishing, or fishing by poisoning, as well as higher sedimentation on the inner slope of the GRT (Maina et al. 2012, Andréfouët et al. 2013, Sheridan et al. 2014, Ranaivomanana et al. 2023). Overfishing and sedimentation also impact the patch reefs and the outer slope in this area, but to a lesser extent the coral assemblages, likely due to the higher hydrodynamic and greater depths in these habitats compared to the inner slope (Botosoamananto et al. 2021). Moreover, higher cover of turf and macroalgae at inner slopes likely reduce the abundance of corals through spatial competition (Botosoamananto et al. 2021). The higher diversity and cover of coral assemblages recorded along the outer slopes and patch reefs are also explained by the more favorable environmental conditions along these sites (Botosoamananto et al. 2021). For coral recruits, the importance of benthic components on the spatial patterns has also been largely documented (Birrell et al. 2005, Kuffner et al. 2006, Arnold et al. 2010, Jorissen et al. 2020). On the GRT, cover of algae and other living taxa such as sponges have been identified as important drivers of the spatial patterns of coral recruitment (Todinanahary et al. 2021, Botosoamananto et al. unpubl. data). The higher cover of algae on the inner slopes likely inhibits larval settlement and increases the post-settlement mortality. Moreover, macroalgae have negative physical effects on young coral colonies through abrasion, shading, and smothering (McCook et al. 2001). In contrast, higher hydrodynamic and water circulation, present along outer slopes and patch reefs, creates more favorable conditions for coral recruitment (Edmunds 2000, Penin & Adjeroud 2013). However, these potential controlling environmental factors of the spatial variability of coral assemblages should be more closely examined, for example through dedicated water quality monitoring surveys in the GRT. Such environmental surveys will not only improve our understanding of the spatial patterns and dynamics of coral assemblages and other reef communities, but will also help identify which threats to prioritize reducing for better conservation and management of these reefs.

Our survey also highlighted a marked interannual variation in the abundance of recruit, juvenile, and adult coral colonies. However, the temporal patterns differed between the three life stages. Recruits were most abundant during the first year of the study (2018–2019), whereas highest abundances for adults were generally recorded in 2019, and in 2020 for juveniles. The interannual changes in coral assemblages are often associated with either large scale disturbances, such as cyclones, thermally induced bleaching events, or predator outbreaks, or to local stressors, such as sudden deterioration of substrate composition or water quality. For coral recruitment, a large part of the temporal variability is also linked to variation in fecundity of adult colonies, which is driven by seasonal and interannual changes in climatic and oceanographic conditions. However, during the study period, no such disturbances or stressors can be associated with the observed temporal changes in coral abundance. Elevated sea surface temperatures (~31°C) were recorded in January and February 2020 (Botosoamananto et al. unpubl. data), but caused neither a significant reduction in recruitment rates the following year (October 2020–January 2021) nor a decrease in juvenile and adult corals the following months (July–August 2020). Rigorous data collection on other potential drivers of the temporal changes in the abundance coral assemblages, such as interannual variation in sedimentation discharges by the two main rivers, should be pursued and examined to determine influence.

### 6.4.2. Regulation of coral assemblages

Similar to studies of coral reefs in other regions, our results identify discrepancies among families and genera for maintenance processes within the same area, likely due to differences in life history traits and strategies such as reproductive modes, stress tolerance, growth capacities, or competitive abilities (Penin et al. 2010, Edmunds et al. 2010, Penin & Adjeroud 2013, Doropoulos et al. 2015, 2022, Moustaka et al. 2019). When examining overall coral assemblages (all taxa pooled), the links between spatial variation of the three life stages (recruits, juveniles, and adults) were weak, with only one significant correlation between abundance of adult corals and recruits in the following reproductive season suggesting a stock-recruitment relationship. This lack of strong and consistent correlation likely results from the mixing of various coral taxa with contrasting life history traits and maintenance processes.

For Acroporidae, indications of stock-recruitment relationships were found, with the abundance of adults correlated with those of recruits and juveniles of subsequent years, with no evidence recorded for recruitment-limitation relationships (i.e., when young stages drive the abundance of adults). The juvenile-adult relationship was restricted to *Montipora*, whereas no significant correlation was recorded for *Acropora*, the other dominant genera of this family. The limited positive correlations between young stages and adults may be partially explained by the high rate of asexual reproduction through fragmentation in this family, which may mask potential recruitment-limitation relationships (Smith & Hughes 1999, Kayal et al. 2015).

In contrast, we recorded indications of recruitment-limitation relationships for Poritidae corals and its dominant genera *Porites*, although restricted to significant correlations between the abundance of juvenile stages and those of adults of the subsequent years. The lack of positive correlations between recruits and other life stages may be explained by lower offspring compared to other opportunistic taxa and the extended period of reproduction and spawning of *Porites* in the SWIO region (Mangubhai et al. 2007, Gress et al. 2014), which dilutes the larval pool over long periods of the year and is likely a large contributor to the low abundance of Poritidae recruits on our recruitment tiles, immersed for four months (Botosoamananto et al. in review). As most Poritidae corals are characterized by relatively lower mortality rates and higher resistance to environmental stressors after reaching a certain size (Kayal et al. 2015), our results suggest that most juvenile colonies also grow into the adult stage in reef habitats of the Toliara region.

For Pocilloporidae, we found strong links between all three life stages, indicative of both recruitment-limitation and stock-recruitment relationships, that are likely driven by *Seriatopora*. This family is generally characterized by high recruitment rates and relatively low mortality rates, except during occasional acute stressors such as bleaching events (Kayal et al. 2015), which may explain the direct translation of young colonies to the adult stage. Moreover, the positive correlations between young and adult colonies may also result from self-seeding occurring at the local scale (Doropoulos et al. 2015, Gibbs & Hay 2015). In fact, the most abundant species of Pocilloporidae in the reefs of Toliara include brooders *Pocillopora damicornis*, *Seriatopora histrix*, and *Stylophora pistillata*, which release larvae with short competency periods that often settle near their parents (Harrison & Wallace 1990, Harriott 1999).

On the other hand, no significant correlations were recorded between life stages for the category ‘other’, which is again likely the result of mixing various families with different life history traits and variable tolerance to environmental stressors. In fact, the positive correlations between juveniles and adults recorded for *Galaxea*, *Cycloseris*, and *Pavona*, the three dominant genera which make up this ‘other’ families category, clearly indicate that this latter category contains coral taxa with contrasting life history strategies. For those coral taxa that failed to show significant positive correlations between young stages and adult corals, we may assume that the differential post-settlement events are sufficiently strong to distort the pattern established at settlement (Chong-Seng et al. 2014, Adjeroud et al. 2017, Grimsditch et al. 2017, Pedersen et al. 2019). Reproduction through colony fragmentation at our study sites, likely frequent for branching corals such as *Acropora* and most Poritidae, a family dominated by *Porites cylindrica* and *P. rus* at Toliara, may also mask the association between recruits and adults (Caley et al. 1996, Penin et al. 2007). Relationship between recruits and adults may also break down for coral taxa with long larval duration in large open systems where advection tends to mix larvae from natal and distant reefs, a likely case for *Acropora* corals that are mostly broadcast spawners with long-dispersal larvae (Hughes et al. 2000, Fraschetti et al. 2002). Such lack of correlation between young and adult stages may also reflect the contrasting habitat preferences and the differential effects of environmental stressors on these distinct life stages (Penin et al. 2007, Trapon et al. 2013, Pedersen et al. 2019, Jouval et al. 2020).

Our results have provided some indication of mechanisms of population regulation, that are not only important for a better understanding of the structure and dynamics of coral assemblages, but also for the implementation of appropriate conservation actions. However, this study is based on correlation analyses, and further sampling and field experiments should be conducted to rigorously examine the ultimate causes of the relationships between spatial variation in the abundance of the three life stages of corals. For example, assessment of stock-recruitment relationships should be complemented by monitoring fecundity, density-dependent interactions, and early post-settlement mortality events within local coral populations. Data on reproduction modes and connectivity patterns should also be collected to better examine mechanisms of population regulation, data which are also necessary to estimate recovery capacities and improve conservation actions (Palumbi 2003, Van Oppen & Gates 2006, Almany et al. 2009, Mumby et al. 2011, Lequeux et al. 2018). Moreover, as these relationships may fluctuate with time, the present study should be complemented by a long-term interannual study on the demography of coral assemblages (Shlesinger & van Woesik 2021).

### 6.4.3. Implications for conservation strategies

The discrepancies of regulation processes among coral families and genera highlighted here call for conservation actions that include all benthic life stages, rather than specific actions targeting one phase of the coral life cycle. Conservation strategies incorporating life-history processes are likely to be more successful than those based on promoting the abundance of adult corals alone (Adjeroud et al. 2017). Thus, the outcomes of this survey suggest implementing conservation actions to increase the settlement rates of coral larvae, reduce early post-settlement mortality, and reduce local threats that affect the health of coral colonies, notably the growth and fecundity of adult colonies. Although some of these actions may be more selective and effective for one life stage, most are in fact beneficial to all coral life stages, as well as other reef communities.

In the context of coral reefs of Toliara, fishing activities are particularly intense, and their management should be a priority (Ranaivomanana et al. 2023). Conservation actions to maintain the biomass and diversity of herbivorous fishes and invertebrates at a sufficient level to control algal biomass is one of the most effective means to promote coral recruitment by offering more adequate substrate for coral larvae to settle (Mumby & Steneck 2008, McClanahan et al. 2012, Edmunds & Riegl 2020). Reducing algal biomass will also decrease, for both young and adult stages, mortality caused by spatial competition, abrasion, and allelopathy with fleshy algae (Kuffner et al. 2006, Dixson et al. 2014). Destructive fishing methods should also be urgently addressed, as this is the main cause of habitat degradation in the Toliara region (Harris et al. 2010, Bruggemann et al. 2012, Sheridan et al. 2014). Practices such as gleaning, mosquito net trawl, and fishing by poisoning, that have direct and indirect negative effects on all coral life stages, should be banned, with alternative income-generating activities, such as aquaculture, proposed to local fishermen (Todinanahary et al. 2016, Ratsimbazafy et al. 2019).

Local environmental conditions can also be improved by conservation measures regarding land use (Mumby et al. 2006b, 2007), with specific actions to reduce nutrients and sediment loads from the two main rivers, the Fiherenana and Onilahy (Bruggemann et al. 2012, Sheridan et al. 2014). These actions will benefit overall coral assemblages, as both young and adult corals are sensitive to increasing levels of sedimentation and nutrients (Wakwella et al. 2020, Evensen et al. 2021), and other reef communities.

Given limited human and financial resources, managers are generally constrained to select the most effective areas to protect and the critical periods to minimize stressors. Our results suggest that sites on the outer slope and on patch reefs, which show higher recruitment rates and abundance and cover of adult colonies, could be considered as recruitment hotspots (Botosoamananto et al. 2021 in review) to prioritize for protection. Our results also suggest that austral summer, when most corals finalize their gametogenesis and spawn (Botosoamananto et al. unpubl. data), and when larvae settle and start their benthic life (Botosoamananto et al. in review), is a critical period when all conservation measures mentioned prior should be particularly reinforced.

However, as coastal human population is largely dependent on reef resources in Madagascar, these conservation measures should be designed and implemented with the strong involvement of end-users through, for example, Locally Marine Managed Areas, which have proven their effectiveness in the Malagasy context (Mahafina 2011, Todinanahary et al. 2016, McClanahan & Jadot 2017, Cochrane et al. 2019, Ratsimbazafy et al. 2019).

# Chapitre 7 :
# Discussion générale et perspectives

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## 7.1. Structure, dynamique, et régulation des communautés coralliennes

La persistance des récifs coralliens dépend étroitement de la santé des assemblages coralliens, et notamment du succès des processus de reproduction et de recrutement, et de leur capacité à résister et à se rétablir suite aux perturbations de grande ampleur et aux stress locaux (Connell et al. 1997, Baird et al. 2009c, Harrison 2011). La reproduction est une phase essentielle pour le renouvellement des populations locales, mais permet également la colonisation de nouveaux récifs et le maintien de la diversité génétique des coraux (Richmond 1990, Sola 2018). Examiner les mécanismes de reproduction, de recrutement, et de régulation des populations coralliennes est donc fondamental pour mieux comprendre la structure, la dynamique et les capacités de résilience des coraux (Adjeroud et al. 2017, Edmunds & Riegl 2020). Par ailleurs, ces informations sont nécessaires pour établir des mesures de gestion et de conservation efficaces. Dans ce travail de thèse, nous avons documenté la structure spatiale des communautés coralliennes (Chapitre 3), la chronologie de la reproduction des coraux (Chapitre 4), la variabilité spatio-temporelle du recrutement des coraux (Chapitre 5), et les mécanismes de régulation des populations coralliennes (Chapitre 6). Notre étude sur les récifs de la région de Toliara s'inscrit donc dans le contexte de ces avancées récentes, en démontrant l'importance des processus de recrutement et de régulation pour la structure et la dynamique des populations coralliennes et pour la conservation de ces récifs (Adjeroud et al. 2017, Edmunds & Riegl 2020).

Les résultats obtenus durant cette thèse ont mis en évidence une saisonnalité importante de la maturation des gamètes chez quatre espèces coralliennes, *Acropora digitifera*, *A. nasuta*, *Platygyra daedalea*, et *Galaxea fascicularis*, et une ponte multispécifique et synchronisée des espèces du genre *Acropora*. Ce phénomène de synchronisation de la ponte chez les coraux a été largement documenté dans plusieurs récifs de l'Indo-Pacifique (Harrison et al. 1984, Baird et al. 2009b, Harrison 2011), mais nos résultats sont les premiers aussi détaillés dans cette région du sud-ouest de l'Océan Indien. Comme dans la plupart des récifs (Richmond & Hunter 1990, Harrison 2011, Keith et al. 2016, Sakai et al. 2020, Ibrahim et al. 2021), la reproduction des coraux dans la région de Toliara est étroitement liée aux variations des conditions environnementales, et notamment la température pour la maturation des gamètes, et la phase de la lune et la vitesse du vent pour le jour de ponte. En revanche, le calendrier précis de la maturation des gamètes et des périodes de pontes peut varier entre les années, en lien avec des décalages de quelques semaines de l'augmentation des températures saisonnières à la fin de l'hiver austral. Néanmoins, notre suivi de la ponte des coraux n'a concerné que deux années consécutives, et il conviendrait de poursuivre les observations pour mieux caractériser les stratégies reproductives des coraux de la région de Toliara. La saisonnalité et la variabilité interannuelle de la reproduction se retrouvent également dans les processus de recrutement. Les pontes relativement massives et synchrones d'*Acropora* sont à relier à la dominance des Acroporidae dans les assemblages de recrues. Et nos résultats montrent clairement une variabilité interannuelle de l'abondance des recrues, des juvéniles, et des adultes pour la plupart des genres coralliens, et dans l'ensemble de nos sites d'étude.

A cette variabilité temporelle se surimpose une forte hétérogénéité spatiale, à toutes les échelles abordées dans ce travail. La diversité, l'abondance, le recouvrement, ou la structure de taille des adultes, de même que le recrutement montrent une variation significative au sein et entre les trois principaux habitats récifaux échantillonnés dans ce travail. L'ensemble de ces résultats démontre une fois de plus la forte structuration spatiale des communautés récifales, et notamment les espèces sessiles et sensibles aux changements des conditions environnementales, comme les coraux.

La pente externe et les massifs coralliens lagonaires sont les habitats où les plus fortes diversité et abondance des trois stades de vie des coraux, recrues, juvéniles et adultes, ont été enregistrées. Ces habitats sont moins dégradés que les récifs internes, qui sont eux plus fortement soumis aux pressions d'origine humaine telles que la pollution, la surpêche, la sédimentation et l'extraction des blocs de coraux (Vasseur 1997, Gabrié et al. 2000, Ranaivomanana 2006, Maharavo 2009, Bruggemann et al. 2012, Maina et al. 2012, 2013, Andréfouët et al. 2013, Sheridan et al. 2014). Sur ces récifs internes, la biomasse algale est généralement plus élevée, ce qui induit une compétition spatiale défavorable aux coraux et perturbe l'installation des larves coralliennes (Birrell et al. 2005, Arnold et al. 2010, Doropoulos et al. 2017b).

Tous les résultats acquis durant ce travail de recherche doctorale confortent les innombrables études précédentes qui ont mis en évidence la forte hétérogénéité spatiale et temporelle des communautés coralliennes (Zvuloni et al. 2010, McClanahan et al. 2014, Adjeroud et al. 2019, Karisa et al. 2020). Les récifs de Toliara, comme la plupart des autres récifs à travers le monde, sont constitués d'une mosaïque d'assemblages coralliens hétérogènes, que ce soit en termes de composition spécifique et de diversité, d'abondance ou de structure de taille, ou de processus de recrutement et de régulation. Et même si notre suivi ne concerne que trois années, il est fort probable que ces mosaïques aient des trajectoires temporelles distinctes. Cette structuration en « patchwork » contribue grandement à la complexité du fonctionnement écologique des écosystèmes coralliens.

A l'origine florissantes, les communautés coralliennes du Grand Récif de Toliara ont connu depuis les années 1980 une phase de déclin de près de trois décennies. Nos résultats, issus d'observation de 2017 à 2020, montrent certain signe de rétablissement, comme le retour à une dominance d'*Acropora* et des densités coralliennes élevées dans certains habitats, notamment la pente externe et les massifs coralliens lagonaires. Les taux de recrutement des Acroporidae et des Pocilloporidae sont relativement élevés, comparativement à d'autres récifs du sud-ouest de l'Océan Indien, ce qui suggère une bonne capacité de résilience. Mais ces constations plutôt positives et rassurantes doivent être prises avec précaution, dans la mesure ou tous les travaux prévoient une augmentation de l'intensité et de la fréquence des perturbations de grande ampleur, comme les phénomènes de blanchissement corallien, et des stress locaux comme la surpêche dans les zones où les populations locales sont fortement dépendantes des ressources récifales, comme à Madagascar.

## 7.2. Implication pour la gestion des récifs coralliens

La forte hétérogénéité spatiale et temporelle de la structure, du recrutement et de la régulation des assemblages coralliens a des conséquences sur la gestion et la conservation des récifs, en termes de type de mesures et d'échelle spatiale de mise en place. Idéalement, des mesures de conservation spécifiques devraient être prises pour les différents sites et habitats récifaux, où les assemblages coralliens et les pressions sont différents. Mais faute de moyens financiers et humains, et parfois de connaissances scientifiques, un tel degré de précision dans l'élaboration et la mise en place de mesures de conservation est rarement observé dans les récifs coralliens.

Nos résultats montrent que les assemblages coralliens des récifs de pente externe et de massifs coralliens lagonaires sont plus diversifiés et abondants, et que le recrutement y est plus élevé. Ce qui suggère de mettre en place des mesures de conservation qui maintiennent l'état de santé de ces habitats et leur potentiel pour ensemencer d'autres récifs et pour assurer la recolonisation à la suite de perturbations. Pour les récifs internes plus dégradés, les conditions ne sont pas réunies pour une installation pérenne des coraux, et nos résultats plaident plutôt pour la mise en place, dans un premier temps, de projet de restauration corallienne, par transplantations de coraux par exemple. Les actions de conservation doivent focaliser sur les facteurs directs et locaux de dégradation des récifs dans la région de Toliara, et notamment :

- la réduction, et à terme le bannissement, des pratiques destructrices qui causent des dommages physiques, tels que le retournement des coraux, la collecte des invertébrés (pour la consommation, l'artisanat et le tourisme) et l'extraction de blocs de coraux pour la construction de tombeaux, maisons et puisards (Mcleod et al. 2019) ;
- la réduction de l'hyper-sédimentation et de la pollution côtière (chimique et organique), par la mise en place d'une politique de gestion qui prend en compte non seulement la zone en aval, mais aussi les facteurs d'agression, tels que la déforestation, les activités minières et le développement urbain, en amont des deux principales rivières (Fabricius 2005, Maina et al. 2013, Mcleod et al. 2019) ;
- la protection des poissons et invertébrés herbivores, qui contrôlent la biomasse des algues qui ont un impact négatif sur la survie des jeunes de coraux et qui entrent en compétition pour l'espace avec les colonies adultes (Steneck et al. 2019).

Mais pour être efficaces, ces actions de conservation doivent être acceptées et mises en place avec le consentement et l'implication des populations locales, et doivent s'accompagner de mesures compensatoires pour ces populations. La mise en place d'aires marines protégées basées sur l'approche de résilience écologique et sociale est une perspective intéressante (Cinner et al. 2009, Maynard et al. 2010, 2015, Bruggemann et al. 2012, Anthony et al. 2015, Lam et al. 2017, 2020). Dans le contexte malgache, il est important de prendre en compte la pérennité des sources de financement, l'accord et la coordination avec les parties prenantes que sont les communautés de pêcheurs, les opérateurs économiques et touristiques, les ONG, et les institutions publiques, et d'inclure les réglementations locales et ancestrales (Dina et Tabous), et nationales. L'implication des communautés locales peut se faire par le biais d'une sensibilisation environnementale continue et de la promotion de la science participative, comme pour les projets de restauration ou les suivis écologiques des milieux marins (Cinner et al. 2009, Mcleod et al. 2019, McLeod et al. 2021). Le modèle d'aires marines localement gérées (*Locally Managed Marine Areas*), qui a montré un certain succès pour gérer les populations de poissons et les pêcheries locales à Toliara (Mahafina 2011, McClanahan & Jadot 2017, Cochrane et al. 2019, Ratsimbazafy et al. 2019), pourrait être un outil intéressant pour la gestion des communautés coralliennes.

## 7.3. Perspectives

Les résultats issus de ce travail de recherche doctoral ont permis d'améliorer nos connaissances sur la structure, la dynamique et la régulation des communautés coralliennes dans la région de Toliara, et constitue une base solide pour évaluer les futurs changements. Les conclusions de ce travail sont également cruciales pour la mise en place et l'amélioration des mesures de conservation et de gestion de ces récifs. Mais cette étude, dont l'échantillonnage a été réalisé entre 2017 et 2020, ne constitue qu'une image instantanée dans un écosystème très dynamique. Par conséquent, il conviendrait de compléter le suivi sur la reproduction, pour mieux appréhender les relations entre la variation des conditions environnementales (température de l'eau, phase lunaire, vent, marée, courant et hauteur des vagues) et la saisonnalité de la gamétogénèse et de la ponte. Le suivi à Toliara pourrait judicieusement être complété par d'autres suivis dans les récifs plus au nord, afin de tester l'hypothèse d'une variation latitudinale des modes de reproduction chez les coraux.

Cette perspective s'applique également pour le suivi du recrutement précoce, échantillonné à l'aide de plaques de substrat artificiel. Même si leur installation est plus difficile que des transects ou des quadrats pour le comptage de juvéniles, il serait intéressant de mettre en place un suivi du recrutement corallien dans d'autres récifs autour de Madagascar, et notamment à Nosy Be et à Masoala où les communautés coralliennes ont été récemment étudiées (Randrianarivo et al. 2022, 2023), et qui permettrait de tester l'effet des aires marines protégées sur le recrutement précoce chez les coraux.

Notre étude sur les processus de régulation des populations était basée sur des analyses de corrélations entre les variations d'abondance des recrues, juvéniles, et adultes. La mise en évidence des relations stock-recrutement chez certaines populations coralliennes devrait être complétée par un suivi de la fécondité des colonies adultes. Par ailleurs, les facteurs de mortalité post-fixation, comme la compétition spatiale avec d'autres organismes récifaux et la prédation par les espèces corallivores, et l'importance des relations de densité-dépendance pourraient être abordés par des expérimentations *in situ* (Vermeij et al. 2010, Penin et al. 2011, Sarribouette et al. 2022).

L'étude de la connectivité, au travers notamment de la structure génétique des populations, est également une thématique de recherche qu'il conviendrait de développer dans la région de Toliara. Des informations sur les échelles de dispersion larvaire, l'intensité des flux géniques et la clonalité au sein et entre populations permettraient en effet de mieux comprendre la contribution du recrutement autochtone et du recrutement allochtone dans le maintien des populations locales, de déterminer d'éventuels « récifs sources » et « récifs puits », et de mieux estimer les capacités de résilience des communautés coralliennes de la région (Frys et al. 2020, Berkström et al. 2022). Et encore une fois, ces données seront également d'une grande utilité pour dimensionner les mesures de conservation et de gestion de ces récifs (Bonin et al. 2016, Balbar & Metaxas 2019).

Ce travail de thèse a grandement contribué à la connaissance des récifs coralliens de la région de Madagascar. Un autre programme de recherche doctoral, récemment entrepris, a permis de caractériser les communautés coralliennes des récifs de Masoala, au nord-est, de Nosy Be, au nord-ouest, et de Salary Nord sur la côte sud-ouest (Randrianarivo et al. 2022, 2023). Mais vu l'étendue et la diversité des formations récifales entourant Madagascar, il conviendrait de développer des recherches sur d'autres récifs peu ou pas étudiés jusqu'à présent, comme ceux de Belo-sur-Mer et de l'île Barren, dans la région centre-ouest, ou ceux d'Androy et d'Anosy dans les régions du sud et du sud-est de l'île. Ces études permettraient non seulement d'enrichir nos connaissances sur les communautés coralliennes, mais sont également très attendues par les populations locales dépendantes des ressources récifales et de leur bonne gestion.

Ce développement des suivis des communautés coralliennes et des aires marines protégées, nécessaire pour une meilleure connaissance et gestion des récifs de Madagascar, doit s'accompagner d'un effort d'homogénéisation des protocoles d'échantillonnage, de la bancarisation, de l'analyse, et de la restitution des résultats. Cet effort de standardisation doit être porté par la récente initiative *Coral Reef Network*, ou par des programmes de suivis pluriannuels gérés par les organismes de recherche malgaches, comme le Laboratoire Mixte International Mikaroka.

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# Annexes

**Annexe 1.** Récapitulatif de l'effort d'échantillonnage pour le chapitre 3 (structure des communautés) et 6 (régulation des populations). Pour les juvéniles et adultes, il s'agit du nombre de transect-couloirs, et pour les photo-quadrats, il s'agit du nombre de photos analysées par stations.

| Dates | Années | Stations | Juvéniles/Adultes | Photo-quadrat |
|---|---|---|---|---|
| 04/07/2018 | 2018 | OS4 | 3 | 30 |
| 04/07/2018 | 2018 | PR2 | 3 | 30 |
| 05/07/2018 | 2018 | IS1 | 3 | 30 |
| 05/07/2018 | 2018 | PR1 | 3 | 30 |
| 05/07/2018 | 2018 | PR3 | 3 | 30 |
| 21/07/2018 | 2018 | OS2 | 3 | 30 |
| 24/07/2018 | 2018 | PR4 | 3 | 30 |
| 24/07/2018 | 2018 | OS1 | 3 | 30 |
| 27/07/2018 | 2018 | IS2 | 3 | 30 |
| 28/07/2018 | 2018 | OS3 | 3 | 30 |
| 14/07/2019 | 2019 | OS2 | 3 | 30 |
| 20/07/2019 | 2019 | PR4 | 3 | 30 |
| 01/08/2019 | 2019 | OS3 | 3 | 30 |
| 11/08/2019 | 2019 | OS4 | 3 | 30 |
| 11/08/2019 | 2019 | PR1 | 3 | 30 |
| 11/08/2019 | 2019 | OS1 | 3 | 30 |
| 12/08/2019 | 2019 | PR2 | 3 | 30 |
| 12/08/2019 | 2019 | PR3 | 3 | 30 |
| 18/08/2019 | 2019 | IS1 | 3 | 30 |
| 20/08/2019 | 2019 | PR4 | 3 | 30 |
| 07/07/2020 | 2020 | IS1 | 3 | 30 |
| 07/07/2020 | 2020 | IS2 | 3 | 30 |
| 13/07/2020 | 2020 | PR3 | 3 | 30 |
| 14/07/2020 | 2020 | OS4 | 3 | 30 |
| 14/07/2020 | 2020 | PR2 | 3 | 30 |
| 15/07/2020 | 2020 | PR1 | 3 | 30 |
| 16/07/2020 | 2020 | OS2 | 3 | 30 |
| 16/07/2020 | 2020 | OS3 | 3 | 30 |
| 08/08/2020 | 2020 | OS1 | 3 | 30 |
| 08/08/2020 | 2020 | PR4 | 3 | 30 |

**Annexe 2.** Récapitulatif de l'effort d'échantillonnage pour le chapitre 5 (variabilité spatio-temporelle du recrutement) et 6 (régulation des populations) : date de collecte, année de suivi, stations et nombre des plaques de recrutement.

| Dates | Années | Stations | No. de plaques |
|---|---|---|---|
| 27/01/2019 | 2018-2019 | IS1 | 12 |
| 27/01/2019 | 2018-2019 | OS1 | 17 |
| 27/01/2019 | 2018-2019 | PR4 | 20 |
| 28/01/2019 | 2018-2019 | IS2 | 18 |
| 28/01/2019 | 2018-2019 | OS2 | 17 |
| 28/01/2019 | 2018-2019 | OS3 | 19 |
| 29/01/2019 | 2018-2019 | OS4 | 13 |
| 29/01/2019 | 2018-2019 | PR1 | 9 |
| 29/01/2019 | 2018-2019 | PR2 | 13 |
| 29/01/2019 | 2018-2019 | PR3 | 13 |
| 27/01/2020 | 2019-2020 | OS4 | 17 |
| 27/01/2020 | 2019-2020 | PR4 | 12 |
| 28/01/2020 | 2019-2020 | IS2 | 8 |
| 28/01/2020 | 2019-2020 | OS2 | 15 |
| 28/01/2020 | 2019-2020 | OS3 | 15 |
| 29/01/2020 | 2019-2020 | IS1 | 9 |
| 29/01/2020 | 2019-2020 | PR2 | 17 |
| 29/01/2020 | 2019-2020 | PR3 | 8 |
| 30/01/2020 | 2019-2020 | OS1 | 18 |
| 30/01/2020 | 2019-2020 | PR1 | 14 |
| 27/01/2021 | 2020-2021 | OS1 | 7 |
| 27/01/2021 | 2020-2021 | PR4 | 14 |
| 28/01/2021 | 2020-2021 | IS2 | 8 |
| 28/01/2021 | 2020-2021 | OS2 | 7 |
| 29/01/2021 | 2020-2021 | OS3 | 10 |
| 30/01/2021 | 2020-2021 | OS4 | 14 |
| 30/01/2021 | 2020-2021 | PR2 | 8 |
| 30/01/2021 | 2020-2021 | PR3 | 7 |
| 31/01/2021 | 2020-2021 | IS1 | 10 |
| 31/01/2021 | 2020-2021 | PR1 | 6 |

**Annexe 3.** Récapitulatif de l'effort d'échantillonnage pour le chapitre 4 (reproduction sexuée des coraux).

| Dates | Saisons | Nb d'échantillons (fragments de coraux observés) |
|---|---|---:|
| 01/02/2019 | Eté 2018-2019 | 13 |
| 10/11/2018 | Eté 2018-2019 | 20 |
| 10/12/2018 | Eté 2018-2019 | 92 |
| 11/01/2019 | Eté 2018-2019 | 34 |
| 11/02/2019 | Eté 2018-2019 | 62 |
| 11/10/2018 | Eté 2018-2019 | 47 |
| 12/10/2018 | Eté 2018-2019 | 31 |
| 12/11/2018 | Eté 2018-2019 | 41 |
| 12/12/2018 | Eté 2018-2019 | 8 |
| 17/02/2019 | Eté 2018-2019 | 19 |
| 18/02/2019 | Eté 2018-2019 | 6 |
| 21/12/2018 | Eté 2018-2019 | 27 |
| 22/01/2019 | Eté 2018-2019 | 6 |
| 24/09/2018 | Eté 2018-2019 | 22 |
| 25/09/2018 | Eté 2018-2019 | 91 |
| 26/09/2018 | Eté 2018-2019 | 66 |
| 02/11/2020 | Eté 2018-2019 | 2 |
| 02/12/2019 | Eté 2018-2019 | 56 |
| 05/11/2020 | Eté 2018-2019 | 23 |
| 07/10/2019 | Eté 2018-2019 | 41 |
| 08/09/2020 | Eté 2018-2019 | 1 |
| 08/10/2019 | Eté 2018-2019 | 35 |
| 10/10/2019 | Eté 2018-2019 | 22 |
| 10/12/2019 | Eté 2018-2019 | 61 |
| 11/09/2019 | Eté 2018-2019 | 41 |
| 12/09/2019 | Eté 2018-2019 | 28 |
| 14/11/2019 | Eté 2018-2019 | 20 |
| 19/12/2019 | Eté 2018-2019 | 66 |
| 23/09/2019 | Eté 2018-2019 | 9 |
| 24/02/2020 | Eté 2018-2019 | 50 |
| 24/09/2019 | Eté 2018-2019 | 14 |
| 27/01/2020 | Eté 2018-2019 | 39 |
| 27/09/2019 | Eté 2018-2019 | 36 |
| 28/09/2019 | Eté 2018-2019 | 16 |
| 30/01/2020 | Eté 2018-2019 | 17 |
| 31/01/2020 | Eté 2018-2019 | 19 |

**Annexe 4.** Résultats des analyses statistiques réalisé dans le chapitre 3 (structure des communautés). Nested ANOVA pour tester la variabilité spatiale du pourcentage de couverture des catégories benthiques entre les habitats et les stations. Les résultats significatifs ($p < 0,05$) sont indiqués en gras.

| Source of variation | **Df** | **Sum Sq** | **Mean Sq** | **F value** | **P value** |
|---|---|---|---|---|---|
| **Hard corals** | | | | | |
| Habitats | 2 | 1299.2 | 649.6 | 3.9 | **0.036** |
| Habitats:Stations | 7 | 5608.6 | 801.2 | 4.8 | **0.002** |
| Residuals | 20 | 3306.4 | 165.3 | | |
| **Macroalgae** | | | | | |
| Habitats | 2 | 8.9 | 4.4 | 59.0 | **<0.001** |
| Habitats:Stations | 7 | 6.0 | 0.9 | 11.3 | **<0.001** |
| Residuals | 20 | 1.5 | 0.1 | | |
| **Turf algae** | | | | | |
| Habitats | 2 | 2.0 | 1.0 | 1.6 | 0.236 |
| Habitats:Stations | 7 | 46.1 | 6.6 | 10.2 | **<0.001** |
| Residuals | 20 | 12.9 | 0.6 | | |
| **Crustose coralline algae** | | | | | |
| Habitats | 2 | 11.0 | 5.5 | 9.4 | **0.001** |
| Habitats:Stations | 7 | 41.5 | 5.9 | 10.1 | **<0.001** |
| Residuals | 20 | 11.7 | 0.6 | | |
| **Others** | | | | | |
| Habitats | 2 | 0.4 | 0.2 | 0.3 | 0.720 |
| Habitats:Stations | 7 | 10.0 | 1.4 | 2.3 | 0.060 |
| Residuals | 20 | 12.3 | 0.6 | | |
| **Sand** | | | | | |
| Habitats | 2 | 2.8 | 1.4 | 2.8 | 0.080 |
| Habitats:Stations | 7 | 42.9 | 6.1 | 12.3 | **<0.001** |
| Residuals | 20 | 10.0 | 0.5 | | |
| **Rubble** | | | | | |
| Habitats | 2 | 114.6 | 57.3 | 81.2 | **<0.001** |
| Habitats:Stations | 7 | 62.5 | 8.9 | 12.7 | **<0.001** |
| Residuals | 20 | 14.1 | 0.7 | | |
| **Dead corals** | | | | | |
| Habitats | 2 | 0.01 | 0.01 | 0.9 | 0.432 |
| Habitats:Stations | 7 | 0.13 | 0.02 | 2.7 | **0.039** |
| Residuals | 20 | 0.13 | 0.01 | | |
| **Soft corals** | | | | | |
| Habitats | 2 | 6.4 | 3.2 | 16.4 | **<0.001** |
| Habitats:Stations | 7 | 19.0 | 2.7 | 13.9 | **<0.001** |
| Residuals | 20 | 3.9 | 0.2 | | |

**Annexe 5.** Résumé des tests *t* appariés visant à identifier les différences significatives du pourcentage de couverture des catégories benthiques entre habitats. Les résultats significatifs (p < 0,05) sont indiqués en gras.

| Source of variation | Hard corals | Macroalgae | Turf algae | Crustose coralline algae | Other | Sand | Rubble |
|---|---:|---:|---:|---:|---:|---:|---:|
| Outer slope - Inner slope | **0.008** | **0.006** | 0.347 | **<0.001** | 0.803 | 0.613 | **0.001** |
| Patch reefs - Inner slope | 0.084 | 0.557 | 0.748 | **0.029** | 0.551 | 0.404 | 0.089 |
| Patch reefs - Outer slope | 0.62 | **<0.001** | 0.511 | 0.806 | 0.619 | 0.492 | **0.001** |

**Annexe 6.** Résumé des tests *t* appariés visant à identifier les différences entre les stations pour le pourcentage de couverture des catégories benthiques. Les résultats significatifs ($p < 0,05$) sont indiqués en gras.

| Source of variation | Hard corals | Macroalgae | Turf algae | Crustose coralline algae | Others | Sand | Rubble | Dead corals | Soft corals |
|---|---|---|---|---|---|---|---|---|---|
| IS2 - IS1 | 0.943 | **<0.001** | 0.072 | 0.920 | 0.363 | **<0.001** | 0.032 | 1.000 | 1.000 |
| OS1 - IS1 | 0.357 | **<0.001** | 0.175 | 0.084 | 0.259 | **0.002** | **<0.001** | 1.000 | **0.009** |
| OS2 - IS1 | **0.042** | 0.056 | 0.729 | **0.034** | 0.462 | 0.590 | **<0.001** | 1.000 | **<0.001** |
| OS3 - IS1 | **0.003** | 0.394 | 0.260 | **0.009** | 0.827 | 1.000 | **<0.001** | 0.130 | **0.001** |
| OS4 - IS1 | 0.868 | 0.058 | **0.014** | 0.069 | 0.330 | **<0.001** | **<0.001** | 1.000 | **0.005** |
| PR1 - IS1 | **0.007** | **<0.001** | 0.516 | 0.789 | 0.076 | **0.002** | **0.005** | 1.000 | 1.000 |
| PR2 - IS1 | **0.016** | 0.342 | 0.092 | **0.030** | 0.259 | 0.857 | **<0.001** | **0.005** | **<0.001** |
| PR3 - IS1 | 0.547 | **<0.001** | 0.901 | 0.592 | 0.690 | 0.019 | 0.517 | 1.000 | 1.000 |
| PR4 - IS1 | 0.270 | 0.127 | **<0.001** | **<0.001** | 0.757 | 1.000 | **<0.001** | 1.000 | 0.773 |
| OS1 - IS2 | 0.322 | **<0.001** | **0.004** | 0.069 | 0.819 | **0.017** | **<0.001** | 1.000 | **0.009** |
| OS2 - IS2 | **0.036** | **<0.001** | **0.036** | **0.027** | 0.109 | **<0.001** | **<0.001** | 1.000 | **<0.001** |
| OS3 - IS2 | **0.003** | **<0.001** | **0.006** | **0.007** | 0.263 | **<0.001** | **<0.001** | 0.130 | **0.001** |
| OS4 - IS2 | 0.812 | **<0.001** | 0.436 | 0.057 | 0.946 | 0.158 | **<0.001** | 1.000 | **0.005** |
| PR1 - IS2 | **0.006** | 0.640 | **0.018** | 0.868 | **0.011** | **0.022** | 0.389 | 1.000 | 1.000 |
| PR2 - IS2 | **0.013** | **0.003** | **0.002** | **0.024** | 0.819 | **<0.001** | 0.059 | **0.005** | **<0.001** |
| PR3 - IS2 | 0.501 | 0.971 | 0.091 | 0.525 | 0.606 | **0.002** | **0.008** | 1.000 | 1.000 |
| PR4 - IS2 | 0.302 | **0.012** | **0.014** | **<0.001** | 0.545 | **<0.001** | **<0.001** | 1.000 | 0.773 |
| OS2 - OS1 | 0.233 | **0.033** | 0.305 | 0.650 | 0.070 | **0.008** | 1.000 | 1.000 | 0.190 |
| OS3 - OS1 | **0.025** | **0.003** | 0.809 | 0.287 | 0.182 | **0.002** | 0.714 | 0.130 | 0.409 |
| OS4 - OS1 | 0.448 | **0.032** | **0.001** | 0.920 | 0.871 | 0.271 | 0.830 | 1.000 | 0.782 |
| PR1 - OS1 | 0.055 | **<0.001** | 0.466 | 0.050 | **0.007** | 0.903 | **<0.001** | 1.000 | **0.009** |
| PR2 - OS1 | 0.104 | **<0.001** | 0.718 | 0.606 | 1.000 | **0.004** | **<0.001** | **0.005** | **<0.001** |
| PR3 - OS1 | 0.745 | **<0.001** | 0.142 | 0.217 | 0.458 | 0.372 | **<0.001** | 1.000 | **0.009** |
| PR4 - OS1 | 0.051 | **<0.001** | **<0.001** | **<0.001** | 0.406 | **0.002** | 0.879 | 1.000 | **0.018** |
| OS3 - OS2 | 0.245 | 0.259 | 0.429 | 0.534 | 0.602 | 0.590 | 0.714 | 0.130 | 0.613 |
| OS4 - OS2 | 0.059 | 0.982 | **0.006** | 0.723 | 0.096 | **0.001** | 0.830 | 1.000 | 0.295 |
| PR1 - OS2 | 0.426 | **<0.001** | 0.760 | **0.019** | 0.276 | **0.006** | **<0.001** | 1.000 | **<0.001** |
| PR2 - OS2 | 0.641 | **0.007** | 0.171 | 0.950 | 0.070 | 0.719 | **<0.001** | **0.005** | **0.001** |
| PR3 - OS2 | 0.135 | **<0.001** | 0.638 | 0.098 | 0.262 | 0.058 | **<0.001** | 1.000 | **<0.001** |
| PR4 - OS2 | **0.004** | **0.002** | **<0.001** | **<0.001** | 0.300 | 0.590 | 0.879 | 1.000 | **0.001** |
| OS4 - OS3 | **0.005** | 0.269 | **0.001** | 0.333 | 0.237 | **<0.001** | 0.879 | 0.130 | 0.580 |
| PR1 - OS3 | 0.705 | **<0.001** | 0.623 | **0.005** | 0.115 | **0.002** | **<0.001** | 0.130 | **0.001** |
| PR2 - OS3 | 0.478 | 0.080 | 0.548 | 0.576 | 0.182 | 0.857 | **0.001** | 0.130 | **<0.001** |
| PR3 - OS3 | **0.012** | **<0.001** | 0.213 | **0.028** | 0.538 | **0.019** | **<0.001** | 0.130 | **0.001** |
| PR4 - OS3 | **<0.001** | **0.023** | **<0.001** | **<0.001** | 0.599 | 1.000 | 0.830 | 0.130 | **0.003** |
| PR1 - OS4 | **0.011** | **<0.001** | **0.003** | **0.040** | **0.010** | 0.325 | **<0.001** | 1.000 | **0.005** |
| PR2 - OS4 | **0.022** | **0.007** | **<0.001** | 0.677 | 0.871 | **<0.001** | **0.001** | **0.005** | **<0.001** |
| PR3 - OS4 | 0.661 | **<0.001** | **0.018** | 0.184 | 0.560 | 0.054 | **<0.001** | 1.000 | **0.005** |
| PR4 - OS4 | 0.208 | **0.002** | 0.074 | **<0.001** | 0.502 | **<0.001** | 0.950 | 1.000 | **0.010** |
| PR2 - OS4 | 0.738 | **0.001** | 0.280 | **0.017** | **0.007** | **0.003** | 0.275 | **0.005** | **<0.001** |
| PR3 - OS4 | **0.028** | 0.615 | 0.441 | 0.425 | **0.034** | 0.313 | **0.001** | 1.000 | 1.000 |
| PR4 - OS4 | **0.001** | **0.004** | **<0.001** | **<0.001** | **0.041** | **0.002** | **<0.001** | 1.000 | 0.773 |
| PR3 - PR2 | 0.056 | **0.003** | 0.072 | 0.087 | 0.458 | **0.027** | **<0.001** | **0.005** | **<0.001** |
| PR4 - PR2 | **0.001** | 0.543 | **<0.001** | **<0.001** | 0.406 | 0.857 | **0.001** | **0.005** | **<0.001** |
| PR4 - PR3 | **0.013** | **0.013** | **<0.001** | **<0.001** | 0.928 | **0.019** | **<0.001** | 1.000 | 0.773 |

**Annexe 7.** Résumé de l'ANOVA emboîtée visant à tester la variabilité spatiale de la richesse générique entre les habitats et les stations. Les résultats significatifs ($p < 0,05$) sont indiqués en gras.

| Source of variation | Df | Sum Sq | Mean Sq | F value | P value |
|---|---|---|---|---|---|
| Habitats | 2 | 115.45 | 57.73 | 6.21 | **0.008** |
| Habitats:Stations | 7 | 344.42 | 49.20 | 5.29 | **0.002** |
| Residuals | 20 | 186.00 | 9.30 | | |

**Annexe 8.** Résumé des tests *t* appariés visant à identifier les différences entre les habitats en ce qui concerne la richesse générique. Les résultats significatifs ($p < 0,05$) sont indiqués en gras.

| Source of variation | P value |
|---|---:|
| Outer slope - Patch reefs | **0.032** |
| Inner slope - Patch reefs | **0.032** |
| Inner slope - Outer slope | 0.911 |

**Annexe 9.** Résumé des tests *t* appariés visant à identifier les différences entre les stations en ce qui concerne la richesse générique. Les résultats significatifs (p < 0,05) sont indiqués en gras.

| Source of variation | P value |
|---|---:|
| PR2 - PR1 | **0.034** |
| PR3 - PR1 | **0.003** |
| PR4 - PR1 | 0.792 |
| OS1 - PR1 | 0.297 |
| OS2 - PR1 | **<0.001** |
| OS3 - PR1 | **0.045** |
| OS4 - PR1 | **<0.001** |
| IS1 - PR1 | **0.034** |
| IS2 - PR1 | **0.001** |
| PR3 - PR2 | 0.297 |
| PR4 - PR2 | 0.058 |
| OS1 - PR2 | 0.242 |
| OS2 - PR2 | **0.026** |
| OS3 - PR2 | 0.895 |
| OS4 - PR2 | **0.034** |
| IS1 - PR2 | 0.895 |
| IS2 - PR2 | 0.156 |
| PR4 - PR3 | **0.006** |
| OS1 - PR3 | **0.034** |
| OS2 - PR3 | 0.196 |
| OS3 - PR3 | 0.242 |
| OS4 - PR3 | 0.242 |
| IS1 - PR3 | 0.297 |
| IS2 - PR3 | 0.692 |
| OS1 - PR4 | 0.431 |
| OS2 - PR4 | **<0.001** |
| OS3 - PR4 | 0.076 |
| OS4 - PR4 | **<0.001** |
| IS1 - PR4 | 0.058 |
| IS2 - PR4 | **0.002** |
| OS2 - OS1 | **0.002** |
| OS3 - OS1 | 0.297 |
| OS4 - OS1 | **0.002** |
| IS1 - OS1 | 0.242 |
| IS2 - OS1 | **0.014** |
| OS3 - OS2 | **0.019** |
| OS4 - OS2 | 0.895 |
| IS1 - OS2 | **0.026** |
| IS2 - OS2 | 0.360 |
| OS4 - OS3 | **0.026** |
| IS1 - OS3 | 0.895 |
| IS2 - OS3 | 0.124 |
| IS1 - OS4 | **0.034** |
| IS2 - OS4 | 0.431 |
| IS2 - IS1 | 0.156 |

**Annexe 10.** Résumé de l'ANOVA emboîtée visant à tester la variabilité spatiale de l'abondance globale des colonies coralliennes entre les habitats et les stations. Les résultats significatifs ($p < 0,05$) sont indiqués en gras.

| Source of variation | Df | Sum Sq | Mean Sq | F value | P value |
|---|---|---|---|---|---|
| Habitats | 2 | 16175.05 | 8087.53 | 4.07 | **0.032** |
| Habitats:Stations | 7 | 53072.42 | 7581.77 | 3.81 | **0.008** |
| Residuals | 20 | 39771.33 | 1988.57 | | |

**Annexe 11.** Résumé des tests *t* appariés visant à identifier les différences entre les habitats en ce qui concerne l'abondance des colonies coralliennes. Les résultats significatifs ($p < 0,05$) sont indiqués en gras.

| Source of variation | P value |
|---|---:|
| Outer slope - Patch reefs | 0.102 |
| Inner slope - Patch reefs | 0.592 |
| Inner slope - Outer slope | **0.045** |

**Annexe 12.** Résumé des tests *t* appariés visant à identifier les différences entre les stations pour l'abondance des colonies coralliennes. Les résultats significatifs (p < 0,05) sont indiqués en gras.

| Source of variation | P value |
|---|---:|
| PR2 - PR1 | **0.024** |
| PR3 - PR1 | 0.070 |
| PR4 - PR1 | 0.238 |
| OS1 - PR1 | 0.814 |
| OS2 - PR1 | **0.002** |
| OS3 - PR1 | **0.001** |
| OS4 - PR1 | **0.042** |
| IS1 - PR1 | 0.094 |
| IS2 - PR1 | 0.878 |
| PR3 - PR2 | 0.601 |
| PR4 - PR2 | 0.234 |
| OS1 - PR2 | **0.039** |
| OS2 - PR2 | 0.234 |
| OS3 - PR2 | 0.147 |
| OS4 - PR2 | 0.786 |
| IS1 - PR2 | 0.500 |
| IS2 - PR2 | **0.033** |
| PR4 - PR3 | 0.495 |
| OS1 - PR3 | 0.109 |
| OS2 - PR3 | 0.094 |
| OS3 - PR3 | 0.055 |
| OS4 - PR3 | 0.800 |
| IS1 - PR3 | 0.878 |
| IS2 - PR3 | 0.094 |
| OS1 - PR4 | 0.339 |
| OS2 - PR4 | **0.023** |
| OS3 - PR4 | **0.013** |
| OS4 - PR4 | 0.352 |
| IS1 - PR4 | 0.595 |
| IS2 - PR4 | 0.301 |
| OS2 - OS1 | **0.003** |
| OS3 - OS1 | **0.001** |
| OS4 - OS1 | 0.068 |
| IS1 - OS1 | 0.144 |
| IS2 - OS1 | 0.935 |
| OS3 - OS2 | 0.779 |
| OS4 - OS2 | 0.149 |
| IS1 - OS2 | 0.070 |
| IS2 - OS2 | **0.002** |
| OS4 - OS3 | 0.089 |
| IS1 - OS3 | **0.040** |
| IS2 - OS3 | **0.001** |
| IS1 - OS4 | 0.685 |
| IS2 - OS4 | 0.058 |
| IS2 - IS1 | 0.125 |

**Annexe 13.** Résumé de l'ANOSIM pour la comparaison par paire de la composition et de l'abondance des genres de coraux entre les habitats.

| | | | | | |
|---|---|---|---|---|---|
| *Global test* | | | | | |
| Sample statistic (Global R): 0.606 | | | | | |
| Significance level of sample statistic: 0.6% | | | | | |
| Number of permutations: 999 (Random sample from 1575) | | | | | |
| Number of permuted statistics greater than or equal to Global R: 5 | | | | | |
| *Pairwise Tests* | | | | | |
| Groups | R | Significance level % | Possible permutations | Actual permutations | Number ≥ Observed |
| Inner slope - Outer slope | 0.857 | 6.7 | 15 | 15 | 1 |
| Inner slope - Patch reefs | 0.071 | 46.7 | 15 | 15 | 7 |
| Outer slope - Patch reefs | 0.688 | 2.9 | 35 | 35 | 1 |

**Annexe 14.** Composition et abondance (nombre moyen de colonies par station) des assemblages coralliens dans les 10 stations utilisées pour les nMDS.

| | **IS1** | **IS2** | **OS1** | **OS2** | **OS3** | **OS4** | **PR1** | **PR2** | **PR3** | **PR4** |
|---|---|---|---|---|---|---|---|---|---|---|
| *Acanthastrea* | 0 | 0 | 8 | 2 | 0 | 19 | 0 | 2 | 3 | 1 |
| *Acropora* | 44 | 56 | 80 | 208 | 359 | 101 | 116 | 160 | 0 | 87 |
| *Astreopora* | 0 | 0 | 22 | 35 | 24 | 0 | 0 | 0 | 0 | 0 |
| *Blastomussa* | 0 | 0 | 3 | 0 | 0 | 4 | 0 | 0 | 0 | 0 |
| *Coscinarea* | 0 | 0 | 11 | 4 | 0 | 15 | 0 | 3 | 3 | 1 |
| *Cycloseris* | 30 | 0 | 2 | 2 | 0 | 0 | 9 | 31 | 85 | 90 |
| *Cyphastrea* | 0 | 0 | 4 | 0 | 0 | 10 | 1 | 1 | 2 | 8 |
| *Echinophyllia* | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 2 | 1 | 0 |
| *Echinopora* | 12 | 1 | 7 | 21 | 11 | 17 | 1 | 2 | 4 | 11 |
| *Euphyllia* | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 2 | 0 | 0 |
| *Favia* | 2 | 12 | 30 | 48 | 2 | 49 | 0 | 12 | 3 | 3 |
| *Favites* | 1 | 4 | 22 | 40 | 5 | 50 | 3 | 2 | 2 | 2 |
| *Fungia* | 2 | 53 | 1 | 9 | 1 | 6 | 2 | 14 | 2 | 6 |
| *Galaxea* | 2 | 1 | 37 | 104 | 238 | 35 | 6 | 10 | 2 | 0 |
| *Gardineroseris* | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 2 |
| *Gardinoseris* | 0 | 2 | 6 | 0 | 6 | 6 | 0 | 1 | 0 | 5 |
| *Goniastrea* | 2 | 1 | 5 | 17 | 0 | 7 | 0 | 0 | 3 | 2 |
| *Goniopora* | 1 | 1 | 3 | 0 | 3 | 4 | 0 | 3 | 0 | 0 |
| *Herpolitha* | 0 | 3 | 0 | 1 | 0 | 0 | 1 | 1 | 0 | 0 |
| *Hydnophora* | 9 | 0 | 15 | 29 | 3 | 8 | 1 | 0 | 3 | 0 |
| *Leptastrea* | 1 | 0 | 6 | 6 | 0 | 13 | 0 | 2 | 1 | 0 |
| *Leptoria* | 0 | 1 | 0 | 16 | 9 | 8 | 0 | 1 | 0 | 0 |
| *Lobophyllia* | 0 | 0 | 1 | 0 | 1 | 1 | 0 | 7 | 7 | 0 |
| *Merulina* | 0 | 3 | 0 | 0 | 0 | 0 | 0 | 2 | 1 | 0 |
| *Millepora* | 0 | 15 | 0 | 12 | 6 | 0 | 3 | 0 | 0 | 0 |
| *Montastrea* | 0 | 0 | 0 | 1 | 0 | 4 | 0 | 2 | 0 | 0 |
| *Montipora* | 9 | 0 | 35 | 38 | 2 | 33 | 3 | 10 | 18 | 1 |
| *Pavona* | 30 | 85 | 12 | 4 | 2 | 10 | 11 | 4 | 28 | 55 |
| *Physogyra* | 0 | 2 | 0 | 0 | 0 | 5 | 0 | 1 | 0 | 0 |
| *Platygyra* | 3 | 0 | 14 | 32 | 2 | 29 | 0 | 3 | 9 | 0 |
| *Plerogyra* | 0 | 2 | 6 | 0 | 0 | 9 | 1 | 5 | 1 | 0 |
| *Pocillopora* | 5 | 6 | 47 | 75 | 27 | 51 | 2 | 23 | 13 | 55 |
| *Porites* | 19 | 9 | 95 | 123 | 38 | 23 | 0 | 2 | 10 | 0 |
| *Psammacora* | 3 | 0 | 8 | 2 | 0 | 20 | 0 | 10 | 4 | 1 |
| *Seriatopora* | 5 | 81 | 1 | 63 | 229 | 3 | 30 | 75 | 30 | 1 |
| *Stylophora* | 9 | 23 | 3 | 9 | 8 | 1 | 18 | 16 | 31 | 16 |
| *Turbinaria* | 0 | 0 | 4 | 3 | 0 | 1 | 0 | 0 | 0 | 0 |

**Annexe 15.** Résumé de l'ANOVA par permutation pour la comparaison de la distribution des fréquences de taille dans chaque habitat sur la base de l'abondance des colonies. Les résultats significatifs ($p < 0,05$) sont indiqués en gras.

| Source of variation | Df | R Sum Sq | R Mean Sq | Iter | P value |
|---|---|---|---|---|---|
| Habitats | 2 | 29318 | 14658.8 | 5000 | **0.001** |
| Size classes | 5 | 127345 | 25469 | 5000 | **0.001** |
| Habitats × Size classes | 10 | 33564 | 3356.4 | 5000 | **0.001** |
| Residuals | 162 | 163297 | 1008 | | |

**Annexe 16.** Résumé du test *t* appariés de la distribution de la fréquence des tailles dans chaque habitat sur la base de l'abondance des colonies. Les résultats significatifs ($p < 0,05$) sont indiqués en gras.

| Source of variation | P value |
|---|---:|
| Outer slope - Inner slope | **0.006** |
| Patch reefs - Inner slope | 0.414 |
| Patch reefs - Outer slope | **0.006** |

**Annexe 17.** Résumé du test apparié de la distribution des fréquences de taille basée sur l'abondance des colonies. Les résultats significatifs ($p < 0,05$) sont indiqués en gras.

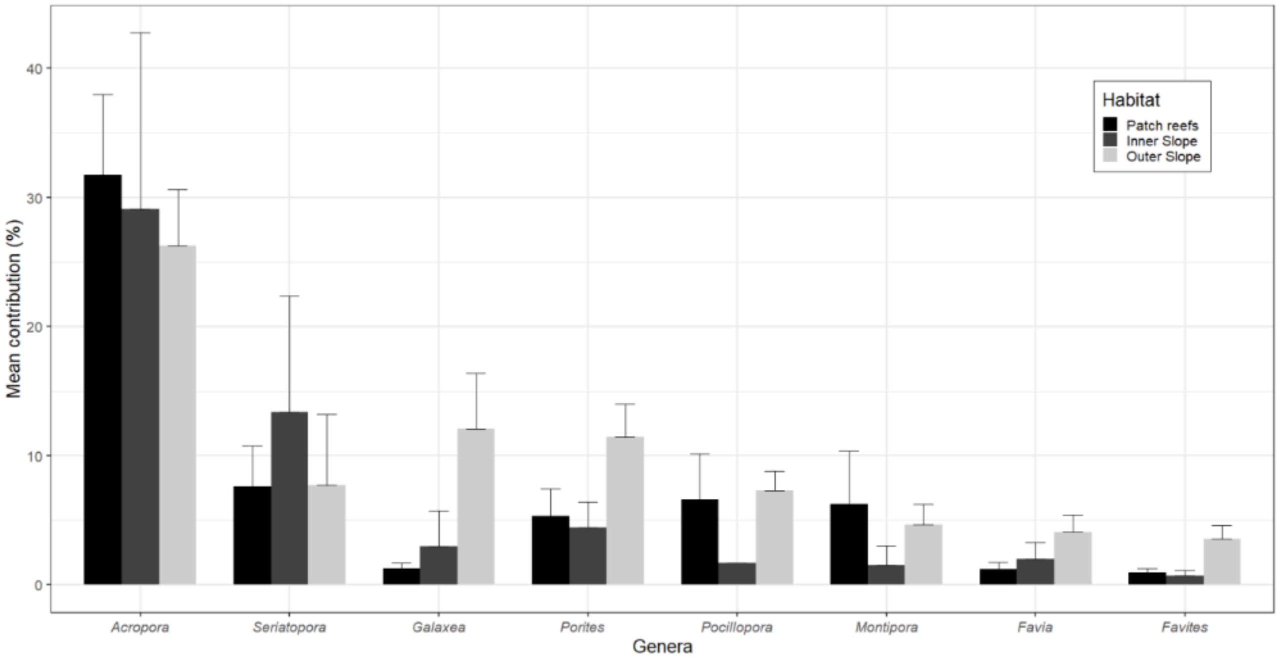
| Source of variation | P value |
|---|---:|
| [11-20]-[6-10] | **0.012** |
| [11-20]-[21-40] | **0.002** |
| [11-20] - [41-80] | **0.002** |
| [11-20] - [81-160] | **0.002** |
| [11-20] - [161-320] | **0.002** |
| [21-40]-[41-80] | **0.017** |
| [21-40]-[6-10] | 0.068 |
| [21-40]-[81-160] | **0.002** |
| [6-10]-[81-160] | **0.002** |
| [41-80]-[6-10] | **0.002** |
| [41-80]-[81-160] | **0.002** |
| [161-320]-[21-40] | **0.002** |
| [161-320]-[41-80] | **0.002** |
| [161-320]-[6-10] | **0.002** |
| [161-320]-[81-160] | **0.017** |

**Annexe 18.** Genres de coraux (scléractiniaires et l'hydrocoralliaire *Millepora*) recensés dans la région de Toliara au sud-ouest de Madagascar en 2017 (présente étude) et en 1961-1970 (Pichon 1978), dans la région d'Andavadoaka (Harding et al. 2006), dans la région nord-ouest par Veron & Turak (2003), et dans la région nord-est par Obura et al. (2011).

| Regions | SW Madagascar | SW Madagascar | SW Madagascar | NW Madagascar | NE Madagascar |
|---|---|---|---|---|---|
| Sites | Toliara | Toliara | Andavadoaka | | |
| Sampling periods | 2017 | 1961-1970 | 2005 | 2002 | 2010 |
| References | Present study | Pichon (1978) | Harding et al. (2006) | Veron & Turak (2003) | Obura et al. (2011) |
| *Acanthastrea* | √ | √ | √ | √ | √ |
| *Acropora* | √ | | | √ | √ |
| *Agariciella* | | √ | | | |
| *Alveopora* | | √ | | √ | √ |
| *Anacropora* | | | | √ | √ |
| *Anomastraea* | | √ | | √ | √ |
| *Astreopora* | √ | √ | √ | √ | √ |
| *Balanophyllia* | | √ | | | |
| *Barabattoia* | | | | | √ |
| *Blastomussa* | √ | √ | √ | √ | |
| *Cantharellus* | | | | √ | |
| *Catalaphyllia* | | | | √ | √ |
| *Caulastrea* | √ | √ | √ | √ | √ |
| *Coeloseris* | | | | √ | √ |
| *Coscinaraea* | √ | √ | √ | √ | √ |
| *Craterastrea* | | | √ | | |
| *Ctenella* | | | | √ | |
| *Cycloseris* | √ | √ | √ | √ | √ |
| *Cynarina* | | √ | | √ | √ |
| *Cyphastrea* | √ | √ | √ | √ | √ |
| *Dendrophyllia* | | √ | | | |
| *Diaseris* | | √ | | √ | √ |
| *Diploastrea* | | √ | √ | √ | √ |
| *Echinophyllia* | √ | √ | √ | √ | √ |
| *Echinopora* | √ | √ | √ | √ | √ |
| *Euphyllia* | √ | | | √ | √ |
| *Favia* | √ | √ | √ | √ | √ |

|  |  |  |  |  |  |
|---|---|---|---|---|---|
| *Favites* | √ | √ | √ | √ | √ |
| *Fungia* | √ | √ | √ | √ | √ |
| *Galaxea* | √ | √ | √ | √ | √ |
| *Gardineroseris* | √ |  | √ | √ | √ |
| *Goniastrea* | √ | √ | √ | √ | √ |
| *Goniopora* | √ | √ | √ | √ | √ |
| *Gyrosmilia* |  | √ | √ | √ | √ |
| *Halomitra* | √ | √ | √ | √ | √ |
| *Herpolitha* | √ | √ | √ | √ | √ |
| *Heterocyathus* |  | √ |  |  | √ |
| *Heteropsammia* |  | √ |  | √ | √ |
| *Horastrea* |  | √ | √ | √ | √ |
| *Hydnophora* | √ | √ | √ | √ | √ |
| *Isopora* |  |  |  |  |  |
| *Leptastrea* | √ | √ | √ | √ | √ |
| *Leptoria* | √ | √ | √ | √ | √ |
| *Leptoseris* | √ | √ | √ | √ | √ |
| *Lithophyllon* |  |  | √ |  |  |
| *Lobophyllia* | √ | √ | √ | √ | √ |
| *Madracis* |  | √ |  | √ | √ |
| *Merulina* | √ | √ | √ | √ | √ |
| *Micromussa* |  |  |  |  | √ |
| *Millepora* | √ | √ | √ | √ | √ |
| *Montastrea* | √ | √ | √ | √ | √ |
| *Montipora* | √ | √ | √ | √ | √ |
| *Mycedium* | √ | √ | √ | √ | √ |
| *Nemenzophyllia* | √ |  | √ |  |  |
| *Oulophyllia* | √ | √ | √ | √ | √ |
| *Oxypora* |  | √ | √ | √ | √ |
| *Pachyseris* |  | √ | √ | √ | √ |
| *Parascolymia* |  | √ |  |  |  |
| *Pavona* | √ | √ | √ | √ | √ |
| *Pectinia* |  | √ | √ | √ | √ |
| *Physogyra* | √ | √ | √ | √ | √ |
| *Platygyra* | √ | √ | √ | √ | √ |
| *Plerogyra* | √ | √ | √ | √ | √ |
| *Plesiastrea* | √ |  | √ | √ | √ |

| | | | | | |
|---|---|---|---|---|---|
| *Pocillopora* | √ | √ | √ | √ | √ |
| *Podabacia* | √ | √ | √ | √ | √ |
| *Polyphyllia* | | | | √ | √ |
| *Porites* | √ | √ | | √ | √ |
| *Poritipora* | | | √ | √ | √ |
| *Psammocora* | √ | √ | √ | √ | √ |
| *Pseudosiderastrea* | | | | √ | √ |
| *Sandalolitha* | | | | | |
| *Scolymia* | | √ | √ | √ | √ |
| *Seriatopora* | √ | √ | √ | √ | √ |
| *Siderastrea* | | √ | √ | √ | √ |
| *Stylaraea* | | | | √ | √ |
| *Stylocoeniella* | | √ | √ | √ | √ |
| *Stylophora* | √ | √ | √ | √ | √ |
| *Symphyllia* | | | | √ | √ |
| *Trachyphyllia* | | √ | | √ | √ |
| *Tubastrea* | | √ | √ | | |
| *Turbinaria* | √ | √ | √ | √ | √ |
| Total | 44 | 61 | 54 | 69 | 69 |



**Annexe 19.** Contribution à l'abondance globale (exprimée en %) des huit principaux genres de coraux dans les trois principaux habitats (PR : massifs lagonaires, IS : pente interne, et OS : pente extérieure). Les barres d'erreur représentent l'erreur standard.

**Annexe 20.** Proportion (%) de colonies matures (gamètes de grande taille et pigmentés prêts à pondre), immatures (gamètes blancs non prêts à être libérés) et vides (pas de gamètes visibles) d'*Acropora digitifera* pendant les deux périodes estivales (septembre 2018 - février 2019, septembre 2019 - février 2020).

| Season | Month | Empty | Mature | Immature |
|---|---|---|---|---|
| Summer18-19 | Sep | 85.71 | 0.00 | 14.29 |
| | Oct | 64.29 | 0.00 | 35.71 |
| | Nov | 33.33 | 66.67 | 0.00 |
| | Dec | 92.31 | 3.85 | 3.85 |
| | Jan | 100.00 | 0.00 | 0.00 |
| | Feb | 100.00 | 0.00 | 0.00 |
| Summer19-20 | Sep | 24.14 | 20.69 | 55.17 |
| | Oct | 33.33 | 5.56 | 61.11 |
| | Nov | 100.00 | 0.00 | 0.00 |
| | Dec | 89.47 | 2.63 | 7.89 |
| | Jan | 100.00 | 0.00 | 0.00 |
| | Feb | 100.00 | 0.00 | 0.00 |

**Annexe 21.** Proportion (%) de colonies matures (gamètes de grande taille et pigmentés prêts à frayer), immatures (gamètes blancs non prêts à être libérés) et vides (pas de gamètes visibles) d'*Acropora nasuta* pendant les deux périodes estivales (septembre 2018 - février 2019, septembre 2019 - février 2020).

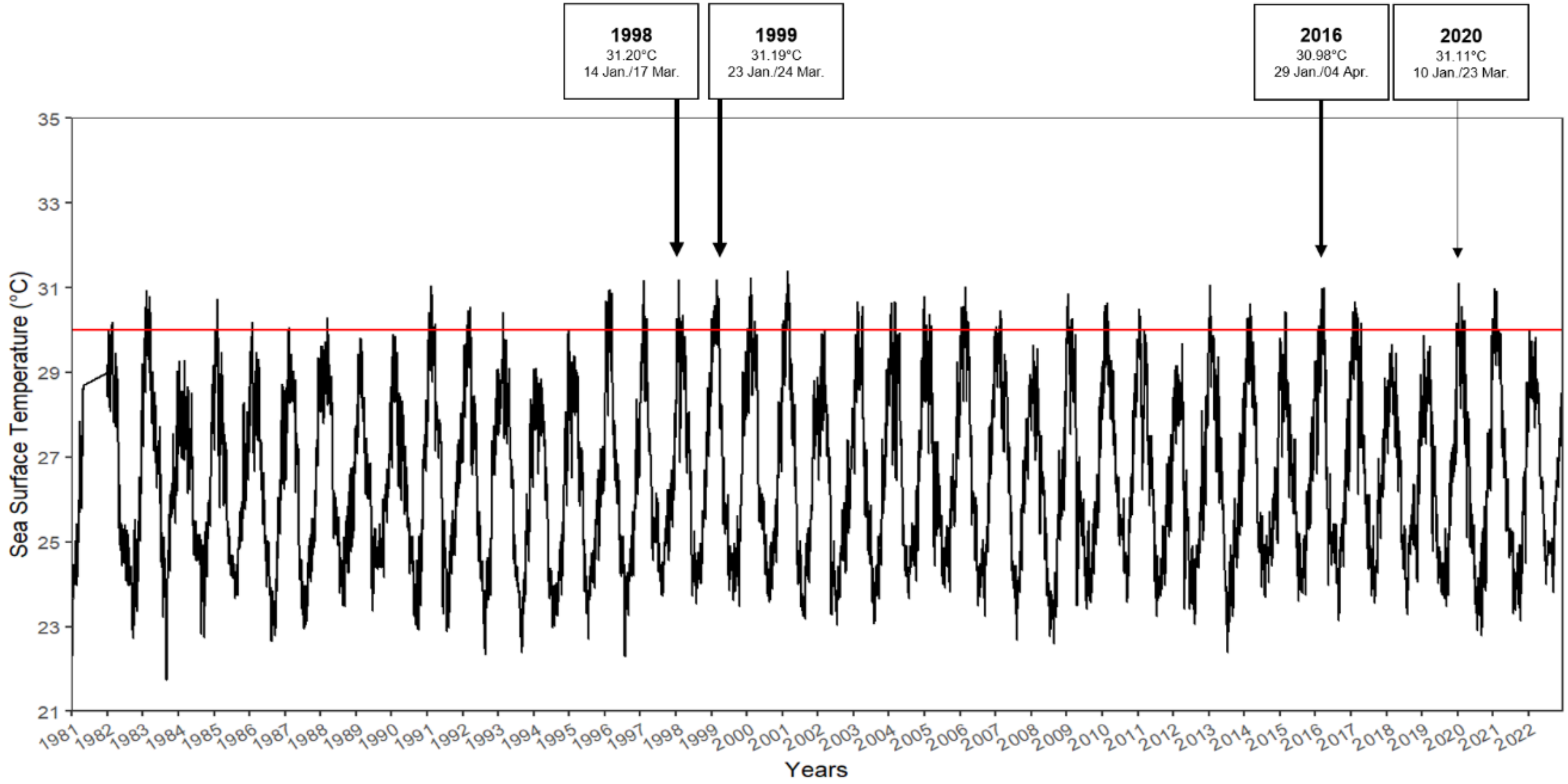
| Season | Month | Empty | Immature | Mature |
|---|---|---|---|---|
| Summer18-19 | Sep | 92.21 | 0.00 | 7.79 |
| | Oct | 91.67 | 0.00 | 8.33 |
| | Nov | 63.64 | 0.00 | 36.36 |
| | Dec | 96.67 | 0.00 | 3.33 |
| | Jan | 100.00 | 0.00 | 0.00 |
| | Feb | 100.00 | 0.00 | 0.00 |
| Summer19-20 | Sep | 12.73 | 34.55 | 52.73 |
| | Oct | 32.14 | 21.43 | 46.43 |
| | Nov | 66.67 | 33.33 | 0.00 |
| | Dec | 98.59 | 1.41 | 0.00 |
| | Jan | 100.00 | 0.00 | 0.00 |
| | Feb | 100.00 | 0.00 | 0.00 |

**Annexe 22.** Proportion (%) de colonies matures (gamètes de grande taille et pigmentés prêts à frayer), immatures (gamètes blancs non prêts à être libérés) et vides (pas de gamètes visibles) de *Galaxea fascicularis* pendant les deux périodes estivales (septembre 2018 - février 2019, septembre 2019 - février 2020).

| Season | Month | Empty | Immature | Mature |
|---|---|---|---|---|
| Summer18-19 | Sep | 94.74 | 0.00 | 5.26 |
| | Oct | 82.35 | 0.00 | 17.65 |
| | Nov | 57.14 | 14.29 | 28.57 |
| | Dec | 75.00 | 10.71 | 14.29 |
| | Jan | 64.71 | 23.53 | 11.76 |
| | Feb | 66.67 | 19.05 | 14.29 |
| Summer19-20 | Sep | 40.91 | 45.45 | 13.64 |
| | Oct | 11.76 | 64.71 | 23.53 |
| | Nov | 0.00 | 0.00 | 0.00 |
| | Dec | 42.31 | 53.85 | 3.85 |
| | Jan | 0.00 | 50.00 | 50.00 |
| | Feb | 20.00 | 46.67 | 33.33 |

**Annexe 23.** Proportion (%) de colonies matures (gamètes de grande taille et pigmentés prêts à frayer), immatures (gamètes blancs non prêts à être libérés) et vides (pas de gamètes visibles) de *Platygyra daedalea* pendant les deux périodes estivales (septembre 2018 - février 2019, septembre 2019 - février 2020).

| Season | Month | Maturation Empty | Immature | Mature |
|---|---|---|---|---|
| Summer18-19 | Sep | 76.66 | 10.00 | 13.33 |
| | Oct | 53.33 | 0.00 | 46.66 |
| | Nov | 77.77 | 16.66 | 5.55 |
| | Dec | 85.71 | 14.28 | 0.00 |
| | Jan | 52.94 | 35.29 | 11.76 |
| | Feb | 76.47 | 11.76 | 11.76 |
| Summer19-20 | Sep | 5.88 | 76.47 | 17.64 |
| | Oct | 15.38 | 42.30 | 42.30 |
| | Nov | 28.57 | 57.14 | 14.28 |
| | Dec | 2.94 | 58.82 | 38.23 |
| | Jan | 8.33 | 25.00 | 66.66 |
| | Feb | 0.00 | 0.00 | 100.00 |



**Annexe 24.** Températures journalières de surface de la mer (°C) autour de Toliara, au sud-ouest de Madagascar, du début 1981 à la fin 2022. Données satellitaires de la NOAA (https://psl.noaa.gov/data/gridded/). Des événements majeurs de blanchissement corallien ont été signalés en 1998, 1999 et 2016, et un événement mineur en 2020. La ligne horizontale rouge indique le seuil thermique hypothétique pour Toliara (30,0 °C). Pour chaque événement, l'amplitude de l'anomalie de température (maximale journalière) et sa durée (période > 30°C) sont indiquées dans des encadrés.

**Annexe 25.** Résumé de la sélection de modèles linéaires mixtes généralisés pour tester la variabilité spatiale et temporelle de l'abondance des cinq principales catégories de recrues entre les années, les habitats et les stations.

| | Intercept | Habitats | Stations | Years | Habitats:Years | df | logLik | AICc | Delta | Weight |
|---|---|---|---|---|---|---|---|---|---|---|
| All taxa | 0.03689 | + | + | + | + | 19 | -884.62 | 1809.4 | 0 | 0.528 |
| | 0.1684 | + | + | + | | 15 | -889.828 | 1811 | 1.61 | 0.236 |
| | 1.208 | | + | + | | 15 | -889.828 | 1811 | 1.61 | 0.236 |
| Relative importance | | 0.764 | 1 | 1 | 0.528 | | | | | |
| Acroporidae | 0.1196 | | + | + | | 15 | -592.026 | 1215.4 | 0 | 0.451 |
| | -1.285 | + | + | + | | 15 | -592.026 | 1215.4 | 0 | 0.451 |
| | -1.491 | + | + | + | + | 19 | -589.153 | 1218.4 | 3.06 | 0.098 |
| Relative importance | | 0.549 | 1 | 1 | 0.098 | | | | | |
| Pocilloporidae | -0.7052 | + | + | + | + | 19 | -635.495 | 1311.1 | 0 | 0.335 |
| | -0.6209 | + | + | + | | 15 | -639.906 | 1311.1 | 0.02 | 0.332 |
| | 0.7255 | | + | + | | 15 | -639.906 | 1311.1 | 0.02 | 0.332 |
| Relative importance | | 0.667 | 0.999 | 0.999 | 0.335 | | | | | |
| Poritidae | -1.926 | | | + | | 6 | -109.229 | 230.7 | 0 | 0.595 |
| | -2.401 | | | | | 4 | -112.296 | 232.7 | 2.01 | 0.217 |
| | -1.589 | + | | + | | 8 | -108.297 | 233 | 2.3 | 0.188 |
| Relative importance | | 0.188 | | 0.783 | | | | | | |
| ‘Other’ recruits | -3.260 | + | + | + | + | 19 | -157.648 | 355.4 | 0 | 0.491 |
| | -2.617 | + | | + | + | 12 | -165.547 | 356 | 0.52 | 0.379 |
| | -1.754 | | | + | | 6 | -172.936 | 358.1 | 2.66 | 0.13 |
| Relative importance | | 0.87 | 0.491 | 1 | 0.87 | | | | | |

**Annexe 26.** Résumé du modèle linéaire généralisé à effets mixtes, structuré par des erreurs binomiales négatives, montrant la variabilité spatiale et temporelle des taux de recrutement des coraux pour tous les taxons (all taxa), les Acroporidae, les Pocilloporidae, les Poritidae et les "autres" recrues. LM : log-ration, CI : intervalle de confiance.

| | | **All taxa** | | **Acroporidae** | | **Pocilloporidae** | | **Poritidae** | | **'Other' recruits** | |
|---|---|---|---|---|---|---|---|---|---|---|---|
| *Source of variations* | *Predictors* | *LM* | *CI* | *LM* | *CI* | *LM* | *CI* | *LM* | *CI* | *LM* | *CI* |
| | (Intercept) | **1.22** $^{***}$ | 0.78 – 1.65 | 0.11 | -0.46 – 0.68 | **0.73** $^{**}$ | 0.22 – 1.24 | **-2.07** $^{***}$ | -2.83 – -1.32 | -2.07 | -4.20 – 0.07 |
| Years | 2019 | **-0.79** $^{*}$ | -1.44 – -0.14 | **-1.00** $^{***}$ | -1.47 – -0.53 | **-0.77** $^{*}$ | -1.40 – -0.14 | -0.89 | -1.83 – 0.06 | -15.1 | -3476.52 – 3446.38 |
| | 2020 | **-0.66** $^{*}$ | -1.27 – -0.05 | **-0.32** | -0.77 – 0.13 | **-0.85** $^{*}$ | -1.62 – -0.08 | **-1.21** $^{*}$ | -2.42 – -0.01 | -0.79 | -2.60 – 1.02 |
| Habitats | Outer slope | **0.79** $^{**}$ | 0.23 – 1.35 | **1.58** $^{***}$ | 0.87 – 2.28 | -0.6 | -1.32 – 0.12 | -0.01 | -1.26 – 1.24 | 0.38 | -1.95 – 2.72 |
| | Patch reefs | **-1.14** $^{***}$ | -1.77 – -0.51 | **-1.42** $^{**}$ | -2.34 – -0.51 | **-1.40** $^{***}$ | -2.18 – -0.62 | 0.57 | -0.65 – 1.78 | -0.87 | -3.16 – 1.42 |
| Stations | IS2 | 0.43 | -0.10 – 0.96 | -0.41 | -1.18 – 0.37 | 0.57 | -0.04 – 1.18 | | | 2.14 | -0.03 – 4.31 |
| | OS1 | -0.41 | -1.18 – 0.36 | -0.15 | -1.76 – 1.46 | -0.16 | -1.03 – 0.72 | | | -0.17 | -1.58 – 1.24 |
| | OS2 | -0.28 | -1.05 – 0.48 | -0.47 | -2.09 – 1.15 | 0.55 | -0.29 – 1.40 | | | -0.82 | -2.54 – 0.90 |
| | OS3 | 0.61 | -0.13 – 1.36 | -0.68 | -2.29 – 0.94 | **1.79** $^{***}$ | 0.98 – 2.60 | | | 1 | -0.13 – 2.14 |
| | PR1 | **1.57** $^{**}$ | 0.54 – 2.59 | **1.65** $^{*}$ | 0.08 – 3.22 | **1.56** $^{*}$ | 0.15 – 2.98 | | | 0.47 | -1.03 – 1.96 |
| | PR2 | **2.58** $^{***}$ | 1.58 – 3.57 | **3.22** $^{***}$ | 1.68 – 4.76 | **1.67** $^{*}$ | 0.25 – 3.09 | | | 0.98 | -0.30 – 2.26 |
| | PR3 | **1.44** $^{**}$ | 0.42 – 2.46 | 1.1 | -0.50 – 2.70 | **1.59** $^{*}$ | 0.19 – 2.99 | | | 0.97 | -0.38 – 2.32 |
| | OS4 | **0.72** $^{**}$ | 0.23 – 1.21 | **1.53** $^{***}$ | 0.89 – 2.16 | -0.63 | -1.29 – 0.02 | | | | |
| | PR4 | **-1.04** $^{***}$ | -1.60 – -0.48 | **-1.40** $^{**}$ | -2.29 – -0.52 | **-1.35** $^{***}$ | -2.07 – -0.62 | | | | |
| Habitats:Years | Outer slope:2019 | -0.6 | -1.32 – 0.13 | -0.46 | -1.64 – 0.71 | -0.55 | -1.40 – 0.30 | | | 16.45 | -3694.03 – 3726.94 |
| | Patch reefs:2019 | -0.39 | -1.15 – 0.37 | 0.23 | -0.97 – 1.43 | -0.52 | -1.40 – 0.37 | | | 17.64 | -3692.84 – 3728.13 |
| | Outer slope:2020 | 0.1 | -0.66 – 0.86 | -0.57 | -1.60 – 0.46 | 0.42 | -0.55 – 1.38 | | | 0.5 | -1.56 – 2.56 |
| | Patch reefs:2020 | **0.79** $^{*}$ | 0.01 – 1.56 | 0.22 | -0.85 – 1.29 | **0.99** $^{*}$ | 0.02 – 1.96 | | | **2.71** $^{*}$ | 0.61 – 4.82 |

$^{*}$ *p<0.05* $^{**}$ *p<0.01* $^{***}$ *p<0.001*

**Annexe 27.** Résumé de la sélection de modèles linéaires mixtes généralisés pour tester la variation des recrues coralliennes entre les trois surfaces de plaques de recrutement.

| Intercept | Surface | Years:Surface | Habitats:Surface | Stations:Surface | df | logLik | AICc | Delta | Weight |
|---|---|---|---|---|---|---|---|---|---|
| 3.274 | + | + | + | + | 39 | -267.556 | 675.5 | 0 | 0.5 |
| 3.274 | + | + |  | + | 39 | -267.556 | 675.5 | 0 | 0.5 |
| Relative importance | 1 | 1 | 0.5 | 1 |  |  |  |  |  |

**Annexe 28.** Résumé du modèle d'effets mixtes linéaires généralisés à structure d'erreur binomiale négative, montrant la variabilité spatiale et temporelle de l'abondance des recrues sur les différentes surfaces des plaques de recrutement (côtés, inférieures et supérieures).

| | *Predictors* | *LM* | *CI* |
|---|---|---|---|
| | (Intercept) | **3.29** $^{***}$ | 2.94 – 3.65 |
| | Lower | **-0.67** $^{*}$ | -1.28 – -0.07 |
| Surfaces | Upper | **-2.40** $^{***}$ | -3.28 – -1.52 |
| | Outer slope:Sides | **0.95** $^{***}$ | 0.52 – 1.38 |
| | Outer slope:Lower | **1.04** $^{***}$ | 0.45 – 1.63 |
| | Outer slope:Upper | **1.34** $^{**}$ | 0.45 – 2.23 |
| | Patch reefs:Sides | **-0.87** $^{**}$ | -1.47 – -0.27 |
| | Patch reefs:Lower | -0.34 | -1.09 – 0.41 |
| Habitats × Surfaces | Patch reefs:Upper | -0.34 | -1.54 – 0.87 |
| | IS2:Sides | 0.19 | -0.29 – 0.67 |
| | IS2:Lower | **1.07** $^{***}$ | 0.49 – 1.65 |
| | IS2:Upper | 0.25 | -0.79 – 1.29 |
| | OS1:Sides | -0.24 | -1.27 – 0.79 |
| | OS1:Lower | -1.31 $^{*}$ | -2.61 – -0.00 |
| | OS1:Upper | 1.13 | -0.37 – 2.63 |
| | OS2:Sides | 0.21 | -0.81 – 1.22 |
| | OS2:Lower | -0.55 | -1.75 – 0.66 |
| | OS2:Upper | -0.83 | -2.51 – 0.85 |
| | OS3:Sides | 0.98 | -0.02 – 1.99 |
| | OS3:Lower | 1.08 | -0.06 – 2.21 |
| | OS3:Upper | -0.14 | -1.72 – 1.44 |
| | PR1:Sides | 0.78 | -0.22 – 1.78 |
| | PR1:Lower | **1.12** $^{**}$ | 0.40 – 1.83 |
| | PR1:Upper | **1.02** | -0.03 – 2.08 |
| | PR2:Sides | **2.26** $^{***}$ | 1.28 – 3.23 |
| | PR2:Lower | **1.20** $^{***}$ | 0.49 – 1.91 |
| | PR2:Upper | **3.09** $^{***}$ | 2.15 – 4.04 |
| | PR3:Sides | **1.16** $^{*}$ | 0.17 – 2.15 |
| | PR3:Lower | 0.2 | -0.60 – 1.00 |
| | PR3:Upper | 0.79 | -0.29 – 1.88 |
| | OS4:Sides | **0.95** $^{***}$ | 0.52 – 1.38 |
| | OS4:Lower | **1.04** $^{***}$ | 0.45 – 1.63 |
| | OS4:Upper | **1.34** $^{**}$ | 0.45 – 2.23 |
| | PR4:Sides | **-0.87** $^{**}$ | -1.47 – -0.27 |
| | PR4:Lower | -0.34 | -1.09 – 0.41 |
| Stations × Surfaces | PR4:Upper | -0.34 | -1.54 – 0.87 |
| | 2019:Sides | **-1.00** $^{***}$ | -1.22 – -0.78 |
| | 2019:Lower | **-1.37** $^{***}$ | -1.68 – -1.06 |
| | 2019:Upper | **-0.49** $^{*}$ | -0.89 – -0.08 |
| | 2020:Sides | **-1.01** $^{***}$ | -1.23 – -0.79 |
| | 2020:Lower | **-1.46** $^{***}$ | -1.78 – -1.14 |
| Years × Surfaces | 2020:Upper | 0.21 | -0.14 – 0.56 |

* $p<0.05$   ** $p<0.01$   *** $p<0.001$

**Annexe 29**. Résumé de la sélection de modèles linéaires mixtes généralisés pour tester l'effet de la couverture du substrat benthique sur la densité de l'ensemble des recrues (tous taxons confondus).

| Intercept | Hard corals | Crustose coralline algae | Macroalgae | Other living taxa | Soft corals | Turf | df | logLik | AICc | Delta | Weight |
|---|---|---|---|---|---|---|---|---|---|---|---|
| 3.493 |  | -0.30 |  |  | -0.14 |  | 5.00 | -93.45 | 200.40 | 0.00 | 0.25 |
| 3.497 |  | -0.29 |  |  |  |  | 4.00 | -95.15 | 200.50 | 0.10 | 0.24 |
| 3.494 |  | -0.33 |  |  |  | 0.10 | 5.00 | -94.44 | 202.40 | 1.99 | 0.09 |
| 3.474 | 0.35 | -0.30 | 0.33 |  |  | 0.36 | 7.00 | -90.75 | 203.00 | 2.53 | 0.07 |
| 3.493 |  | -0.30 |  | 0.05 |  |  | 5.00 | -94.88 | 203.30 | 2.85 | 0.06 |
| 3.496 |  | -0.29 | 0.04 |  |  |  | 5.00 | -95.01 | 203.60 | 3.13 | 0.05 |
| 3.491 |  | -0.32 |  |  | -0.12 | 0.07 | 6.00 | -93.18 | 203.60 | 3.18 | 0.05 |
| 3.491 |  | -0.30 | 0.06 |  | -0.14 |  | 6.00 | -93.18 | 203.60 | 3.19 | 0.05 |
| 3.497 | 0.02 | -0.28 |  |  |  |  | 5.00 | -95.10 | 203.70 | 3.31 | 0.05 |
| 3.49 |  | -0.30 |  | 0.04 | -0.13 |  | 6.00 | -93.31 | 203.90 | 3.45 | 0.05 |
| 3.493 | -0.01 | -0.30 |  |  | -0.14 |  | 6.00 | -93.44 | 204.10 | 3.70 | 0.04 |
| Relative importance | 0.16 | 1.00 | 0.17 | 0.11 | 0.44 | 0.22 |  |  |  |  |  |

**Annexe 30**. Résumé de la sélection de modèles linéaires mixtes généralisés pour tester l'effet de la couverture du substrat benthique sur la densité des recrues d'Acroporidae.

| Intercept | Acroporidae | Crustose coralline algae | Macroalgae | Other living taxa | Soft corals | Turf | df | logLik | AICc | Delta | Weight |
|---|---|---|---|---|---|---|---|---|---|---|---|
| 2.17 | | -0.36 | | 0.16 | | | 5.00 | -64.10 | 142.00 | 0.00 | 0.41 |
| 2.16 | | -0.35 | 0.13 | 0.16 | | | 6.00 | -63.02 | 143.60 | 1.68 | 0.18 |
| 2.18 | | -0.37 | | | | | 4.00 | -67.11 | 144.60 | 2.61 | 0.11 |
| 2.17 | | -0.36 | 0.13 | | | | 5.00 | -65.97 | 145.70 | 3.75 | 0.06 |
| 2.16 | 0.20 | -0.35 | 0.25 | | | | 6.00 | -64.06 | 145.70 | 3.78 | 0.06 |
| 2.17 | | -0.37 | | 0.16 | -0.02 | | 6.00 | -64.07 | 145.70 | 3.78 | 0.06 |
| 2.17 | | -0.37 | | 0.16 | | 0.01 | 6.00 | -64.10 | 145.80 | 3.84 | 0.06 |
| 2.17 | 0.00 | -0.36 | | 0.16 | | | 6.00 | -64.10 | 145.80 | 3.85 | 0.06 |
| Relative importance | 0.12 | 1.00 | 0.30 | 0.77 | 0.06 | 0.06 | | | | | |

**Annexes 31**. Résumé de la sélection de modèles linéaires mixtes généralisés pour tester l'effet de la couverture du substrat benthique sur la densité des recrues de Pocilloporidae.

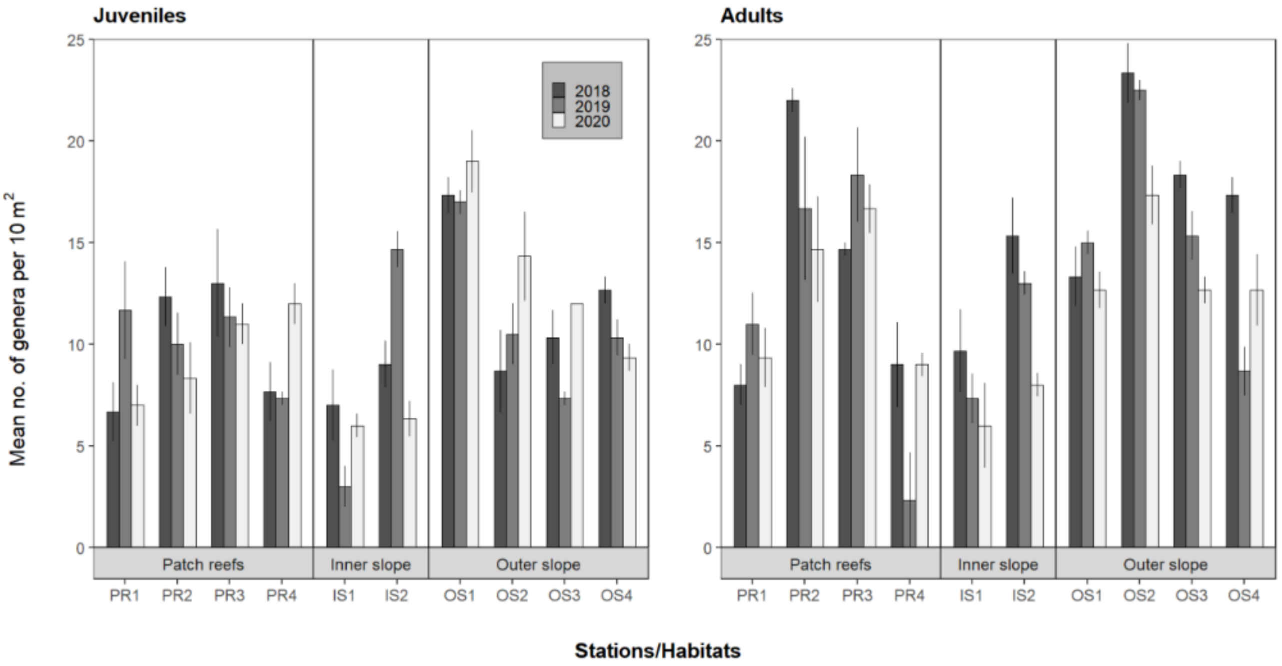
| Intercept | Pocilloporidae | Crustose coralline algae | Macroalgae | Other living taxa | Soft corals | Turf | df | logLik | AICc | Delta | Weight |
|---|---|---|---|---|---|---|---|---|---|---|---|
| 2.89 | 0.33 | -0.28 | -0.16 |  | 0.10 | -0.14 | 7.00 | -160.67 | 340.70 | 0.00 | 0.64 |
| 2.90 | 0.31 | -0.29 | -0.17 |  |  | -0.16 | 6.00 | -163.45 | 342.70 | 2.04 | 0.23 |
| 2.89 | 0.33 | -0.28 | -0.16 | 0.03 | 0.10 | -0.14 | 8.00 | -160.30 | 343.80 | 3.14 | 0.13 |
| Relative importance | 1.00 | 1.00 | 1.00 | 0.13 | 0.77 | 1.00 |  |  |  |  |  |

**Annexe 32**. Résumé de la sélection de modèles linéaires mixtes généralisés pour tester l'effet de la couverture du substrat benthique sur la densité des recrues de Poritidae.

| Intercept | Poritidae | Crustose coralline algae | Macroalgae | Other living taxa | Soft corals | Turf | df | logLik | AICc | Delta | Weight |
|---|---|---|---|---|---|---|---|---|---|---|---|
| -0.8171 | | | | | | -0.36 | 4 | -34.26 | 78.30 | 0.00 | 0.17 |
| -0.7818 | | | | | | | 3 | -35.72 | 78.40 | 0.17 | 0.16 |
| -0.8112 | | | | 0.14 | | -0.39 | 5 | -33.53 | 79.80 | 1.52 | 0.08 |
| -0.7663 | | | | 0.13 | | | 4 | -35.08 | 79.90 | 1.62 | 0.08 |
| -0.8743 | -0.20 | | | | | -0.46 | 5 | -33.60 | 79.90 | 1.65 | 0.08 |
| -0.8475 | | 0.15 | | | | -0.38 | 5 | -33.72 | 80.20 | 1.90 | 0.07 |
| -0.7876 | | 0.15 | | | | | 4 | -35.22 | 80.20 | 1.92 | 0.07 |
| -0.7706 | | | 0.10 | | | | 4 | -35.55 | 80.80 | 2.57 | 0.05 |
| -0.7807 | -0.09 | | | | | | 4 | -35.59 | 80.90 | 2.65 | 0.05 |
| -0.7777 | | | | | 0.05 | | 4 | -35.67 | 81.10 | 2.81 | 0.04 |
| -0.816 | | | | | 0.02 | -0.36 | 5 | -34.26 | 81.20 | 2.98 | 0.04 |
| -0.8166 | | | 0.01 | | | -0.35 | 5 | -34.26 | 81.30 | 2.98 | 0.04 |
| -0.8685 | -0.25 | | | 0.17 | | -0.53 | 6 | -32.63 | 81.30 | 2.99 | 0.04 |
| -0.8461 | | 0.18 | | 0.16 | | -0.43 | 6 | -32.81 | 81.60 | 3.36 | 0.03 |
| -0.794 | | 0.17 | | 0.15 | | | 5 | -34.45 | 81.60 | 3.36 | 0.03 |
| Relative importance | 0.16 | 0.20 | 0.09 | 0.26 | 0.08 | 0.54 | | | | | |

**Annexe 33**. Résumé de la sélection de modèles linéaires mixtes généralisés pour tester l'effet de la couverture du substrat benthique sur la densité des "autres" recrues.

| Intercept | Other corals | Crustose coralline algae | Macroalgae | Other living taxa | Soft corals | Turf | df | logLik | AICc | Delta | Weight |
|---|---|---|---|---|---|---|---|---|---|---|---|
| 0.07761 | | | | | 0.343 | 0.346 | 5 | -35.025 | 83 | 0 | 0.127 |
| 0.1759 | | | | | | | 3 | -38.365 | 83.8 | 0.77 | 0.087 |
| 0.1408 | | | | | | 0.251 | 4 | -37.106 | 84.1 | 1.07 | 0.075 |
| 0.1154 | | -0.4317 | | | | | 4 | -37.12 | 84.1 | 1.1 | 0.074 |
| 0.1411 | | | | | 0.2513 | | 4 | -37.143 | 84.2 | 1.14 | 0.072 |
| 0.0446 | | | 0.2595 | | 0.4096 | 0.41 | 6 | -34.136 | 84.7 | 1.64 | 0.056 |
| 0.0888 | | -0.4048 | | | | 0.231 | 5 | -35.974 | 84.9 | 1.9 | 0.049 |
| 0.07865 | -0.2722 | -0.5093 | | | | | 5 | -36.158 | 85.3 | 2.27 | 0.041 |
| 0.04974 | | -0.2899 | | | 0.2957 | 0.319 | 6 | -34.48 | 85.4 | 2.33 | 0.04 |
| 0.1471 | | | | -0.2965 | | | 4 | -37.776 | 85.5 | 2.41 | 0.038 |
| 0.1556 | -0.2135 | | | | | | 4 | -37.785 | 85.5 | 2.43 | 0.038 |
| 0.05073 | | | | -0.2943 | 0.3456 | 0.327 | 6 | -34.543 | 85.5 | 2.46 | 0.037 |
| 0.09942 | | -0.3514 | | | 0.2003 | | 5 | -36.36 | 85.7 | 2.67 | 0.033 |
| 0.08671 | | -0.4306 | | -0.3107 | | | 5 | -36.463 | 85.9 | 2.88 | 0.03 |
| 0.102 | | | | -0.3522 | 0.2643 | | 5 | -36.473 | 85.9 | 2.9 | 0.03 |
| 0.1182 | | | | -0.2626 | | 0.236 | 5 | -36.628 | 86.3 | 3.21 | 0.026 |
| 0.1724 | | | 0.0827 | | | | 4 | -38.249 | 86.4 | 3.35 | 0.024 |
| 0.07761 | -0.01477 | | | | 0.3392 | 0.341 | 6 | -35.023 | 86.5 | 3.42 | 0.023 |
| 0.1301 | | | 0.1521 | | | 0.278 | 5 | -36.768 | 86.5 | 3.49 | 0.022 |
| 0.1294 | -0.1656 | | | | 0.2236 | | 5 | -36.82 | 86.6 | 3.59 | 0.021 |
| 0.1312 | | | 0.1319 | | 0.2765 | | 5 | -36.858 | 86.7 | 3.67 | 0.02 |
| 0.1338 | -0.1308 | | | | | 0.216 | 5 | -36.903 | 86.8 | 3.76 | 0.019 |
| 0.1092 | | -0.4432 | 0.07993 | | | | 5 | -37.011 | 87 | 3.97 | 0.017 |
| Relative importance | 0.142 | 0.284 | 0.139 | 0.161 | 0.459 | 0.474 | | | | | |



**Annexe 34.** Variation spatiale et temporelle du nombre moyen de genres (juvéniles et adultes) dans les 10 stations situées sur les trois habitats principaux (PR : massifs lagonaires, IS : pente interne, et OS : pente externe). Les barres d'erreur représentent l'erreur standard.

**Annexe 35.** Résumé du modèle linéaire généralisé à effets mixtes structuré par l'erreur binomiale négative, montrant la variabilité spatiale et temporelle des taux de recrutement corallien pour l'ensemble des taxons (all taxa), Acroporidae, Pocilloporidae, Poritidae et "autres" recrues. LM : log-ration, CI : intervalle de confiance.

| | | **All taxa** | | **Acroporidae** | | **Pocilloporidae** | | **Poritidae** | | **'Other' recruits** | |
|---|---|---|---|---|---|---|---|---|---|---|---|
| *Source of variation* | *Predictors* | *LM* | *CI* | *LM* | *CI* | *LM* | *CI* | *LM* | *CI* | *LM* | *CI* |
| | (Intercept) | **1.22** $^{***}$ | 0.78 – 1.65 | 0.11 | -0.46 – 0.68 | **0.73** $^{**}$ | 0.22 – 1.24 | **-2.07** $^{***}$ | -2.83 – -1.32 | -2.07 | -4.20 – 0.07 |
| Years | 2019 | **-0.79** $^{*}$ | -1.44 – -0.14 | **-1.00** $^{***}$ | -1.47 – -0.53 | **-0.77** $^{*}$ | -1.40 – -0.14 | -0.89 | -1.83 – 0.06 | -15.1 | -3476.52 – 3446.38 |
| | 2020 | **-0.66** $^{*}$ | -1.27 – -0.05 | **-0.32** | -0.77 – 0.13 | **-0.85** $^{*}$ | -1.62 – -0.08 | **-1.21** $^{*}$ | -2.42 – -0.01 | -0.79 | -2.60 – 1.02 |
| Habitats | Outer slope | **0.79** $^{**}$ | 0.23 – 1.35 | **1.58** $^{***}$ | 0.87 – 2.28 | -0.6 | -1.32 – 0.12 | -0.01 | -1.26 – 1.24 | 0.38 | -1.95 – 2.72 |
| | Patch reefs | **-1.14** $^{***}$ | -1.77 – -0.51 | **-1.42** $^{**}$ | -2.34 – -0.51 | **-1.40** $^{***}$ | -2.18 – -0.62 | 0.57 | -0.65 – 1.78 | -0.87 | -3.16 – 1.42 |
| Stations | IS2 | 0.43 | -0.10 – 0.96 | -0.41 | -1.18 – 0.37 | 0.57 | -0.04 – 1.18 | | | 2.14 | -0.03 – 4.31 |
| | OS1 | -0.41 | -1.18 – 0.36 | -0.15 | -1.76 – 1.46 | -0.16 | -1.03 – 0.72 | | | -0.17 | -1.58 – 1.24 |
| | OS2 | -0.28 | -1.05 – 0.48 | -0.47 | -2.09 – 1.15 | 0.55 | -0.29 – 1.40 | | | -0.82 | -2.54 – 0.90 |
| | OS3 | 0.61 | -0.13 – 1.36 | -0.68 | -2.29 – 0.94 | **1.79** $^{***}$ | 0.98 – 2.60 | | | 1 | -0.13 – 2.14 |
| | PR1 | **1.57** $^{**}$ | 0.54 – 2.59 | **1.65** $^{*}$ | 0.08 – 3.22 | **1.56** $^{*}$ | 0.15 – 2.98 | | | 0.47 | -1.03 – 1.96 |
| | PR2 | **2.58** $^{***}$ | 1.58 – 3.57 | **3.22** $^{***}$ | 1.68 – 4.76 | **1.67** $^{*}$ | 0.25 – 3.09 | | | 0.98 | -0.30 – 2.26 |
| | PR3 | **1.44** $^{**}$ | 0.42 – 2.46 | 1.1 | -0.50 – 2.70 | **1.59** $^{*}$ | 0.19 – 2.99 | | | 0.97 | -0.38 – 2.32 |
| | OS4 | **0.72** $^{**}$ | 0.23 – 1.21 | **1.53** $^{***}$ | 0.89 – 2.16 | -0.63 | -1.29 – 0.02 | | | | |
| | PR4 | **-1.04** $^{***}$ | -1.60 – -0.48 | **-1.40** $^{**}$ | -2.29 – -0.52 | **-1.35** $^{***}$ | -2.07 – -0.62 | | | | |
| Habitats:Years | Outer slope:2019 | -0.6 | -1.32 – 0.13 | -0.46 | -1.64 – 0.71 | -0.55 | -1.40 – 0.30 | | | 16.45 | -3694.03 – 3726.94 |
| | Patch reefs:2019 | -0.39 | -1.15 – 0.37 | 0.23 | -0.97 – 1.43 | -0.52 | -1.40 – 0.37 | | | 17.64 | -3692.84 – 3728.13 |
| | Outer slope:2020 | 0.1 | -0.66 – 0.86 | -0.57 | -1.60 – 0.46 | 0.42 | -0.55 – 1.38 | | | 0.5 | -1.56 – 2.56 |
| | Patch reefs:2020 | **0.79** $^{*}$ | 0.01 – 1.56 | 0.22 | -0.85 – 1.29 | **0.99** $^{*}$ | 0.02 – 1.96 | | | **2.71** $^{*}$ | 0.61 – 4.82 |

$^{*}p<0.05$   $^{**}p<0.01$   $^{***}p<0.001$

**Annexe 36.** Résumé du modèle d'effets mixtes linéaires généralisés à structure d'erreur binomiale négative, montrant la variabilité spatiale et temporelle de la richesse générique (RG) et de l'abondance des coraux juvéniles et adultes (tous taxons confondus).

| | | **Juvenile GR** | | **Adult GR** | | **Juvenile abundance** | | **Adult abundance** | |
|---|---|---|---|---|---|---|---|---|---|
| *Source of variation* | *Predictors* | *LM* | *CI* | *LM* | *CI* | *LM* | *CI* | *LM* | *CI* |
| | (Intercept) | **2.20** *** | 1.94 – 2.47 | **1.97** *** | 1.69 – 2.25 | **3.59** *** | 3.18 – 3.99 | **4.14** *** | 3.78 – 4.51 |
| Years | 2019 | 0.02 | -0.24 – 0.27 | -0.1 | -0.33 – 0.12 | 0.11 | -0.29 – 0.52 | **0.96** *** | 0.59 – 1.32 |
| | 2020 | -0.03 | -0.29 – 0.22 | -0.08 | -0.30 – 0.15 | 0.39 | -0.01 – 0.80 | 0.2 | -0.16 – 0.57 |
| Habitats | Inner slope | **-0.49** * | -0.93 – -0.04 | 0.3 | -0.11 – 0.70 | **-1.01** ** | -1.65 – -0.37 | **0.73** * | 0.17 – 1.29 |
| | Outer slope | 0.16 | -0.19 – 0.52 | **0.72** *** | 0.37 – 1.07 | 0.09 | -0.48 – 0.67 | **1.21** *** | 0.69 – 1.72 |
| Stations | IS2 | **0.63** *** | 0.28 – 0.98 | **0.46** ** | 0.16 – 0.76 | **1.30** *** | 0.82 – 1.77 | 0.13 | -0.29 – 0.56 |
| | OS1 | **0.50** *** | 0.25 – 0.75 | 0.06 | -0.20 – 0.31 | **0.47** * | 0.00 – 0.93 | -0.17 | -0.59 – 0.25 |
| | OS2 | 0.03 | -0.26 – 0.32 | **0.48** *** | 0.24 – 0.72 | 0.1 | -0.38 – 0.58 | **0.65** ** | 0.22 – 1.08 |
| | OS3 | -0.09 | -0.37 – 0.20 | 0.18 | -0.07 – 0.43 | **1.08** *** | 0.62 – 1.54 | **0.49** * | 0.07 – 0.90 |
| | PR1 | -0.06 | -0.38 – 0.25 | **0.33** * | 0.00 – 0.66 | 0.06 | -0.40 – 0.53 | **0.75** *** | 0.33 – 1.18 |
| | PR2 | 0.13 | -0.17 – 0.43 | **0.96** *** | 0.67 – 1.26 | 0.14 | -0.33 – 0.60 | **1.42** *** | 1.00 – 1.84 |
| | PR3 | 0.27 | -0.02 – 0.56 | **0.89** *** | 0.60 – 1.19 | 0.25 | -0.21 – 0.72 | **1.39** *** | 0.97 – 1.82 |
| Habitats:Years | Inner slope: 2019 | 0.08 | -0.38 – 0.55 | -0.1 | -0.51 – 0.30 | 0.23 | -0.48 – 0.95 | -0.54 | -1.17 – 0.09 |
| | Inner slope: 2020 | -0.23 | -0.73 – 0.27 | **-0.50** * | -0.94 – -0.06 | 0.45 | -0.26 – 1.16 | -0.58 | -1.22 – 0.05 |
| | Outer slope: 2019 | -0.1 | -0.45 – 0.25 | -0.07 | -0.37 – 0.23 | -0.02 | -0.60 – 0.56 | 0.08 | -0.44 – 0.60 |
| | Outer slope: 2020 | 0.14 | -0.20 – 0.48 | -0.19 | -0.49 – 0.11 | 0.14 | -0.43 – 0.71 | **-0.59** * | -1.11 – -0.08 |

* $p<0.05$ ** $p<0.01$ *** $p<0.001$

**Annexe 37.** Résumé du modèle d'effets mixtes linéaires généralisés à structure d'erreur binomiale négative, montrant la variabilité spatiale et temporelle de l'abondance des coraux juvéniles pour les Acroporidae, Pocilloporidae, Poritidae et les "autres" taxons.

| | | **Acroporidae** | | **Pocilloporidae** | | **Poritidae** | | **Other taxa** | |
|---|---|---|---|---|---|---|---|---|---|
| *Source of variation* | *Predictors* | *LM* | *CI* | *LM* | *CI* | *LM* | *CI* | *LM* | *CI* |
| | (Intercept) | **1.85** $^{***}$ | 1.30 – 2.39 | **2.33** $^{***}$ | 1.85 – 2.80 | -0.69 | -1.64 – 0.25 | **3.02** $^{***}$ | 2.55 – 3.49 |
| Years | 2019 | -0.19 | -0.72 – 0.35 | 0 | -0.46 – 0.46 | 0.6 | -0.02 – 1.23 | 0.27 | -0.21 – 0.76 |
| | 2020 | 0.25 | -0.27 – 0.78 | 0.14 | -0.32 – 0.60 | 0.19 | -0.47 – 0.85 | 0.38 | -0.10 – 0.87 |
| Habitats | Inner slope | **-0.97** $^{*}$ | -1.88 – -0.06 | **-0.82** $^{*}$ | -1.61 – -0.04 | -0.58 | -2.23 – 1.06 | **-1.45** $^{***}$ | -2.22 – -0.68 |
| | Outer slope | 0.6 | -0.14 – 1.35 | -0.77 $^{*}$ | -1.47 – -0.06 | **2.47** $^{***}$ | 1.42 – 3.52 | -0.14 | -0.80 – 0.52 |
| Stations | IS2 | **0.78** $^{*}$ | 0.13 – 1.43 | **1.91** $^{***}$ | 1.30 – 2.52 | **2.26** $^{***}$ | 1.00 – 3.51 | **0.90** $^{**}$ | 0.34 – 1.45 |
| | OS1 | 0.01 | -0.57 – 0.59 | 0.19 | -0.40 – 0.77 | 0.46 | -0.02 – 0.94 | **0.80** $^{**}$ | 0.28 – 1.33 |
| | OS2 | 0.26 | -0.33 – 0.85 | 0.56 | -0.02 – 1.15 | -0.32 | -0.87 – 0.22 | -0.07 | -0.63 – 0.48 |
| | OS3 | **0.94** $^{**}$ | 0.37 – 1.50 | **2.24** $^{***}$ | 1.69 – 2.79 | **-1.61** $^{***}$ | -2.30 – -0.92 | **0.60** $^{*}$ | 0.07 – 1.12 |
| | PR1 | -0.07 | -0.71 – 0.57 | **1.02** $^{***}$ | 0.48 – 1.55 | 0.92 | -0.10 – 1.93 | **-1.03** $^{***}$ | -1.59 – -0.48 |
| | PR2 | **1.06** $^{***}$ | 0.46 – 1.66 | 0.3 | -0.25 – 0.85 | **1.72** $^{***}$ | 0.77 – 2.66 | **-0.86** $^{**}$ | -1.41 – -0.31 |
| | PR3 | 0.24 | -0.39 – 0.86 | **0.88** $^{**}$ | 0.34 – 1.42 | **1.89** $^{***}$ | 0.95 – 2.82 | -0.46 | -1.00 – 0.07 |
| Habitats:Years | Inner slope: 2019 | 0.96 | -0.02 – 1.95 | 0.12 | -0.71 – 0.95 | 0.32 | -0.84 – 1.47 | 0.3 | -0.56 – 1.16 |
| | Inner slope: 2020 | 0.62 | -0.35 – 1.59 | **-0.89** $^{*}$ | -1.76 – -0.02 | -1.68 | -3.46 – 0.09 | **1.24** $^{**}$ | 0.40 – 2.08 |
| | Outer slope: 2019 | 0.15 | -0.59 – 0.89 | 0.52 | -0.16 – 1.20 | -0.49 | -1.29 – 0.31 | -0.43 | -1.11 – 0.24 |
| | Outer slope: 2020 | 0.3 | -0.42 – 1.01 | **0.69** $^{*}$ | 0.03 – 1.36 | 0.44 | -0.37 – 1.25 | -0.02 | -0.68 – 0.64 |

* $p<0.05$ ** $p<0.01$ *** $p<0.001$

**Annexe 38**. Résumé du modèle d'effets mixtes linéaires généralisés à structure d'erreur binomiale négative, montrant la variabilité spatiale et temporelle de l'abondance des coraux adultes pour les Acroporidae, Pocilloporidae, Poritidae et les "autres" taxons.

| *Source of variation* | *Predictors* | **Acroporidae** | | **Pocilloporidae** | | **Poritidae** | | **Other taxa** | |
|---|---|---|---|---|---|---|---|---|---|
| | | *LM* | *CI* | *LM* | *CI* | *LM* | *CI* | *LM* | *CI* |
| | (Intercept) | **2.59** *** | 2.01 – 3.17 | **2.48** *** | 2.00 – 2.96 | -0.19 | -1.03 – 0.65 | **3.57** *** | 3.22 – 3.93 |
| Years | 2019 | **1.21** *** | 0.64 – 1.77 | **1.09** *** | 0.63 – 1.55 | **1.18** *** | 0.52 – 1.85 | **0.84** *** | 0.49 – 1.19 |
| | 2020 | 0.17 | -0.40 – 0.74 | 0.34 | -0.12 – 0.81 | **0.81** * | 0.14 – 1.48 | 0.16 | -0.19 – 0.52 |
| Habitats | Inner slope | 0.77 | -0.10 – 1.65 | 0 | -0.74 – 0.74 | **2.46** *** | 1.33 – 3.59 | **0.85** ** | 0.31 – 1.39 |
| | Outer slope | **0.84** * | 0.03 – 1.65 | 0.19 | -0.48 – 0.87 | **3.55** *** | 2.51 – 4.60 | **1.27** *** | 0.77 – 1.77 |
| Stations | IS2 | -0.31 | -0.97 – 0.34 | **1.24** *** | 0.68 – 1.80 | 0.11 | -0.63 – 0.85 | 0.01 | -0.39 – 0.42 |
| | OS1 | 0.09 | -0.56 – 0.74 | 0.33 | -0.21 – 0.88 | -0.26 | -0.97 – 0.44 | -0.28 | -0.68 – 0.13 |
| | OS2 | **0.85** * | 0.19 – 1.52 | **1.31** *** | 0.76 – 1.87 | -0.14 | -0.87 – 0.59 | **0.70** *** | 0.29 – 1.11 |
| | OS3 | **0.70** * | 0.06 – 1.35 | **1.68** *** | 1.14 – 2.21 | **-1.79** *** | -2.53 – -1.06 | **0.49** * | 0.09 – 0.89 |
| | PR1 | 0.43 | -0.23 – 1.09 | **1.00** *** | 0.46 – 1.54 | **2.92** *** | 2.05 – 3.79 | **0.49** * | 0.08 – 0.90 |
| | PR2 | **1.38** *** | 0.72 – 2.03 | **1.10** *** | 0.56 – 1.64 | **3.03** *** | 2.16 – 3.91 | **1.43** *** | 1.02 – 1.83 |
| | PR3 | **1.17** *** | 0.51 – 1.83 | **1.32** *** | 0.78 – 1.86 | **3.09** *** | 2.22 – 3.96 | **1.38** *** | 0.97 – 1.79 |
| Habitats:Years | Inner slope: 2019 | -0.85 | -1.83 – 0.13 | **-1.14** ** | -1.96 – -0.32 | -0.87 | -2.00 – 0.26 | -0.35 | -0.95 – 0.26 |
| | Inner slope: 2020 | -0.24 | -1.23 – 0.75 | **-0.84** * | -1.67 – -0.01 | -0.66 | -1.79 – 0.48 | **-0.85** ** | -1.47 – -0.24 |
| | Outer slope: 2019 | 0.07 | -0.73 – 0.87 | 0.05 | -0.61 – 0.70 | 0.45 | -0.47 – 1.37 | -0.07 | -0.57 – 0.43 |
| | Outer slope: 2020 | -0.54 | -1.35 – 0.26 | -0.56 | -1.22 – 0.10 | -0.39 | -1.31 – 0.53 | **-0.75** ** | -1.24 – -0.25 |

* $p<0.05$ ** $p<0.01$ *** $p<0.001$